

POPULATION AND HABITAT VIABILITY ASSESSMENT BRIEFING BOOK

Minnesota Valley Wildlife Refuge

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BRIEFING BOOK

SECTION 1
PROBLEM STATEMENT AND AGENDA



Captive Breeding Specialist Group

Species Survival Commission
IUCN -- The World Conservation Union

U. S. Seal, CBSG Chairman

KIRTLAND'S WARBLER POPULATION AND HABITAT VIABILITY ASSESSMENT WORKSHOP STATEMENT OF GOALS AND OBJECTIVES

PROBLEM STATEMENT:

Kirtland's Warbler (*Dendroica kirtlandii*) is a threatened species whose population is currently estimated at 700-1000 adult birds. Over the last 40 years the populations has fluctuated with a low-point in the mid-1970's of perhaps 350-400 adults. The species is migratory with its breeding ground limited to 13 counties in the northern part of the lower peninsula of Michigan. The winter grounds of this remnant population are in the Bahamas. Evidence indicates that the species was formerly (late 19th century) more widely distributed in the jack-pine forests at least in Wisconsin and Ontario. Estimates of the population for this period are perhaps a few thousands of breeding pairs. Major threats to the survival and recovery of this species include: parasitism by cowbirds (*Molothrus ater*); loss of habitat in the breeding ground range; limited habitat and environmental fluctuations/catastrophes (drought, hurricanes) in the winter grounds as well as rigors and hazards of the annual migration.

WORKSHOP GOALS:

The goals of the Workshop include:

- 1. Conducting a Population and Habitat Viability Assessment (PHVA) of the Kirtland's Warbler.
- 2. Formulating quantitative strategies with risk assessments to prevent extinction and achieve the establishment or maintenance of viable, self-sustaining populations within the historic range of the birds.

The overall purpose of the workshop is to develop a Conservation Strategy that will assure, with high probability, the continued survival and adaptive evolution of the Kirtland's Warbler. The final document will include specific recommendations and priorities for research and management of the species. The plan will be developed by detailed examination of natural history, biogeography, life-history characteristics, status of all wild populations, and threats to the species continued existence. Computer models will be used to assist in evaluating the vulnerability of the species to extinction.

A draft of the final workshop document will be prepared during the workshop. It is a goal of the workshop that this document be reviewed and revised by all participants during the workshop as many times as necessary to achieve agreement on its contents before departure.

PHVA OBJECTIVES:

- 1. Determine the number of breeding individuals required for specific probabilities of survival and preservation of genetic diversity for specified periods of time (i.e., 25, 50, 100, 200 years). Do current data support the recovery goal of 1000 breeding pairs?
- 2. Project the potential expansion or decline of Kirtland's Warbler numbers under various management regimes. Consider how possible interventions in the wild population and its habitat might change the mortality and recruitment rate, and loss of genetic diversity.
- 3. Determine the number and geographic dispersion of subpopulations with specific focus on the desirability of a Wisconsin population. Outline metapopulation structure needed to establish additional viable populations. Indicate management consequences of this approach.
- 4. Consider the importance of maintaining and enhancing genetic diversity.
- 5. Consider the need or importance of establishing captive populations. In particular, consider how captive propagation can:
 - a. Accelerate expansion of the population,
 - b. Enhance preservation of genetic diversity,
 - c. Protect population gene pool against fluctuations due to environmental vicissitudes in the wild,
 - d. Provide birds for augmenting wild populations or establishing new populations.
- 6. Identify problems or issues that need continuing analysis and research, such as predation, wintering habitat, genetics, and habitat strategies.

KIRTLAND'S WARBLER (Dendroica kirtlandii) PHVA WORKSHOP

JANUARY 7-9, 1992

MINNESOTA VALLEY NATIONAL WILDLIFE REFUGE VISITOR CENTER

AGENDA

TUESDAY - 7 JANUARY:

- Welcome John Blankenship, Assistant Regional Director, FWS
- Introduction to PVA Workshops Hilda Diaz-Soltero, Deputy Assistant Regional Director, FWS
- Welcome Craig Johnson, Endangered Species Chief, FWS
- Problems and Goals of the Workshop Ulysses Seal, Chair-Captive Breeding Specialist Group, IUCN
 - Small Population Biology Overview Jan Eldridge, Division of Endangered Species, FWS
 - Overview:
 - 1. Historic Overview Lawrence Walkinshaw, Nickolas Cuthbert
 - 2. Census and Population Data Jerry Weinrich, Sharon Moen
 - 3. Predation and Parasitism Michael DeCapita, Wesley Jones
 - 4. Summer Habitat John Probst, William Mahalak, Charlene Gieck, Richard Urbanek, Burton Barnes, Tom Weise, Philip Huber
 - 5. Wintering Ground Habitat Paul Sykes
 - 6. Recruitment Carrol Bocetti, Sharon Moen
 - 7. Mortality Cameron Kepler, Sharon Moen
 - 8. Dispersal Paul Aird

- 9. Catastrophe Kenneth Ennis
- 10. Captive Populations and Reintroductions Bocetti
- Establishment of Working Groups
- Introductory Run on Vortex:
- Evening: Working Groups meet and start refining model values; begin working on reports.

WEDNESDAY - 8 JANUARY:

- Discussion of Vortex results from the previous day. Review of the first day minutes.
- Working groups meetings and preparation for reports.
- Group reports
- Incorporate specifics in the Vortex model and rerun simulation.
- Evening: Working Groups Continue to Refine Reports. Vortex Simulation Will Run Overnight

THURSDAY - 9 JANUARY:

- Presentation of results from simulations and analysis: Ulysses Seal and Sharon Moen. Distribution of Day 2 minutes.
- Review and revision of draft documents.
- Identification of conservation priorities and schedule of actions. Identification of major policy, political, and financial constraints and effects on biological scenarios.
- Final review of documents. Consensus language on the Summary and Recommendations. Note any items that are dependent upon further data, analyses, and simulations to be completed after the workshop.
- Complete review of the Consensus Agreement as a primary product of the Workshop.
- Distribute final draft of individual documents. Minutes. Close

Complete draft document will be distributed to participants for final review after the workshop.

BRIEFING BOOK

SECTION 2
BASIC BACKGROUND ON WARBLERS
&
THEIR ENVIRONMENT

HARRISON, H.H. 1984, WOOD WARBLERS' WORLD. SIMEN & SCHUSTER, NY 336pp. pgs 172-178

27. Kirtland's Warbler

Dendroica kirtlandii

PLATE 12

No Wood Warbler, and possibly no other North American bird, has received as much media attention and public interest as the endangered Kirtland's Warbler. Annually, newspaper, magazine, and television coverage is given to the nesting success or failure of this species in its limited breeding area in about five or six counties in the northern half of Michigan's lower peninsula.

In the 1950s, when my son and I went to Michigan in search of Kirtland's Warbler, no measures were taken to protect this rare and endangered bird from the public. We were free to tramp the jack pine forests without any restrictions. Fortunately, the area is now closed to the public from May 1 to August 15. Guided tours are conducted to permit birders to see the warblers, but under controlled conditions.

The United States Forest Service, the United States Fish and Wildlife Service, the Michigan Department of Natural Resources, and the Michigan Audubon Society are involved in management efforts. A Kirtland's Warbler Recovery Team heads the project. An area of 135,000 acres of jack pine habitat has been designated for attention in the Kirtland's Warbler's historical breeding range in Michigan. The eventual goal is to increase the population to one thousand pairs, a goal that seems far away at present.

It has been estimated that the total weight of all the Kirtland's Warblers in the world would be less than twelve pounds, for an adult weighs only one-half ounce. In the entire history of this warbler, all the nests found have been in only thirteen adjacent counties. However, in 1982 and in 1983 a singing male was heard for the first time in the Upper Peninsula near Gwinn. Singing males, but no females and



Kirtland's Warbler demands large stands of jack pine six to twenty feet tall and porous soil with low, dense ground cover. At present its entire breeding range is confined to five or six counties in Michigan.



A male Kirtland's Warbler lands on the author's hand as a nest is examined. This picture, taken in 1950, would not be possible under strict regulations enforced today.

Kirtland's Warbler



The total weight of all the Kirtland's Warblers in the world is less than twelve pounds. An adult weighs only a half ounce.

no nests, have been reported from Wisconsin in 1978, 1979, and 1980; from Ontario, in 1977 and 1978; and from Quebec, in 1978. Old migration records strongly suggest that in the nineteenth century the species may have had a larger breeding range, including suitable jack pine areas in Wisconsin and Ontario.

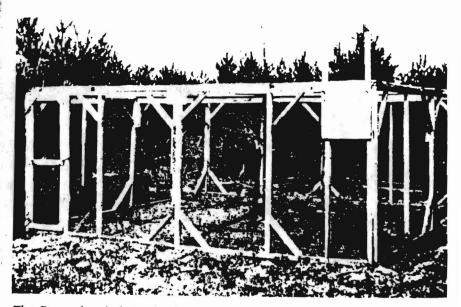
The first count, in 1951, indicated 432 males. In 1961, this count reached 502 males. Ten years later the total was 201. Starting that year, counts have been made annually. Over a twelve-year span, 1971 through 1982, the population of singing male Kirtland's has remained remarkably stable. The lowest count was in 1974, when only 167 males were reported, and the highest was 242 in 1980. The official count for 1983 placed the number of singing males in Michigan at 215. This was an increase of 8 over the 207 recorded in 1982.

Census taking consists of systematically searching for singing males in suitable habitat in mid-June. According to Harold Mayfield, author of a book devoted entirely to the species, this is a feasible method of estimating total population: count singing males and double the number, figuring one female for each male. As he cautions, however, this method may be off as much as 20 percent. Unmated females and males in the breeding area are imponderables.

Unquestionably the exacting demands of nesting Kirtland's War blers have been responsible for limiting its population. In young jack pine forests (*Pinus banksiana*) Kirtland's Warbler will eventually sur vive or perish, for it is only in this very specialized environment that the warblers will nest. This drama has so caught the public's attention that Mayfield declares that it is one of the best understood songbirds in America.

The Jack Pine Warbler, as it is popularly known, has these special requirements for its nesting area: jack pines must predominate; the pines must be six to twenty feet tall; the pines must be in large stands ideally two hundred acres or more; and the ground beneath and between the pines must be sandy and porous with low ground cover. The natural provider of these ideal conditions is forest fire. Since natural fires are stopped if possible, forest management practices for preserving the Kirtland's Warbler now include controlled burns.

The warbler population faces two other major problems in its struggle for survival: the Brown-headed Cowbird and a practically unknown factor, the dangers in its widespread winter range in the



The Brown-headed Cowbird problem that plagued Kirtland's Warblers for many years has been solved by using traps like this to capture the parasites before they lay eggs in warblers' nests.

Bahamas, an area of about forty-five hundred square miles in hundreds of scattered islands and cays. Although the wintering area has been searched on numerous occasions, investigators have had difficulty even finding the tiny bird in this sprawling range.

The Brown-headed Cowbird problem has been attacked successfully. As the cowbird extended its range northward in the last century, it found conditions ideal for parasitizing the Kirtland's Warbler. When a crisis was recognized in 1971, concerned friends of the warbler moved the next year to eliminate cowbirds by trapping them. That year, twenty-two hundred were taken in large chicken-wire traps and were asphyxiated. Since that time cowbirds have been destroyed each spring at Kirtland's nesting sites, and beneficial results appeared immediately in higher production of young warblers. However, of the hundreds of adults and young that leave Michigan in August and September, only about two hundred pairs have returned to breed the following year. The survival rate through two migrations and a winter spent in the tropics is about 65 percent for adults but unusually low for yearlings, and thus perplexing.



Female Kirtland's Warblers build their nests on the ground in a thick cover such as grass, sweet fern, and blueberries under jack pine trees.



This fledgling Kirtland's Warbler will spend the winter in the Bahamas with others of its kind. The survival rate for yearlings is low.

To the surprise of many not well acquainted with this bird, it does not nest in the jack pine trees that are so crucial to its breeding. The birds nest on the ground under the trees where the nest is hidden in a thick cover of grass, sweet fern, or blueberries. The female Kirtland's alone incubates the eggs for fourteen days, the longest incubation period reported for any North American warbler. The male feeds the incubating female and assists in feeding the young. It is known that occasionally pairs have had two successful broods in a summer, but this is not common.

Mayfield declares that Kirtland's Warbler "can scarcely be called an accomplished singer." He continues, "The song is not truly musical but, rather, loud, clear, emphatic, and frequently repeated. It has none of the buzz and trill so common among Wood Warblers, but reminds the listener of the chattering quality of a House Wren's song, though it is briefer. Field students are reminded of the Northern Waterthrush and some notes of the House Wren, but the resemblance

usually is not close enough to cause one to mistake the Kirtland's.
Warbler for either."

The first specimen of Kirtland's Warbler was given to Dr. Jared P. Kirtland by his son-in-law, Charles Pease, who had collected it near Cleveland, Ohio, on May 13, 1851. Kirtland turned the specimen over to Spencer F. Baird, who, in 1852, described the bird for science and gave it its name. Years later it was learned that Dr. Samuel Cabot of Boston had captured a male on shipboard near the Bahamas in October, 1841. The first nest and eggs were collected by James A. Parmalee on June 6, 1904, after which oologists paid as much as twenty-five dollars each for Kirtland's Warbler eggs. A nest with young birds had been discovered in 1903 by Norman A. Wood, but nests with eggs had more import to egg collectors of that period.



Breeding Range of Kirtland's Warbler

28. Prairie Warbler

Dendroica discolor

PLATE 12

The depth of study that may be given a single species is indicated in a \$95-page monograph by Val Nolan, Jr., entitled The Ecology and Be-bavior of the Prairie Warbler (Dendroica discolor). Nolan, a biology professor at Indiana University, pursued his study over fourteen years intense field work. The results may be more than the average bird ratcher wants to know about this species, but I have had no question the Prairie Warbler that Nolan has failed to answer.

Judging by the habitat the bird prefers, *Prairie* seems to be a misomer. It is not an inhabitant of western prairies or grassy plains, but parently that is not what Alexander Wilson had in mind when he proposed its English name. Wilson found the species near Bowling Green in the "barrens of southwestern Kentucky," an area known to heal residents as "prairie country."

The nesting environment preferred by the Prairie Warbler inudes forest edges, dry, brushy clearings, pine barrens, sproutlands,

author prepares to photograph the nest of a Prairie Warbler in silky corwood in western Pennsylvania.



Mayfield, Harold, *The Kirtland's Warbler* (Bloomfield Hills, Michigan Cranbrook Institute of Science, 1960), p. 125.

MORSE, N.H. 1989 American Warblers: An Ecological and Behavioral Perspective. Harvard U. Press

11 Rare Species

European colonization of North America has probably affected population sizes of most native birds, but it has been especially marked in some warbler species. Certain species are also rare as a consequence of extreme habitat specialization, and presumably their numbers were small prior to human disturbance. This rarity may be the hallmark of species well on their way to natural extinction, perhaps as a consequence of the receding of Pleistocene glaciation and changes in climate and vegetation. Species that are common today but were rare in the recent past may also be extreme specialists, the only difference being that human modifications to the environment have greatly increased their access to favorable conditions. In this chapter I present brief case histories of several species that are or formerly were rare. My intent is to elucidate the basis for rarity.

Rare North American warblers can be divided into two groups: local endemics and species with a wide range but low density. The latter can naturally change into the former, but some species also attain high densities within a restricted area. Among the former group I survey Kirtland's and Golden-cheeked warblers. An example of the latter group is the Bachman's Warbler, which occupied damp forests in the southern United States before declining in number over the past century. I will also discuss another species of the same region, Swainson's Warbler, which chooses habitats similar to Bachman's Warbler but has not declined drastically over the same period.

Kirtland's Warbler

The Kirtland's Warbler has probably been decreasing in numbers for hundreds or thousands of years; it may properly be said to be a "relict" or senescent species. Ironically, as a result of its endangered state, we know more about it than most other warblers. Kirtland's Warblers have certain traits characteristic of endangered species: their habitat specifications are circumscribed, at least in the breeding season, and they occupy a limited

range within their chosen habitat type. Hatching success of undisturbed eggs is 85 percent (Mayfield 1960); for comparison, Prairie Warblers have a success of 97 percent (Nolan 1978). Kirtland's Warblers have recently experienced nest parasitism from Brown-headed Cowbirds (up to 70–75 percent: Walkinshaw 1983).

The reason for this species' rareness in the first place, which almost certainly preceded the cowbird menace, is puzzling. The bird is confined to Jack Pine forests, though sometimes it nests in Red Pine (Pinus resinosa) plantations within its limited breeding range of a few counties in Michigan (northern part of the lower peninsula). It breeds only within the small southern isolate of Jack Pine in Michigan, perhaps 200,000 hectares in area, separated from other stands by Lakes Michigan and Huron. It is not yet clear how or if this locality differs from all others; certainly it has not supported Jack Pines more than 6,000-8,000 years, when the pines followed the receding glacier northward. Within its range Kirtland's Warbler is largely confined to stands of greater than 32 hectares (80 acres); it occupies trees 6-22 years of age in areas that have burned recently, with heights of 1.3-6.0 meters. It is further confined to forests growing on Grayling sand, a particularly porous soil, which enables the warbler to recess its nests in the ground, a trait unusual in this genus. As a result of these and other constraints, no more than 10 percent of the Jack Pine area in Michigan may be satisfactory habitat. Colonies on plots smaller than 32 hectares are usually unsuccessful; more often than not, their inhabitants are unmated males, apparently unable to find or to attract females to these sites. This pattern of females being more discriminating in site choice than males is widespread among passerine birds (Morse 1985). Areas of young pines larger than 32 hectares were formerly characteristic of northern lower Michigan because of the wide sweep of level land, which results in large fires because there are no natural boundaries to stop them. It is unlikely that northern lower Michigan is unique in this regard.

Mayfield (1960) and Walkinshaw (1983) pointed out that an important aspect of a young Jack Pine stand after burning is that no other species are characteristic of it. This habitat is marginal for the relatively few species found with Kirtland's Warblers, suggesting that Kirtland's Warblers have been unable to compete successfully for space in other kinds of habitats. If so, this status is not new, in that their habitat selection has become so finely honed. Mayfield suggested that areas less than 32 hectares may be so small that excessive competition and predation infringes from adjacent

areas, making them untenable sites. This prediction historically precedes arguments about the consequence of forest fragmentation on the species diversity of Neotropical migrants in small plots (see Whitcomb et al. 1981; Ambuel and Temple 1982). However, Probst (pers. comm., 1987) knows of no evidence that directly supports Mayfield's explanation.

Within large tracts of young pines the Kirtland's Warblers are colonial, eschewing seemingly similar sites to nest in loose groups within other similar areas, although they possibly differ in subtle ways. One routinely finds clusters of between 2 and 30 pairs separated by substantial distances of similar habitat (Figure 11.1). Once colonized, sites are occupied for several years, although sometimes sites in seemingly satisfactory habitats have been abandoned because of nest failure or chance local extinction.

Historical records, plus regular censuses in recent years, give a sense of trends in this species' population size over the past century (see Mayfield

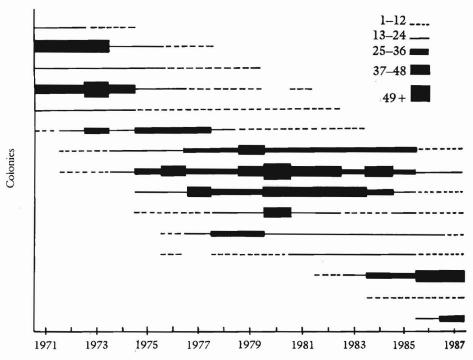
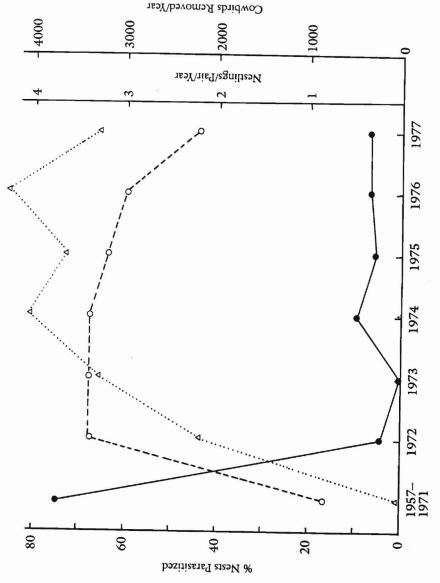


Figure 11.1 Sizes of several colonies of Kirtland's Warblers over time. (Modified from Probst 1986; Probst, pers. comm., 1987.)

1960; Walkinshaw 1983). The vast majority of reports in spring migration, as well as the extralimital records (away from usual breeding and migration areas), were made in the late 1800s; further, most data on this species from its only known wintering grounds, the Bahamas, come from that period also. Mayfield and Walkinshaw take this information to indicate that numbers of Kirtland's Warblers were higher then than now, although even then there were probably no more than a few thousand pairs. Since the breeding grounds were not known at that time, we have no corroboration of migration and winter data. But this period came just after northern lower Michigan was first lumbered. Jack Pine was considered worthless as a timber tree, but adjacent areas of White (Pinus strobus) and Red pine were extensively lumbered, leaving heaps of inflammable slash that led to large fires throughout the region. These episodes should have been followed by an increase in satisfactory nesting habitats, exceeding the ones available before or after. All one can say is that the timing of the fires fits the numbers of birds recorded in migration and on wintering grounds.

Numbers almost certainly declined between this period and the first census in 1951 (Ryel 1984). Fewer than 500 pairs were recorded in 1951, and by 1971 the population had shrunk to about 200 pairs. This was a time of heavy nest parasitism by Brown-headed Cowbirds: half to three-quarters of the Kirtland's Warblers' nests were parasitized, a higher frequency than the one recorded earlier. Mayfield and Walkinshaw assumed that Kirtland's Warblers never encountered cowbirds until the late 1800s, and records of the cowbird's range expansion (see Mayfield 1960) establish that its impact was low prior to this time. In the early part of this century such students as Wood (Wood and Frothingham 1905) and Leopold (1924) expressed concern about the cowbird's impact. Kirtland's Warblers have no known defenses against cowbirds, which is not surprising in view of their lack of contact with them until recently. Once the ability to reject eggs evolves, it spreads rapidly through a population (Rothstein 1975b), yet Kirtland's Warbler is by no means unique in lacking this ability. By virtue of its small numbers, however, it is much more vulnerable to extinction than are species with extensive ranges that suffer high parasitism when in contact with cowbirds. For instance, the Red-eyed Vireo suffers just as much parasitism when cowbirds are common, but vireo populations in large forests not visited by cowbirds, such as the Canadian deciduous forests, are free from their depredations. Further, the probability that rejecter behavior will evolve in such a small gene pool is bound to be



rasitized by Brown-headed Cowbirds (black circles); and numbers of Kirtland's Warblers reared per pair 54. (Modified from Walkinshaw 1983.) parasitized by (triangles), from 26 to 8 Percentage of Kirtland's Warbler nests Is trapped and removed of yearly sample varied

low. Thus, the Kirtland's Warbler is unusually vulnerable because of its small population size. In such a situation the entire population could easily become extinct before rejection mechanisms evolved.

For this reason cowbird control was undertaken in the 1970s. The program has reduced parasitism from 75 percent to 6 percent, with a corresponding fourfold increase in the number of fledglings produced (Figure 11.2). One might expect this change to be followed by an increase in population size, but that has not happened; rather, over the past several years the population has stabilized at a low level of roughly 200 pairs. The reasons are unclear. Vigor of the breeding adults is probably not a consequence, for mortality of adults on the breeding grounds is extremely low. Probst (1986) noted, however, that previous estimates of annual productivity and recruitment (Ryel 1981) have not separated postfledging losses from those suffered away from the breeding grounds, or taken into account that some males (at least) are unmated and that many abandon territories. Probst estimated that there may be an 18-35 percent fledgling loss prior to migration, on the basis of Walkinshaw and Faust's (1975) reports that 33 percent of fledglings were not seen again after they left their nests and Nolan's (1978) estimate of an 18 percent loss in Prairie Warblers, a congener that occupies a similar habitat. The period immediately after fledging is one of high mortality in other passerines (Lack 1954). Probst and Hayes (1987) noted that at least 15 percent of all males are unmated, especially ones in marginal habitats (40 percent unpaired), although the number might be partially offset by polygynous matings (Radabaugh 1972). All told, the number of juveniles departing their natal areas could be 40 percent or more lower than the number predicted by calculations based on singing males and fledging success.

Another factor affecting the size of breeding pools is the low level of juvenile returns to their area of birth, a trait common to many passerines. Birds not returning to established colonies have a low probability of finding mates. Although data are difficult to gather, observations of singing males in extralimital areas and of young birds in different colonies suggest that many individuals survive the winter and migration yet fail to join a breeding population. Mayfield (1983) maintained that numbers of extralimital birds have risen following cowbird control, citing Kirtland's Warblers observed as far away as Ontario, Quebec, and Wisconsin, some being banded birds from the Michigan population. So long as they fail to meet females, these birds make no more reproductive contribution than those that die young. There is no information on whether any extralimital

individuals eventually find a colony, and it is unrealistic to expect that we will obtain adequate information on this point. One of the Ontario birds sang at the same site at least two years, and a bird on the Upper Peninsula of Michigan probably returned two years also (see Probst 1985).

The problem of locating a breeding colony becomes progressively more serious as breeding ranges decline. During the cowbird-induced decline, the range shrank to one-fourth its former size, and the east-west width shrank to one-third. Perhaps decreasing breeding range is an especially difficult trap for Kirtland's Warblers, since they are a successional species that depends on finding new nesting sites with regularity and is especially inclined to occupy new areas. Although in widely distributed species most vagrants might find mates, the tiny range of Kirtland's Warbler may often preclude it.

The failure of the population to rebound may be due to its being limited elsewhere. This unaccounted mortality probably does not happen on migration lanes, for one would not expect the population to remain as stable as it has if that were so. Two rapid drops, however, one perceived (though not verified) in the late 1920s and early 1930s (Trautman 1979), and one in the winter of 1973–74 (Walkinshaw 1983), may have resulted from hurricanes killing birds either in passage or immediately after their arrival on wintering grounds. Heavy mortality of warblers also may have occurred in the winter of 1970–71 and the spring of 1971, as a result of extreme drought on their Bahamian wintering grounds. The drought took place immediately before the breeding census that recorded the catastrophic 10-year decline (Radabaugh 1974).

The alternative explanation is that wintering grounds are now limiting. Little is known about them, except that the species is apparently confined to the Bahamas. The few workers who have tried to find Kirtland's Warblers recently in the Bahamas have not been very successful. Radabaugh (1974) found one bird in 800 hours of fieldwork on 11 large Bahamian islands, and Emlen (1977) found none in 500 hours of fieldwork on Grand Bahama Island. The older records suggest that they occupy low broadleaf scrub. Whether they would favor young pine is unclear, but pinelands have been extensively cut there. Terborgh (1980) and Rappole et al. (1983) have suggested that this and other species could have dropped to catastrophically low levels as a result of habitat change on their wintering grounds before the birds were known to science. Many of the larger islands were under extensive agriculture from the 1550s, so environmental modifications may have had a major effect on distributions.

Golden-cheeked Warbler

The Golden-cheeked Warbler, another endemic species with a narrow breeding and wintering area, bears similarities and differences to Kirtland's Warbler. It, too, is a narrow habitat specialist, being confined as a breeding species to the "cedar" brakes (Juniperus ashei) of central Texas, on and about the Edwards Plateau (Pulich 1976). Pulich estimated its population to be 15,000–17,000 birds. Its distribution is coincident with that of the Ashe Juniper, and even within that range it nests only in certain types of juniper—it uses mature trees that, according to Pulich's estimate, must be at least 50 years of age. Thus, Pulich's picture suggests that Golden-cheeked Warblers differ from Kirtland's Warblers in requiring mature vegetation.

Pulich proposed that the basis for this species' limited breeding distribution is its use of the fibrous bark of Ashe Juniper for its nests, which, in his experience, constitutes the major building material of the Goldencheeked Warbler. Although two other junipers occupy large areas in Texas, the Redberry Juniper (J. pinchotii) in the western part of the range and the Red Cedar (J. virginiana) in the northeastern part, Pulich found no indication that the birds use them for materials. This putative nesting requirement has not been tested experimentally, and it seems unlikely to have been a limiting factor traditionally. Areas with stringy Ashe Juniper bark may have other critical traits, such as certain foliage growth patterns.

Golden-cheeked Warblers are not locally limited within the areas they currently occupy; but they exhibit a loose colonial distribution, as noted for Kirtland's Warbler. Pulich reported that the groupings usually contained fewer than six territories, separated from other colonies by considerable amounts of identical habitat, but one aggregation consisted of 21 pairs.

Pulich's assertion that the species is confined to only part of the available habitat must be viewed in the context of Kroll's (1980) analysis of used and unused sites. Kroll reported that sites occupied over a five-year period and sites not occupied during that time differed clearly and consistently in multivariate analyses of vegetation variables, though they were similar to the human eye. Key variables included the presence of Ashe Juniper and Bigelow Oak (*Quercus durandii brevioloba*), distance between trees, density of the two tree species, height of stand, and age of juniper. The birds required oaks for foraging and were most active there, although they concentrated on Ashe Juniper for nesting materials and singing

The Effect of Physical Factors on Wintering Populations

Low temperature and related factors have a major impact on birds wintering at high latitudes (Lack 1954; Fretwell 1972), and for that reason probably strongly influence the population dynamics of species like the Yellow-rumped Warbler. Temperature may be significant at lower latitudes, also, and a second physical factor, moisture, may figure in there as well. A third factor, distance to closest wintering area, further affects migrant density on wintering grounds.

Species wintering at high latitudes are constantly subject to the effects of unpredictable winter climate (Morse 1980a). Yellow-rumped Warblers that winter in areas of occasional high snows may even find much of their food covered at times. In spite of the importance of such phenomena in setting the northern limits of wintering populations, little of a precise nature is known about the effect of severe winter weather on these birds. Weather-related population decreases could signify either local mortality or dispersal, and Terrill and Ohmart's (1984) data on western Yellow-rumped Warblers suggest that facultative dispersal may occur under such circumstances.

Pine Warblers winter throughout the southern pine forests in the United States and thus have a more northerly winter distribution than most of the other parulines, except the Yellow-rumped Warbler. They feed heavily on insects during the winter, although they take other food, such as pine seeds and fruits (Bent 1953; Morse 1970a), if available. They are vulnerable to unseasonably cold winter weather, however, and suffered heavy mortality during the unusually cold winters of 1976 and 1977 (Robbins et al. 1986). The loss was corroborated by lowered breeding densities in subsequent years. This disaster indicates clearly the possible costs of northerly wintering.

In addition to species that winter at high latitudes, other warblers are exposed to severe weather because they fail to move southward when their conspecifics do, only to succumb to normal winter conditions or to survive at feeders that provide exotic food supplies (mealworms, citrus fruit, and the like). These stragglers are unlikely to be of evolutionary significance to the populations of which they are a part. Normally they would be culled from the population as a result of their abnormal behavior. Occasionally, however, this type of behavior could be of major importance. Given the tropical origin of warblers, and the return to the tropics of most species in the winter season, it is possible that northerly-wintering popula-

tions of Yellow-rumped Warblers are descended from individuals that had this type of abnormal wintering habit. Diamond (1982) has suggested that some western-wintering populations of eastern Yellow-rumped Warblers may be the result of abnormal migration.

Although temperature has frequently been mentioned as an important variable affecting the suitability of northern areas as wintering grounds, few references discuss its effect on migrants wintering at lower latitudes. The oft-reported tendency for migrants to frequent highlands holds up in the southerly parts of the wintering range (Costa Rica, Panama, and South America), but not in higher-latitude tropics and subtropics, where no correlation occurs in moist areas (Terborgh 1980). In fact, in western Mexico, Hutto (1980) reported many fewer migrants in the uplands than in the lowlands, which led Terborgh (1980) to propose that winter temperatures fall low enough in the uplands to depress insect activity.

The Neotropical region contains areas arid enough to exert a physical effect on individuals living there, and not surprisingly these regions usually have few migrants wintering in them (Russell 1980). A more important factor is the fluctuation of wet and dry seasons, which dictates the availability of both insects (Wolda 1978; Hespenheide 1980) and fruit (Morton 1980).

Even if the regular interposition of wet and dry seasons is the most important moisture-related variable facing migrants in the Neotropics, unusual periods of drought exert an effect, especially in marginally acceptable areas. Orejuela et al. (1980) reported that during an unusually severe dry season in Colombia some wintering migrants did not put on the fat that they normally would accumulate prior to their northward migration. If such stressful conditions were widespread they would have a severe effect on entire populations of these birds. Some species initially in the study area may have avoided this problem by leaving the site before conditions became severe.

The Whitethroat (Sylvia communis), an Old World sylviine warbler, probably provides the best example of the impact of unusual drought on the wintering ground. Whitethroats breed throughout most of Europe and winter in the vast arid Sahel region, south of the Sahara Desert of Africa. During a period of severe drought in the Sahel during the 1960s and 1970s, birds on the breeding grounds declined precipitously (Winstanley et al. 1974), only rebounding somewhat after the drought temporarily ameliorated (Batten and Marchant 1977). Climate-mediated population fluctuations of this sort are not rare on wintering grounds, but often

they can be documented only when they fortuitously happen in the midst of ongoing studies.

Unusual wetness can produce strong effects too. The winter of 1980–81 was the wettest on record (57 years of data) in the Panama Canal area, with substantial rains falling during the usual dry season. The rain inhibited the activity of the pollinators of fruiting trees, with the result that fruit production was low and late. Frugivorous migratory species, including Bay-breasted Warblers, Catbirds, and Wood Thrushes, that normally entered the area in large numbers never appeared (Martin and Karr 1986).

A third factor logically included under this heading is the effect of distance on the numbers of individuals that winter in an area. Although selective pressure should favor individuals that move far enough to escape severe weather, additional travel only increases energetic costs and dangers (Terborgh and Faaborg 1980). Thus, it is not surprising that the proportions of wintering migrants drop from 50 percent or more of the avifauna in Florida, some parts of Mexico, and the Greater Antilles to less than one to a few percent in equatorial South America (Terborgh 1980) (Figure 10.1). Combined with the tremendous distances required to reach the equatorial zone is a diversity of resident species, some of which are ecologically similar to the migrants (Keast 1980b). Equatorial South America has the richest avifauna in the world (Pearson 1980) and large numbers of putative warbler equivalents (Keast 1980c). Terborgh and Faaborg (1980) reported a comparable decline of migrants through the West Indies. Although the Greater Antilles, nearest to the northern mainland source, have high proportions of migrants, their number declines to one percent or less on the most distant of the Lesser Antilles. Even though the Lesser Antillean islands have fewer species than the Greater Antillean islands, within-habitat population densities and species numbers on the Lesser Antilles do not differ significantly from those on the Greater Antilles. The distance effect appears valid, then, although it is perhaps exaggerated by the small land areas of the Lesser Antilles (Terborgh and Faaborg 1980).

Diversity and Partitioning of Wintering Warblers

Many species that breed together are allopatric on their wintering grounds; however, MacArthur (1958) reported that the number of winter overlaps (half or more of wintering ranges in common) of spruce-woods warblers and other northeastern breeding species were about what one

would predict by chance. He thus concluded that the winter community was randomly composed in relation to the summer community. Chipley (1980) noted that MacArthur's assignments of species to allopatric or sympatric categories were conservative and concluded that the frequency of sympatry was lower than would be predicted by chance (Figure 10.2). It fact, each of MacArthur's five study species has a different center of winter abundance (Hutto 1985a). Greenberg (1986) has also noted that 75,000 square-kilometer blocks in the eastern United States routinely encompass 8—II breeding *Dendroica* species. A similar measure of the winter ground

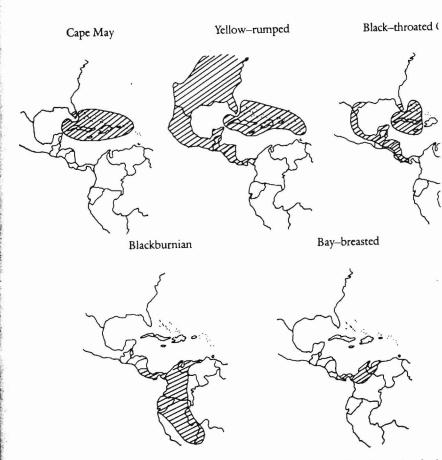
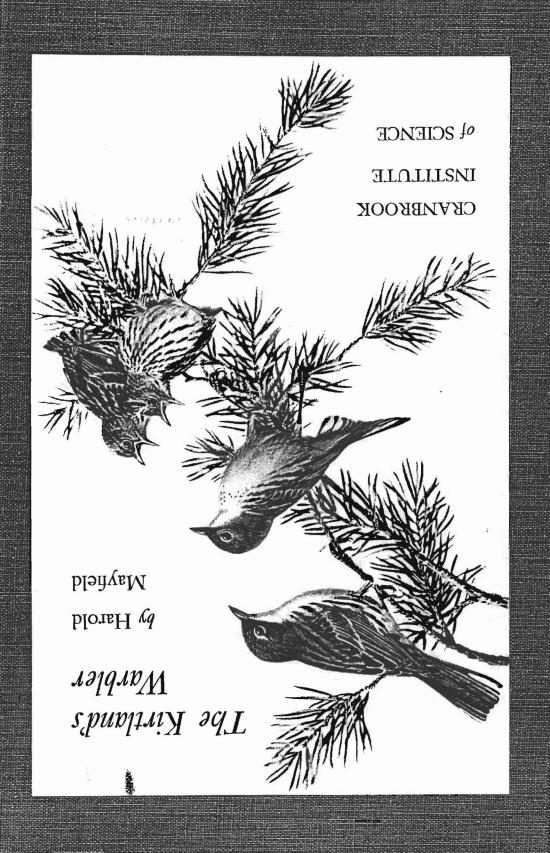


Figure 10.2 Distribution of wintering spruce-woods warblers (cross-hatched areas). (Data from AOU 1983.)



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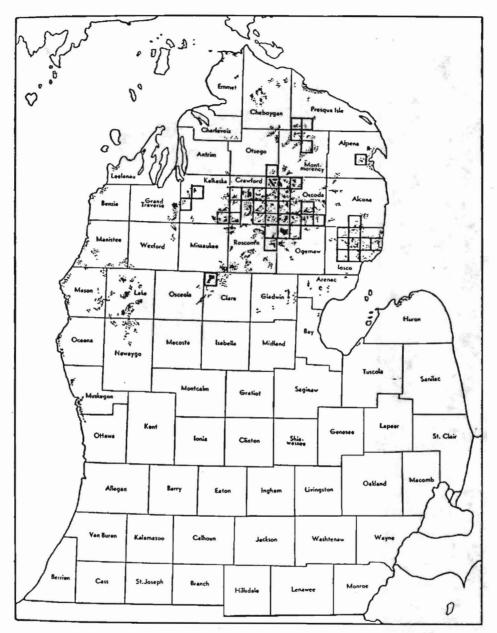
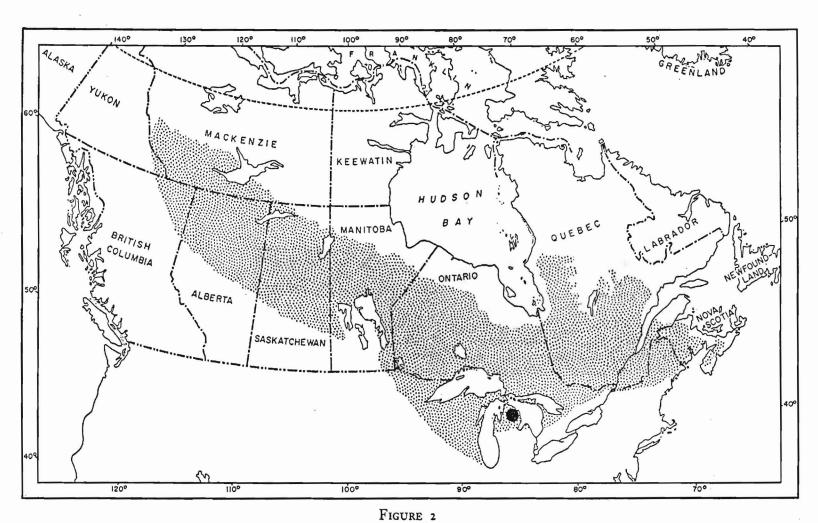


FIGURE 1

Michigan townships (six-mile squares) where Kirtland's Warbler has been known to nest, 1903–1959, small squares. Natural stands of jack pine in northern Lower Michigan dotted (Zimmerman, 1956:265).



Range of the jack pine in North America (Munns, 1938), dotted, and nesting range of Kirtland's Warbler, large dot.

Table 3
Winter Records of Kirtland's Warbler in Bahama Islands

Island	Number taken	Collector	Year
Andros	ľ	C. B. Cory	1879
Berry	3	C. S. Winch '	1891
Caicos	2	C. B. Cory	1891
Cat	1	J. P. Moore	1891
Eleuthera	2	C. J. Maynard	1884
Eleuthera	5	C. S. Winch	1891
Eleuthera	3	C. J. Maynard	1897
Great Abaco	1	C. S. Winch	1891
Green Cay	2	Robert Ridgway	1886
Little Abaco	1	J. L. Bonhote	1902
New Providence	24	C. J. Maynard	1884
New Providence	4	C. B. Cory	1884
New Providence	8	A. H. Jennings	1887
New Providence	2	C. J. Maynard	1893
* New Providence	5	C. J. Maynard	1897
New Providence	1	J. L. Bonhote	1902
New Providence	I	C. J. Maynard	1913
New Providence	1	C. J. Maynard	1915
Watlings	4	Robert Ridgway	1886
Total	71		

^{*} Includes one on Athol.

Although collecting efforts in these islands were not distributed evenly over the decades of the last hundred years, there was considerable field work before and after the period shown. For example, Henry Bryant spent four months (January to May) on these islands in 1859, and a shorter period in 1866, without finding the Kirtland's Warbler. In the more than 40 years since the last specimen was taken (in 1915), several ornithologists have worked in the islands, including Van Tyne and Mayfield, 59 man-days, and James Bond, about 100 days. (Bond saw one Kirtland's Warbler.) These circumstances, along with the fact that collectors of those days called the bird "fairly numerous" or "not uncommon," lead us to believe that the Kirtland's Warbler reached a peak in the 1880's and 1890's.

The Wintering Ground as a Limitation on the Species

It is possible that there have been factors on the wintering ground tending to limit the population of this rare species. But it is difficult

to speculate about them when we know so little about the bird's requirements or behavior in winter. The only factor to be considered here, therefore, is the land area in the Bahama Islands.

This portion of the earth's crust has been stable since the Cretaceous (Eardley, 1951:574); so for many millions of years changes in land area of the Bahamas have come about chiefly from changes in sea level as the glaciers have advanced and retreated. The islands are so low and the surrounding waters mostly so shallow that some major changes have occurred. For example, the Wisconsin glacial stage began about 25,000 years ago and came to a close about 8,000 years ago (Horberg, 1955:281), and in the early portion of it, perhaps 20,000 years ago, the sea dropped 10 fathoms, exposing the Great Bahama Bank and uniting many of the existing islands into a land mass approaching to within ten miles of the shore of Cuba. At that time the bird life was much richer, with perhaps 40 per cent more species than now, a number comparable to that on Cuba or Hispaniola (Brodkorb, 1959:368). However, as discussed in the section on Nesting Ground, there is some doubt whether a richer avifauna would be more favorable to the Kirtland's Warbler. Also, when we go back so far, remembering that the breeding range may have been much larger and displaced several hundreds of miles southward, we are far from certain that the wintering range was located exactly where it is now.

As the Wisconsin glacier receded, the ocean rose and the islands in the Bahamas shrank to approximately their present size. Subsequently, the sea level has been fairly stable. The only significant change in "postglacial" time was a rise of 6 to 8 feet some 4,000 to 6,000 years ago. This Silver Bluff time in geology is also recognizable from botanical evidence. In Michigan it was a warm, dry period, during which a number of Western plants are believed to have become a part of the jack-pine association which we now regard as part of the typical Kirtland's Warbler breeding habitat. The present sea level is thought to be merely a retreat from the Silver Bluff level (MacNeil, 1950:104). Consequently, even though there has been erosion of shores by wave action in some places, it does not appear that the land area in the Bahamas has been greatly larger or smaller during the 6,000 to 8,000 years that the Kirtland's Warbler has probably been nesting in Michigan; that is, the islands have not been so large as to have had a significantly different fauna or so small as to have crowded the birds unduly in "postglacial" times.

(4) Watlings (D Cat Eleuthera

Fall Migration

Verne Dockham, who has lived in the nesting region of the Kirtland's Warbler for many years, finds that they begin to disappear in late August; that the majority leave in the first week of September; and that they become rare after the middle of September, although an occasional straggler may remain until late in the month. The latest record from the nesting range was September 28, 1919 (specimen by Max M. Peet). There are no fall records in Michigan south of the jack-pine country. The latest fall specimen in the United States was recorded on October 29 (1903, South Carolina).

Fall migration records for the species are few in number. All occur in Ontario, Ohio, or the South Atlantic states—that is, in the general direction of the Bahama Islands from central Michigan. The records are shown in the following tabulation.

FALL MIGRATION RECORDS OF THE KIRTLAND'S WARBLER

Point Pelee, Ontario, October 2, 1915 (specimen by W. E. Saunders, letter, December 10, 1934)

Toledo, Ohio, September 22, 1929 (seen by Louis W. Campbell and Edward S. Thomas, 1940:146)

Oberlin, Ohio, August 28, 1902 (Lynds Jones, 1903a:104, incorrectly given by Dawson, 1903:164)

Cleveland, Ohio, October 14, 1886 ("found [dead] under electric light mast," Davies, 1906:118)

Fort Myer, Virginia, September 25, 1887 (specimen by Hugh M. Smith and William Palmer; and another seen October 2 of the same year; 1888:147-148)

Rocky Mount, North Carolina, September 2, 1936, September 22, 1938, September 23, 1941 (seen by Francis H. Craighill, 1942:25-26)

Mt. Pleasant, South Carolina, October 29, 1903 (specimen by A. T. Wayne, 1904:83-84)

Christ Church Parish, South Carolina, October 4, 1910 (seen by A. T. Wayne, 1911:116)

East Goose Creek, Florida, September 9, 1919 (seen by Ludlow Griscom and John T. Nichols, letter, May 15, 1950)

Off the coast of Florida, second week of October, 1841 (specimen taken on shipboard "between Abaco and Cuba" by Samuel Cabot, Jr., Baird, 1865:207)

Table 4
Size of Territory of North American Warblers

	Size of Te		
Species	Range	Average	Authority
Kirtland's Warbler	1.5-16.5	8.4	This work
(Dendroica kirtlandii) Ovenbird	2.5-4.5	3.0	Hann, 1937
(Seiurus aurocapillus)	0.8-4.3	2.3	Stenger & Falls, 195
Northern Waterthrush	2.0-3.7	2.5	Eaton, 1957
(S. noveboracensis) Prairie Warbler	1.2-6.0	3.0	Nolan, letter, Dec. 31, 1958
(Dendroica discolor) Prothonotary Warbler	1.9-6.38	3.66	Walkinshaw, 1953
(Protonotaria citrea) American Redstart		0.19	Sturm, 1945
(Setophaga ruticilla)		0.5-1.0	Hickey, 1940
Yellowthroat	8.1-8.0	1.26	Stewart, 1953
(Geothlypis trichas)		2.0	Hofslund, letter, Dec. 19, 1958
Yellow Warbler	*****	0.4	Kendeigh, 1941
(Dendroica petechia)	0.15-0.94	0.42	Brewer, 1955 Kendeigh, 1947
Tennessee Warbler	0.4-1.7	0.68	110110101011
(Vermivora peregrina) Nashville Warbler	1.2-6.0	2.7	"
(V. ruficapilla) Magnolia Warbler	1.0-1.6	1.4	
(Dendroica magnolia) Cape May Warbler	0.4-2.4	1.1	"
(D. tigrina)			
Black-throated Green	0.8-2.1	1.2	66
Warbler (D. virens) Blackburnian Warbler	2.0-2.2	2.1	"
(D. fusca) Bay-breasted Warbler (D. castanea)	0,1-1.2	0.37	. "

the tree growth is more open, and smaller if hemmed in closely by neighboring territories. Perhaps these two factors may also help to explain why Kirtland's Warbler territories are larger than territories of closely related species; that is, there is less vegetation in Kirtland's Warbler areas than in most forests inhabited by warblers, and there is plenty of habitat available to all without crowding. However, the total amount of vegetation in an area does not seem to give any clue to the small territories of the Yellow Warbler in brush, of the Redstart in forest, or of the Yellowthroat in an open expanse of marshland.

Stenger (1958:335-346) found that the territory of the Ovenbird, which feeds almost entirely on the ground, was smaller where the weight of invertebrates in the leaf litter was higher per unit area. This suggests that availability of food may help determine territory size in that species. However, if food availability is a factor in the size of the Kirtland's Warbler territory, I think it is a minor one. By the time the young have hatched and food needs are greatest, food seems extremely easy to get, and the female, particularly, gathers much of her food within 10 meters of the nest or in equally small feeding areas a short distance away—that is, within a very small part of the territory. Then, when the young have fledged, the family groups wander beyond the territorial boundaries but still seem to utilize only a small fraction of the area available. Lack (1943:100) similarly had the impression that food in the territory was far in excess of the needs of European Robins and their young during an ordinary summer.

By studying birds on small islands, Beer et al. (1956:200-209) found that the species studied were able to raise their young on territories "much smaller when the boundaries are strictly physical barriers rather than invisible lines determined by intraspecific conflict"—in some cases less than one-tenth the minimum area supposedly required on the mainland.

For the Kirtland's Warbler I believe the territory must be large enough to provide insulation from other adults of the species. Unless there is some freedom from the distractions of competition and conflict, I suspect certain delicately poised activities of the mating sequence cannot proceed successfully. These may include nest searching and building, when the female is easily deterred, and meetings of the pair, including copulation, which takes place only in concealment. The fact that many wild birds do not breed in captivity suggests that the requirements may be subtle and precise. Denser vegetation, providing the desired amount of seclusion in a smaller area, would of course also provide a higher concentration of food supply.

The Kirtland's Warbler

ing," periods of 9 to 12 days. Barth (1953:156) reported that the eggs of two small birds, House Martin and Willow Warbler, lost slightly more than one per cent per day during incubation.

The Kirtland's Warbler has the largest eggs of any species in the genus *Dendroica*, as shown by the compilation from Bent (1953) in Table 8.

Table 8

Comparative Size of Eggs in Genus Dendroica
(After Bent)

Species	N	Average length (mm.)	Average breadth (mm.)	Reference in Bent (page)
Yellow Warbler	50	16.6	12.6	168
Magnolia Warbler	50	16.3	12.3	200
Cape May Warhler	50	16.8	12.5	217
Black-throated Blue Warbler	50	16.9	12.8	229
Myrtle Warbler	50	17.5	13.3	244
Audubon's Warbler	50	17.6	13.5	264
Black-throated Gray Warbler	50	16.5	12.5	278
Townsend's Warbler	40	17.4	12.9	285
Black-throated Green Warbler	50	17.0	12.7	296
Golden-cheeked Warbler	50	17.7	13.1	319
Hermit Warbler	50	17.0	13.1	324
Cerulean Warbler	50	17.0	13.0	331
Blackburnian Warbler	50	17.2	12.8	341
Yellow-throated Warbler	50	17.1	13.0	354
Grace's Warbler	38	16.9	12.7	365
Chestnut-sided Warbler	50	16.7	12.4	371
Bay-breasted Warbler	50	17.7	12.9	383
Blackpoll Warbler	50	17.9	13.4	396
Pine Warbler	50	18.1	13.5	410
Kirtland's Warbler	154	18.1	13.9	This study
Prairie Warbler	50	15.9	12.3	432
Palm Warbler	40	17.4	12.9	453

Number of Eggs

Usually the Kirtland's Warbler lays five eggs in the first set and four eggs in a later nest of the same season. Occasionally a nest has six eggs or three eggs. It is always possible that cowbirds have removed eggs from sets examined, but I feel reasonably sure that some sets are complete with only three eggs. To calculate the proportion of sets of various sizes, I have considered only those not containing cowbird eggs and judged complete if observed for at least two days

EGGS

without a gain in number. These 67 nests held 310 eggs, 4.63 eggs per nest, distributed as follows:

Eggs per nest	Nests $N = 67$	Percentage of nests
3	7	10
4	13	19
5	45	67
6	2	3

Further evidence confirms the approximate correctness of the 3 per cent ratio of six-egg nests. In over 200 nests, including parasitized nests and nests seen only after the eggs had hatched, four were known to have received at least six warbler eggs each. Curiously, three of them were found in one year, 1951. One of these had also a cowbird egg and one had six young when found. It is probable that six warbler eggs were laid also in a few more nests that had lost eggs to cowbirds or through hatching failures before they were found.

In a world where variations so often occur in a "normal distribution," it is interesting that many birds with a usual clutch of five eggs have far more four-egg than six-egg clutches. The Ovenbird (Hann, 1937:172), Greenfinch (Monk, 1954:5), and European Robin (Lack, 1943:84) are other examples of such a distribution. However, as will be described later, a large number of four-egg sets are repeat nestings after the loss of earlier five-egg sets. When such repeat nestings are excluded by considering only those 38 unparasitized sets completed by June 14, we have a less skewed distribution:

Eggs per nest	Nest.
6	2
5	31
4	3
3	2

We cannot be sure that there has not been cowbird interference and other damage to some of these eggs after they were laid.

The largest number of eggs found in a Kirtland's Warbler nest was seven. There were four such nests: two with five warbler eggs and two cowbird eggs, one with six warbler eggs and one cowbird egg, and one with four warbler eggs and three cowbird eggs.

Hann (1947:173) once found eight eggs, four of the host bird and four of the cowbird, in the nest of an Ovenbird.

Since repeat sets are usually smaller, the number of eggs per set

region. Thus the cowbird begins laying before the warbler, reaches its peak of egg laying at about the same time as the warbler, and quits laying as the nesting season of the warbler draws to a close.

Thus, since none of the warblers nest outside of the cowbird season, there would appear to be little opportunity for the warbler to develop a more advantageous nesting time through selection.

Variation in Parasitism by Years

Field workers believe that the number of cowbirds in Kirtland's Warbler areas varies from year to year, although no exact counts have been made. Indeed, we should expect the population of any species to fluctuate to some extent, and that the cowbird pressure on Kirtland's Warblers would therefore be higher in some years than in others. Actually, the proportion of parasitized nests on the study areas varied from a statistically significant low point in 1951 (9 out of 33) to a significant high point in 1956 (15 out of 17). However, in general the samples are too small for us to be certain the population of cowbirds varied from year to year in this region. Information of

Table 24

Cowbird Parasitism of Nests of Kirtland's Warbler: Variation by Years 1944–1957

Year	Total Nests	rarasiii:	zed Nests
1 641	N	N	Per cent
1944	6	5	. 83
1945	8	5	63
1946	13	7	54
1947	13	9	69
1948	19	5	26 *
1949	6	3	50
1950	6	3	50
1951	33	9	27 *
	23	8	35
1952	15	6	40
1953	17	3	18 *
1954	15	10	67
1955		15	88 4
1956 1957	17 15	11	73

^{*} Variations not explainable by chance alone (significant at 5 per cent level of confidence).

consecutive years with the greatest number of nests is given in Table 24.

Choice of Nests by Cowbirds

Diligent field work on the parasitic Cuckoo, Cuculus canorus, in England led Chance (1940) to believe one strain ("gens") of Cuckoos confined its attentions to one host species, unless no nests of that species were available, and laid a distinctive type of egg resembling the host's. However, some of his findings were inferred rather than observed directly; for example, the individual birds were not usually marked so that they could be identified with certainty.

Do certain cowbirds specialize in Kirtland's Warblers' nests? Having laid in a nest, does a cowbird tend to return to it, or to avoid the when laying again? We cannot yet answer the first question, but perhaps we can throw some light on the second.

Most attempts to trace the activities of particular cowbirds have been based on the appearance of the eggs. The assumption that imilar eggs were laid by the same cowbird and dissimilar eggs by different cowbirds is speculative, and I have not attempted to use it bere. Certainly, this assumption would not be true of Kirtland's Warbler eggs, for those in the same nest often look so different from one another that one might think they were laid by different females.

A way of examining the work of cowbirds at large is to compare distribution of eggs with that expected by chance. For this purpose we use the elements of a Poisson series, which express the probabilities of successive events when the average expectation is known, as in the following formula:

$$e^{-c}$$
 $(1 + c + \frac{c^2}{2!} + \frac{c^3}{3!} + \frac{c^4}{4!} + \cdots)$

where c is the average expectation and e is the base of natural loga-

In this instance 137 nests received 125 cowbird eggs. Therefore, exerage expectation, c, would be $\frac{125}{137}$ = .91 eggs per nest. However, the observed distribution was as follows: 0 cowbird eggs, 62 cowbird eggs, 36 nests; 2 cowbird eggs, 29 nests; 3 cowbird eggs, 1 nest. Expressing the distribution in centages of 137 nests, and comparing the chance distribution

The Kirtland's Warbler

26 young warblers. Four, with two cowbird eggs each, contained 1.71 young warblers each, or 7 young warblers. So 33 warbler young were not affected adversely by cowbirds. Of these, 30 were fledged.

Consequently, in this hypothetical sample of 100 parasitized nests not destroyed or deserted, of 89 + 112 = 201 warblers hatched, 53 + 30 = 83 (41 per cent) were fledged. Conversely, the mortality among nestlings in parasitized nests was 59 per cent of warblers hatched. But of 201 eggs hatched, 8 per cent would be lost from hatching to fledging as a result of other causes of in-nest mortality; so only 185 eggs should be considered in calculating losses attributed to cowbird nestlings alone. Hence, survival of nestlings in the face of cowbirds, neglecting other hazards of the nestling period, is $\frac{83}{185}$ or 45 per cent of nestlings hatched; and conversely, mortality of warbler nestlings attributed to cowbird nestlings alone is about 55 per cent in nests that are not destroyed or deserted.

Recapitulation of Warbler Losses Caused by the Cowbird

The pressure exerted by the cowbird at different stages in the nesting process is shown in Table 32.

Table 32
Warbler Losses Caused by the Cowbird in Parasitized Nests: Summary

41	
41	
т.	59
6	53
31	22
	-

Thus, as a direct result of the cowbird, 78 per cent of warbler eggs in parasitized nests fail to produce fledglings. Since 55 per cent of all

f about 43 per cent of all lend fledging, in nests not control the fact that many was lost anyway through other desertion of nests. By suppression of the fact disease among of the fact disease among of the form heart disease among of the fact disease disease among of the fact disease among of the fact disease among of the fact disease among disease disea

To show more accurately cowbird—and how much be we compare the production

The average Kirtland's r interference from cowbird fledglings is .32, and the p nest. On the other hand, in will produce fledglings is .6 is .32 per nest. Or, expressings laid in nests without times as likely to produce nests.

Warbler nests would be imence. For this question, we cent of nests parasitized) which probability that eggs whird pressure (p. 201) is stized. Therefore, the procent if there were no co

Incubation Period for

The incubation period nests is in no case known to tion to the hour of hatchi incubation begins, exact a cowbird eggs laid after incubation period is here to have inferred a period of

TABLE 33 - INTERCESTALLY NEST SUCCESS NATURA TAIC.

nd's Warbler

sts have been found sometime after true in most other studies of open-

ors are often silent on this point, it that most nests reported with eggs rse of incubation. If so, the success es will be higher than the true rates. If we could assume that the days of only throughout the incubation pethe true success rate from the obole, because the time of discovery of ag to the habits of the bird and the

s one tending to lower the observed the, is introduced by excluding nests cocedure favors the inclusion of nests ost might have been excluded if they are observer had left the area. Presums in many other studies.

eated the data in another way. Howirtland's Warbler with other species, in the usual manner in Table 33. Here hat the nests found were typical of all ecept as noted, my own observations

rizing 35 major studies of open-nestper cent of the eggs hatched, with a

of wood warblers have shown prollows: Ovenbird, 63 per cent of 322 v Warbler, 71 per cent of 168 eggs thonotary Warbler, a cavity-nesting (Walkinshaw, 1953:168).

with a hatching rate of 52 per cent of interference, has a low production since, unlike many others, it usually season. The activity of the cowbird; in fact, substantially below the 47 cause records based on eggs seen do removed by cowbirds, most of which

REPRODUCTION AND MORTALITY

Table 33

Nest Success during Incubation

	Nests		
	Without C eggs	With C eggs	Total
Total number of nests	79 *	75	154
Nests excluded because outcome unknown	15	12	27
Nests excluded because later parasitized	5	o	5
Nests excluded because of human interference	o	9	9
Nests with outcome known	59	54	113
Nests deserted during incubation	8	8	16
Nests destroyed during incubation	I 1	8	19
Nests hatching no eggs	2	o	2
Nests in which eggs hatched	38	38	76
Percentage of nests with outcome known hatching	-		• /2.501
eggs	64	70‡	67
KW eggs seen in nests with outcome known	273	154 8	427
KW young seen in nests with outcome known	142	58	200
Percentage of KW eggs seen that hatched	52 T	38 †	47
C eggs seen in nests with outcome known	0	78	78
C young seen in nests with outcome known	o	54	54
Percentage of C eggs seen that hatched	o	69	69

* Group of 67 nests on page 147, plus 6 nests from which cowbird eggs had been removed, plus 6 nests in which the set of eggs was not proved complete, although the outcome was known.

† The number of young hatched was undoubtedly higher than this figure, because some of these nests were not seen immediately after hatching.

‡ Larger proportion of parasitized nests hatch eggs because they usually have a shorter incubation period by two days than do nests with KW eggs only.

§ An undetermined number of KW eggs were removed by cowbirds before many of these nests were found.

were removed before the nests were found and which were therefore not seen.

Rates of Success during the Nestling Period (as Customarily Presented)

It is not easy to determine accurately how many young birds have left the nest safely. We seldom witness their leaving, and great effort is required to find them after they leave. Usually we infer that young Kirtland's Warblers have left if the nest becomes empty when the young are old enough to leave; that is, at about eight days of age.

Here (Table 34) I have assumed that young have fledged if they have been seen in the nest over a period of at least seven days. To enlarge the sample as much as possible, I have included several nests found when the young were hatched recently (judged not over two

Table 34

Nest Success during the Nestling Period

	Nests		
	Without cowbirds	With cowbirds	Total
Total number of nests	35	27	62
Nests deserted	2	2	4
Nests destroyed	5	8	13
KW nestlings seen	136	43	179
KW young fledged	104	25	129
Percentage of KW nestlings seen			
that fledged	76	58 *	72 *
C nestlings seen	О	31	31
C young fledged	О	19	19
Percentage of C nestlings seen			
that fledged	О	61 †	61 †

^{*} This small sample yields a fledging rate for warblers that is obviously too high, because many newly hatched warblers are killed by cowbirds and removed by parents without being seen by an observer.

days old). In view of the uncertainties, these figures should be considered approximate. Of 62 nests, 45 (73 per cent) fledged young.

In order to represent properly nest losses from desertion and destruction, only those are included which were lost at such a time that an observer would still have been present if the nest had survived its full period.

In Table 35 are shown further data on nest success, but from ness not seen early enough to be included in previous tables.

Rates of Success from Eggs to Fledging (as Customarily Presented)

To draw from the data shown in Tables 33 and 34 rates of nest and fledging success comparable to those of other studies, the rates of success during incubation and the nestling period, computed in two

REPRODUCTION

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Table 35
Birds Produced per Nest Fledging Young *

	N	Per nest fledging young
Nests without Cs	42	
KW young fledged	164	3.9
Nests with Cs	27	3.9
C young fledged	39	1.4
KW young fledged	27	1.0 †

* Note that all nests in this group succeeded; that is, none that were deserted or destroyed are included.

† This yield is probably too high, since it contains an abnormally successful parasitized group.

earlier sections, are combined. The results are shown in Table 36.

The nest success rate yielded by this method for the Kirtland's Warbler, 49 per cent, is exactly that found by Nice (1957:305-307)

Table 36
Success from Eggs to Fledging *

	,
Nest Success/Egg Success	Rate
To fledging, without Cs (During incubation, 64 per cent; during nestling period, 76 per cent)	.64 × .76 = 49 per cent of nests found with eggs
With half the nests parasitized (During incu- bation, 67 per cent; during nestling period, 73 per cent)	$.67 \times .73 = 49$ per cent of nests found with eggs
KW egg success to fledging, without C's (During incubation, 52 per cent; during nestling period, 76 per cent)	.52 × .76 = 40 per cent of eggs seen
KW egg success to fledging, including para- sitized nests (During incubation, 47 per cent; during nestling period, 72 per cent)	.47 X .72 = 34 per cent of eggs seen

^{*} Note that these figures are certainly too high, because they are based on eggs acen, and do not take account of eggs removed by cowbirds before the nests were found.

for 7,788 open nests of several species of altricial birds. However, she found a fledging success of 46 per cent for 21,951 eggs in various studies of open-nesting altricial birds, with a range of 22.4 to 70.6. Hann (1937:198) gives 43.5 per cent fledging success for the Ovenbird, and Schrantz (1943:386), 54 per cent for the Yellow Warbler,

[†] This small sample yields a fledging rate for cowbirds that is almost certainly too low.



Warbler

ne appreciable, if we assume the ring to be half the rate during seven days would be .987 = .87. It start of construction would be Of course, most of these nests 8 days (an average of about 5 d, but the time available for rededlay in some instances would it would seem reasonable to addownward, say 10 per cent, to 11 67 succeed per year for 100

of 0.9 fledglings each, the young number 135, an average of about Warblers.

birds, the yield would have been ing incubation, 222 fledglings in ir of Kirtland's Warblers. Thus, pird, the Kirtland's Warbler has a

uction of fledglings per year per 8 in several other passerine spethe Ovenbird produced 2.9 fledgought only 1.6 fledglings to the

oduction of young must be suffiadults. It is therefore necessary to

ther of Kirtland's Warblers were To study their survival rate, I adults on three areas, where sufosequent years to make it probable rea would be found. All these birds and were seen in later years, if at al rate is therefore calculated from e next. (See Table 44.)

a minimum survival rate; the true

REPRODUCTION AND MORTALITY

figure will be higher than this one if any birds live undetected in later years.

I believe the true survival rate for adults from one nesting season to the next is about 60 per cent, as shown for the Old Mack Lake area. This area was small enough to allow virtually all of it to be searched each year, and it was at least three miles from any other nesting colony. The other two study areas were so large or so near other nesting areas not searched that warblers which moved even a short distance may have escaped detection.

When we calculate survival rates from numbers of birds seen in the wild, there is always a question about how many birds still living

Table 44
Survival of Adult Kirtland's Warblers: Males and Females

Area	Years N		Banded birds in June N		Previously banded birds present fol- lowing year N		Survival rate per year (Per cent)	
	M	F	M	F	M	F	М	F
Old Mack Lake	9	9	29	36	17	22	59	61
Wakely Bridge Road	4	4	8	24	6	9		
New Mack Lake	2	2	8	1 t	4	6	• •	• •
Total			45	71	27 *	37 *	6o *	52

^{*} Actual survival may have been greater than shown if any birds escaped detection.

are not seen. Certainly there are some. Female Kirtland's Warblers are more likely to escape notice than males. On the Old Mack Lake area, for example, of 22 instances of returns a year later there were four instances of females which were not seen one year but were found the next. On the same area, which was studied intensively, no males were missed one year and found later. However, on the Wakely Bridge Road area, where it was impossible to make a thorough study of the entire populated area, of six returns of males one was missed in two intervening years.

I have two examples of females that nested at distances of almost a mile (1,350 m.) and nineteen miles (31 km.) from the previous year's nests. Ordinarily such females would not be found again. The

Population Change in the Kirtland's Warbler

At present, population size appears to be regulated on the wintering grounds by rainfall.

LAWRENCE A. RYEL

The Kirtland's Warbler (Dendroica kirtlandii) is often referred to as one of the best known songbirds. Two books and about 200 papers have been written about the species. Yet mankind was unaware of their existence until the early 1850's. Neither Wilson nor Audubon ever saw one. Dr. Jared P. Kirtland, for whom the species was named, never observed one alive (Gifford 1975). When he died in 1877, neither the winter range nor the breeding range were known. It was not until 2 years later that the winter range was determined to be in the Bahama Islands. The first colony of breeding birds was discovered in 1903 in the jack-pine (Pinus banksiana) plains of nor thern Lower Michigan (Mayfield 1975). In the next 20 years, apparently only three other colonies were found (Leopold 1924). It appears that the Kirtland's Warbler has been a rare bird for at least the past 100 years.

Although considerable effort was expended on life history studies since the 1930's, no attempts were made to assess the overall number of birds until 1951. That year Harold Mayfield organized a census of singing males the first attempt in the world to census the entire breeding range of any songbird species (Mayfield 1953). Two more censuses were carried out at 10-year intervals (Mayfield 1962, 1972a). A drastic 60% decline from 1961 to 1971 (502 to 201), however, prompted those concerned with the survival of the species to institute annual censuses and provide protection for breeding birds.

An interim committee held forth until 1975 when the Kirtland's Warble Recovery Team was organized under Federal Endangered Species legislation. The team has representatives from the Michigan Department of Natural Resources, U.S. Forest Service, U.S. Fish and Wildlife Service, and the Michigan Audubon Society. Their goal is to increase the population to 1,000 pairs and maintain it at that level (Byelich 1976).

The objective of this paper is to evaluate some hypotheses which need to be dealt with in our attempts to develop a population model—a mathematical approximation of the population dynamics of the species. We do not have information on when the decline between 1961 and 1971 occurred, whether it was abrupt or gradual, or what caused it. Workers theoring a crash generally implicate the weather; while those believing the decline was gradual implicate habitat changes, parasitism, or competition. Since 1971, certain management practices appear to have maintained the population at approximately 1971 levels, but we have wondered why the population has not increased instead. Additional ideas are needed and will be most welcome.

METHODS

Data are available from 12 censuses of singing male Kirtland's Warblers (Mayfield 1953, 1972a, 1973a, 1973b, 1975; Ryel 1976a, 1976b, 1979a, 1980a, 1980b; Burgoyne and Ryel Mayfield actively supervised and participated in all censuses from their inception in 1951 cough 1974. His initiative and far-sightedness have provided us with over a quarter-century population benchmarks. In addition, much published information from the literature as as original data developed by the Kirtland's Warbler Recovery Team, was utilized in this

RESULTS

Recent population trends. — Since 1971, the annual census results have remarkably uniform – an average of 202.9 ± 20.8 (one standard deviation) singing males in Michigan. From 1977 to 1980, one to four singing males, all apparently unmated, were also found outside of Michigan. Data for individual Michigan counties also suggest a rather stable situation (Table 1). Only when the resolution is increased to individual sections (square miles) do sizable changes become evident (Ryel 1979a). The variable evidence suggests that populations in a given area increase largely by recruiting yearlings produced in other areas. Declining populations in an area seem to represent the continual attachment of older males to their territories (Ryel 1979b). One can clearly see the difficulty of assessing the overall success of the species by studying small portions of its breeding tange.

Winter range. — Mayfield (1960) felt that the survival of both adults and fedglings was high on the breeding grounds, which leads one to suspect that sost mortality occurs during migration and/or the winter. Fretwell (1972) points out that the populations of most bird species are limited by conditions during the winter months. Since the population levels of Kirtland's Warblers have remained relatively stable since 1971, in spite of greatly increased nesting success, some people have concluded that the winter range has a limited carrying capacity and that the current population level is close this capacity.

So far as is known, the wintering range of Kirtland's Warbler is restricted to the Bahama Islands and the nearby, geologically similar, Caicos Islands Mayfield 1960). Actually "winter" is not quite the correct term. Kirtland's Warblers spend over 8 months in the Bahamas, generally from mid-August late April. Recently there have also been two curious sightings of Kirtland's Warblers in Mexico. Lane (1975) observed one (perhaps two) hids south of Veracruz on 11 November 1974 and there is a report of three hids observed near Palenque by George Finney (Paul Aird, pers. comm. 1978). Barring further evidence, we must view the Mexican reports as representing aberrant birds. Certainly no indication of a Mexican wintering area is evident from fall migration records (Clench 1973).

Mayfield (1960, 1972b, 1975) and Radabaugh (1974) have summarized the historical winter records for the Bahamas. The only period when the pecies could be found there with any degree of regularity was from 1884 to 1897. During this 14-year span, over 90% of the some 72 known specimens

TABLE 1. Counts of singing male Kirtland's Warblers by County, all censuses to date.

Location	1951	1961	1971	1972	1973	1974	1975	1976	1977	1978	1979
Michigan Counties											1
Crawford	142	52	101	101	114	'88	90	95	78	74	75
Oscoda	103	152	48	48	47	41	35	44	59	62	71
Iosco	74	30	1							2	1 1
Montmorency	43	6 1	1								
Presque Isle	34	34									
Roscommon	4	13				1	4	2	7	2	2
Alcona	4										
Kalkaska	28	32					3	7	11	16	21
Ogemaw		114	47	49	51	35	46	51	62	40	40
Otsego		14	3								
Wexford				2	4	2	1	1	1		- 4
Michigan Total	432	502	201	200	216	167	179	200	218	196	210
Wisconsin Counties Jackson										2	
Ontario Counties Renfrew									1	1	
Quebec Counties Gatineau										_1	
NORTH AMERICAN TOTAL	432	502	201	200	216	167	179	200	219	200	211

from the Bahamas were taken. Since the 1900's, the birds have been ceedingly difficult to find. Both their distribution among the islands and habitat used is virtually unknown.

In the winters of 1972 and 1973, Radabaugh (1974) spent a total of hours in surveying habitat and searching for Kirtland's Warblers on 11 ferent islands. He found only one Kirtland's Warbler, a male, which observed on 3 different days in March, 1973 on Crooked Island. One object tive of Radabaugh's studies was to evaluate the idea that worsening habit conditions in the winter range might be responsible for the decline of warbler population between 1961 and 1971. He noted the most professional habitat change in and just prior to the decade of interest was the lumber of Caribbean pines (*Pinus caribeae*) successively on Grand Bahama, Abas and Andros islands from 1956 to 1974. In all, some 1,690 km² were logge He suggested this activity may have contributed to the population declin Mayfield (1975), however, counters that in most logged over pine state reforestation progressed rapidly and substantial tracts of pine were left cut on each of the islands. Furthermore, Caribbean pine occurs on four of the northernmost islands. Mayfield (1972b, 1975) also notes and annotated observations have placed the birds in young or student broadleaved scrub, even when associated with pines or the pine-like Australian "pine" (Casuarina equisetifolia).

Bahamas consist of about 700 islands and 2,400 cays and rocks. Only 100 of the islands and cays are even minimally inhabited by humans interiors of most of these are uninhabited (Mayfield 1975; Editions 1980). Evidently, as a whole, the Bahama Islands have changed very this century. Kirtland's Warblers have been collected or observed on 16 islands or cays (Radabaugh 1974).

density influences. — One important thing to determine is the ups and downs of the Kirtland's Warbler population are due the ups and downs of the Kirtland's Warbler population are due the ups and downs of the Kirtland's Warbler population are due to the ups and downs of the Kirtland's Warbler population are due to the ups and the population fluctuate about an equilibrium value (density density or vary randomly from one year to the next mostly due to in climate and other environmental factors (density independent)?

The critical control of the ups and t

$$V = \sum_{i=1}^{N} (X_i - \overline{X})^2$$

$$U = \sum_{i=1}^{N-1} (X_{i+1} - X_i)^2$$

logarithm of the population size in year t. V reflects growth rate from the population mean, while U reflects growth rate changes in ve years.

the Kirtland's Warbler, if we assume the spring breeding population the number of singing males counted, then R=.727. The test is The critical value of $R_{\perp}=.543$ at the $\alpha=.05$ level for N=10. Loce this analysis suggests the population, at least at current levels, is longly density dependent; but 10 years of data is not a very long from which to draw conclusions.

hurricanes during the fall migration period were responsible for ling Kirtland's Warbler populations. He feels that a series of ling hurricanes during the late 1920's and early 1930's were responsible decline in Kirtland's Warblers which he is convinced occurred durperiod.

Cruickshank 1939; Hill 1945). Sutton (1945), however, reports that the storm's conditions. Following passage of an October hurdon, florida, he found only one dead bird, a Palm Warbler palmarum), which may or may not have been a victim of the

Hurricanes are almost entirely a fall phenomenon in the North Atlant-Since 1900, no hurricanes or tropical storms have occurred during spring migration period of Kirtland's Warblers (Neumann, et al. 1978). It fall migration period appears to be much more spread out than springing migration (Mayfield 1960; Wallace 1968). The available data are limited but they suggest that most migration occurs during the last half of Augustinough mid-October (Clench 1973).

There were 19 such storms (Table 2) which occurred from 1951 to 1971 during the fall migration period (August 15 to October 15) in the vicinity the Bahama Islands. Data through 1977 were from Neumann et al. (1972) while John Hope of the National Hurricane Center, Coral Gables, Florid kindly supplied me with information on hurricanes and tropical storms for 1978 and 1979. Although the 9-year period, 1952 to 1960, had 13 of the storms, singing male census results for 1961 were 502, some 16% above to 1951 count (432). The population did not show any increasing trends from 1971 to 1979 when only one storm occurred (1979). The decade when warblers declined (1961 to 1971) had five storms.

One might suspect that a storm crossing the northern end of the islandarian would pose the greatest threat to migrants. Examination of hurricatracking charts reveals only two such storms since 1951 – Hurrical Isabella, 14 and 15 October 1964 and Hurricane Betsy, 6 to 8 September 1965. Both of these, however, were in the decade when the populate declined.

Hurricanes and tropical storms are not the only hazardous weat systems for migrating birds. Storms associated with cold fronts during bo spring and fall migrations have been reported to result in unusual migration patterns for many species (Gunn and Crocker 1951), as well as outrimortality at television antennas, smoke stacks, and other high structudue to reduced visibility, high winds, and/or heavy rains (for example Howell et al. 1954; James 1956; Cochran and Graber 1958; Caldwell at Cuthbert 1963; Caldwell and Wallace 1966; Kale et al. 1969; Taylor Anderson 1973; Avery et al. 1977; Broughton 1977; Seets and Bohlen 1977. Both spring and fall migration periods are involved. Warbler species to be particularly affected by such conditions since they are generally

TABLE 2. Hurricanes and tropical storms in the Bahama Islands, August 15 to October 15, to 1979.

				14
Year	Number	Year	Number	
1952	1 H*	1960	1 H, 2 T	
1953	1 T**	1963	1 H	. 5
1954	2 H, 1 T	1964	2·H	
1956	2 T	1965	1 H	.4
1958	1 H, 1 T	1966	1 H	
1959	1 H	1979	1 H	1
on whose the		1.20		- 1

^{*} Hurricanes in vicinity of Bahama Islands.

mil migrants and often appear to travel together in loose assemblages of species.

while no dead Kirtland's Warblers were observed in the above studies, potential is certainly there. In a most dramatic episode, Trautman was thering bird casualties at the base of the Perry Monument, South Bass cland, Ohio (Lake Erie), the evening of 24 May 1954 when a falling trland's Warbler struck him (Mayfield 1960).

In recent years it seems that members of the Kirtland's Warbler Recovery mare apprised of at least one sight record every year, but in the agrate these still amount to a relatively small number of observations over years. Most of these observations are of single birds, either in the hamas or during migration. In 30 years of bird watching in Michigan, I ronally have observed this species only once during migration. On 10 ty 1969, I, together with my wife and son, observed two males on the Erie Game Area, Monroe County.

On the wintering grounds, Kirtland's Warblers are reported to be shy and lary (Mayfield 1960). This might be merely a reflection of their rareness, Eaton (1953) reported that wintering wood warbler species in Cuba be classified into three groups based on behavioral differences: (1) for found singly, (2) those in flocks of one species, or (3) those in flocks several species. He included the Louisiana Waterthrush (Seiurus severalla), Ovenbird (Seiurus aurocapillus), Northern Waterthrush (Seiurus eboracensis), Swainson's Warbler (Limnothlypis swainsonii), and Cape Warbler (Dendroica tigrina) in the solitary group.

Since the birds appear to migrate singly or in small flocks, a single storm add not be likely to affect much of the population. This would be partially true in the fall when the migration period is prolonged. The same stretch for some 750 miles and there are records of Kirtland's arbiers from various islands located throughout the chain. With the stering grounds spread over such a large area, the odds of one storm afting a major portion of the population here seems small.

Drought. — Paul Fluck reported seeing "bushel baskets" of dead birds the Queen's Highway on Grand Bahama in the spring of 1971 adabaugh 1974). He attributed this to reduced insect life after an excely dry winter. In order to gain some insight into the possible effects of ught, I examined the rainfall patterns from the Nassau International port and prior to 1957 from Oakes Airport (National Climatic Center, lous dates). While these may not reflect conditions for the entire island in, no other records were easily available.

Vinter is normally the dry season in the Bahamas, but some years are the drier than others. The November to April period for the 10 years 1951 to 1960 averaged 328.2 mm. of rain. The following decade, when warbler population declined, was decidedly drier, averaging 200.5 mm. 1976 less per year. The past nine winters have been intermediate, average 302.7 mm.

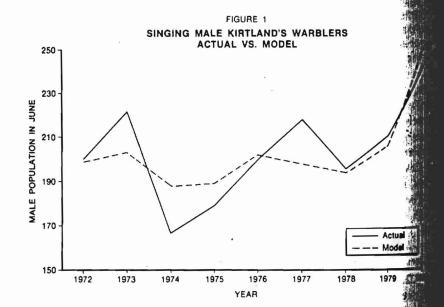
Using stepwise multiple regression (MIDAS statistical package developed the Statistical Research Laboratory, University of Michigan, and run on

^{**} Tropical storms in vicinity of Bahama Islands.

the university's AMDAHL/v8 computer), we constructed a simple based on the number of singing males in Michigan in year $t(X_1)$, estimated number of fledglings produced in year $t(X_2)$, and the sum Nassau rainfall in mm from November to April for years t and t + 1 (restimated number of singing males in Michigan in year t + 1 (restimated number of fledglings (X_2) was calculated by multiplying number of males by the average number of fledglings produced per from field studies. In some years the average number of fledglings per was in turn estimated from the number of fledglings per nest.

The resultant prediction equation is: $\hat{Y} = -.05752 X_1 + .03976 X_2 + .09389 X_3 + .09389 X_4 + .03976 X_4 + .03976 X_5 + .09389 X_6 + .09389 X_7 + .03976 X_6 + .09389 X_7 + .03976 X_$

The partial regression coefficient for the Nassau rainfall variable (significant at the $\alpha = .05$ level, while neither of the other two coefficient approach significance. The simple correlation matrix which was undevelop the regression equation is shown in Table 3. Nassau rainfall in November to April is significantly correlated with the number of significantly



3. Simple correlation matrix of variables used in population model.

(E)						
		Males	Fledglings	Nassau rain	Males year	
		year t	year t	NovApr.	t + 1	
riable		(X_1)	(X ₁)	(X ₁)	(Y)	
des year t	(X ₁)	1.0000				
ings year t	(X_1)	0255	1.0000			
rain	(X_i)	.2690	1813	1.0000	· ·	
MovApr.						
Mes year t + 1	(Y)	.1749	.1734	.7712*	1.0000	
	5 10	Signi	ficance levels:			
			.01 = .7977 **			
		.01	.05 = .6664 *			

which in the following June at the $\alpha = .05$ level. None of the other corrections approach significance.

Hence, there is a strong support for the notion that overwinter survival of thand's Warblers is related in a positive fashion to the winter rainfall. does not mean that there is a direct cause and effect relationship. ther, increased rainfall likely causes increased plant growth which in turn produce larger insect populations. The male that Radabaugh (1974) there over parts of 3 days in March, 1973, spent about 70% of its time wively searching for food. He guessed that the foraging area was at least 7 much larger than the usual breeding territory in Michigan. He also the foraging area was not rich in other bird life and no conflicts (or close approaches) were observed with any other bird. The total rainfall Nassau that winter (November, 1972 through March, 1973) was 258 mm., fourth highest year in the decade (National Climatic Center, various). It's possible that in "dry" winters, so much energy is spent searching food, that it affects survival.

Competition. – At higher population levels, competition might well stome a significant factor. Fretwell (1976, 1977, 1978) hypothesized that petition for food, both from other warbler species, particularly the Warbler and Prairie Warbler (Dendroica discolor), as well as inspecific competition, influenced the number of Kirtland's Warblers that rived the winter. He felt that the population was strongly density dedent and that the more birds that attempted to winter, the higher the mortality. Subsequent population changes did not completely supthis predictions, nor did the test described above reveal density endence at current population levels. In addition, simple correlations table 3) between fledglings in year t and males in year t+1, as well as in year t and males in year t +1 were both positive.

Summer range. — On the breeding range in northern Lower Michigan, Kirtland's Warblers characteristically occur in loose aggregations or "colonies." The birds occur typically in dense stands of Christmas-tree sized jack-pine covering 32 ha or more, which are produced naturally by forest fires. The birds also utilize plantations of jack and occasionally red pine (Pinus resinosa) which simulate this configuration. The birds no longer use an area when the trees are 4.9 to 6.1 m tall. A typical time span of use might be 10 to 12 years, but the range is on the order of 6 to 19 years (Mayfield 1960).

Many workers, notably John Byelich, Recovery Team leader, feel that the breeding habitat is the most critical factor in the birds' survival, Indeed the evidence from bird collectors seems to indicate that the highest populations occurred during the 1880's and 1890's following the dramatic changes that occurred in northern Michigan with the cutting of the pine forests and the many subsequent wild fires (Mayfield 1975). In this century, Michigan forest fire control has become increasingly efficient, greatly reducing the number of large fires, which in turn has reduced the amount of habitat. The birds, however, have never come close to occupying all of the apparently suitable habitat in a given year. Our idea of warbler habitat, however, may well be different from that actually most appropriate for the birds. Jerome Weinrich, Michigan Department of Natural Resources, and William Irvine, U.S. Forest Service, estimated that approximately 2,430 ha were occupied by the birds in 1980. This is almost identical to Mayfield's (1975) estimate for 1974 and Wood's (1926) estimate for 1925. The birds seem to prefer large colonies; but paradoxically, most colonies are small. In 1980, the median size for the 22 colonies was four males, while the mean was 11.0 (extremes 1 to 49). About ³/₄ of the singing males were found on the sites of five wild fires (Ryel 1980b). Mayfield's (1962) studies indicate that the birds prefer natural growth over planted trees. This preference may be related to differences in growth form and spacing of the trees, difference in ground cover, and reduced competition from other species of animals.

Using current forest stand data, David Sorenson, U.S. Forest Service, and Jerome Weinrich were able to project both forwards and backwards to estimate the probable extent of suitable habitat in state and federal ownership at several points from 1961 to 1989. In 1980, 92% of the singing males were found on state or federal land. During the decade when warbler populations declined by 60%, there was a corresponding decline of about 44% in habitat. By 1979, the habitat had increased to 88% of 1961 levels; however, there has been no general increase in warbler populations. Habitat projections indicate a further increase through 1984 followed by another decline (Table 4).

The Recovery Team has designated 51,650 ha (58% state forest and 42% national forest) as critical habitat. Management plans are nearly complete and some work has already been done. An additional 3,040 ha of Michigan

TABLE 4. Estimates of occupiable habitat — Michigan's Kirtland's Warbler range (hectares).

<u> </u>	1961	1971	1979	1984	1989
National Forest	2,480	1,220	1,590	2,180	2,400
State Forest	4,800	2,880	4,460	4,240	1,870
National Guard			380	1,620	1,210
# · · · · · · · · · · · · · · · · · · ·	7,280	4,100	6,430	8,040	5,480

National Guard land has potential for producing habitat through occasional wild fires caused by training maneuvers. Objectives are to regenerate 1,090 ha per year - 690 state and 400 federal. However, there is a time lag of 8 to 10 years before it will be occupiable.

To protect nesting Kirtland's Warblers from human disturbance, the Recovery Team has posted known breeding areas against entry from May 1 to August 15 each summer. No bird watching or bird photography is allowed except by supervised tours conducted by the U.S. Fish and Wildlife Service at Grayling and the U.S. Forest Service at Mio (Ryel 1978). Agreements with the Michigan National Guard have resulted in alterations of their training maneuvers during the nesting season. No research studies have been approved in active colonies except the work of Walkinshaw (1981) and Cuthbert (unpublished) who have monitored nesting success.

Anderson and Storer (1976) analyzed the influence of 47 variables on nesting success using information which had been gathered on 545 nests from 1931 to 1975. They found no variables which significantly affected fledgling success except Brown-headed Cowbird (Molothrus ater) parasitism and two factors which seemed to aid cowbirds: the presence of large trees or snags and hilly terrain. There was also some indication (not statistically significant) that larger colonies had somewhat better success.

It is likely that summer and early fall weather, particularly rainfall, on the breeding grounds may influence fledgling survival, either directly or indirectly, but this has not been investigated to date.

Brown-headed Cowbird. - Leopold (1924), one of the first to study nesting Kirtland's Warblers, listed cowbirds as "common" in the area in losco County where he observed two Kirtland's Warbler nests in 1923, one of which was parasitized. He was apparently the first to blame the cowbird for the scarcity of the species.

Mayfield, Walkinshaw and others also soon came to view the cowbird as the greatest threat to the Kirtland's Warbler. They are convinced that the decline between 1961 and 1971 was due to cowbird parasitism (Walkinshaw 1972; Mayfield 1960, 1961a, 1961b, 1972a, 1972b, 1975, 1977, 1978). Their records indicate parasitism was high in the past and became higher in recent years. Mayfield's (1975) data, largely from the 1940's and 1950's, indicated about half of the nests he found were parasitized. He estimated an average

of 1.35 fledglings were produced per pair during this period. Comparison data from Walkinshaw (1981) for the years 1931 through 1955 show a 250 nest parasitism and a fledgling production of 1.64 per nest. From 1957 1971, however, he found 75% of the nests were parasitized and an overal fledgling rate of less than one (Table 5).

In order to properly evaluate what these production data mean, we to consider survival rates. Roberts (1971) calculated the average and adult survival rate for six eastern warbler species at 64%. Nolan (1978) cluded that the average annual survival of adult Prairie Warblers in Indian was 65% for both sexes. Mayfield (1960) estimated the corresponding for Kirtland's Warbler to be about 60%.

Fledgling survival is much more difficult to evaluate. Most year Kirtland's Warblers apparently do not return to the colony where they fledged (Ryel 1979a), hence, estimation of survival from banding return very difficult. Nolan (1978) estimated that the survival of Prairie Wart fledglings to the following breeding season was about 32%. Roberts (1970) concluded that the first-year survival of fledglings for some "less cessful" species of warblers (including Kirtland's) had to be on the order 45% for a stable population. In most species of wildlife, the survival young of the year is much more variable from year to year than that adults.

As Mayfield (1960) points out, at the fledgling rates he observed in studies from 1944 to 1957 (Table 5), the survival rate for fledglings would need to be about 57% to maintain the population, or nearly equal to 60% he calculated for adults.

TABLE 5. Kirtland's Warbler nesting success.

	Number	Number of nests	Number of Nestlings fledged		×	15
Year	of pairs		per pair	per nest	Source	1
1944-1957		206	1.35	.90	Mayfield	(11
1931-1955		28		1.64	Walkinshaw	(ti
1957-1968		25		.64	Walkinshaw	(H
1969-1971		38		.92	Walkinshaw	(11
1972	26	32	3.35	2.72	Walkinshaw	(11
1973	31	34	2.97	2.71	Walkinshaw	(11
1974	54	63	3.35	2.87	Walkinshaw	(1)
					Orr	(1)
1975	32	37	3.19	2.76	Walkinshaw	4 (11
1976	30•	33	2.97	2.70	Walkinshaw	(1)
1977	29	31	2.21	2.06	Walkinshaw	(1)
1978		25		3.20	Cuthbert	(mate
1979		35		2.69	Cuthbert	(unp

mether trials of the same sort of deterministic simulations also convinced that either fledgling production was underestimated and/or that fledgbervival was extremely high (Table 6). The former, at least, turns out to inially true. Early workers felt Kirtland's Warbler was single brooded field 1960). Radabaugh (1972), however, found that if the first brood by the end of June, about 40% of these pairs may nest again. however, not many pairs attempt to rear two broods. Walkinshaw ound only about 5% of the pairs he studied from 1972 to 1977 tried, Orr (1975) in a 1974 study found 17% did. Per pair and per nest data these studies are shown in Table 5. Of course, as with most bird if the first nest is destroyed, many will renest. Mayfield's (1960) hale 5 take this into account. Determining the true production for pair requires following them closely through the entire breeding Associated errors all tend to depress fledgling rates. Hence, actual ing rates per pair for early years were probably somewhat higher than is indicated. If I had to pick a simulation which best fits the available k would be similar to number 5 in Table 6 which uses a 65% adult sur-35% fledgling survival, and 1.50 fledglings produced per pair. This in a 60% population decline in 10 years. It is obvious that parasitism easily have caused the observed decline.

cowbird control program, based on the work of Nicholas Cuthbert of and Michigan University, was begun with high hopes in 1972 (Shake and 1975). About 3,000 cowbirds per year were removed from a areas. Parasitism rates dropped to near zero. Walkinshaw (1981) only 6% (14) of 230 nests he studied from 1972 to 1977 were tized, and fledgling rates were very high (Table 5). In effect, the had been eliminated as a factor.

Effects of various survival and production rates.

	Assumptions		Needed fledglings produced		
	Annual	Fledgling	per pair to achieve		
Mon	adult . survival	survival to spring	Stable population	60 percent decline in 10 years	
	.60	.25	3.20	2.50	
2	.60	.35	2.29	1.80	
3	.60	.45	1.77	1.40	
4	.60	.55	1.45	1.14	
5	.65	.35	2.00	1.50	
6	.65	.45	1.56	1.17	
7	.65	.55	1.27	.95	
	.65	.65	1.08	.81	

Recovery Team members expected cowbird control to result in increased warbler populations. Since cowbird control was begun in the spring of 1972 it should have influenced the breeding population of 1973 and succeeding years. While the 1973 census was higher than the preceding 2 years, 1974 was the lowest count to date and still holds that distinction. The number of males did not reach the 1973 level again until 1977 (Table 1). Although Kirtland's Warbler populations have not responded as many predicted, Mayfield (1975) argues convincingly that without cowbird control, the species might well be on the verge of extinction.

DISCUSSION

Clearly we cannot conduct carefully designed experiments to test the various hypotheses discussed in this paper. Here we have tried to evaluate them, one at a time, using variously simple models, logic, and information and opinions from the literature.

It appears that cowbird parasitism was the most important factor in causing the population decline from 1961 to 1971. The evidence from nesting studies reveals that not enough fledglings were being produced to maintain a stable population. However, this was also a decade of generally low rainfall on the wintering grounds, as well as declining nesting habitat on the breeding range and these factors probably contributed to the decline.

Since the cowbird control program, initiated in 1972, eliminated the cowbird as a factor, many of us expected to see Kirtland's Warbler populations rebound to previous levels. During the past decade, the amount of suitable or occupiable breeding habitat also increased to near 1961 levels. The conclusion seemed inescapable that something was controlling the population either during migration or on the wintering grounds where the birds spend the majority of the year. Hurricanes and other storms during migration are potential, but seemingly unlikely, agents to accomplish such control. A more logical variable would be the winter food supply, presumably insects, which might vary with weather conditions. Rainfal seemed a good candidate, and a surprisingly good relationship between surviving males and rainfall was found.

Examination of recent population fluctuations indicates that the birds are currently not strongly influenced by density dependent factors. This implies that a consecutive series of winters with average or above average rainfal will allow the population to build up. If and when this happens, however, there must be adequate breeding habitat present for the expanded numbers of breeding pairs. Obviously cowbird control and other protection will need to be continued.

The next step in analysis of population dynamics will be to develop more complex population models which will consider several factors at once. It also makes sense to simulate the effect of various management strategies on the computer, rather than using the trial and error approach on the precarious, real-world population.

SUMMARY

The population of Kirtland's Warblers declined by 60% from 1961 to 1971. A number of hypotheses have been advanced to account for this decline. These were evaluated using simple models, logic, and information from the literature. The most important factor in the decline appears to have been parasitism by Brown-headed Cowbirds which resulted in fledging rates too low to maintain stable population levels. Since 1971, a bowbird trapping program has essentially eliminated the cowbird as a facfor, but the warbler population levels have not increased. Examination of **recent** population fluctuations suggests the species is not currently density dependent. At present it appears that the population is being regulated on the wintering grounds, largely through the agency of rainfall. Relative ever-winter survival seems to vary directly with the amount of rainfall. **Hurricanes** and other storms have a high potential for killing birds, but the chances for mass destruction seem small because of the behavior of the hirds during migration and on the wintering grounds. Winter habitat in the Behamas apparently has not changed much in this century, although there have been extensive pine harvests on three islands beginning in 1956. On the summer range, suitable breeding habitat declined by 44% from 1961 to 1971. This was followed by an increase which is expected to continue until 1984. Another low point is looked for in 1989. Extensive habitat management is now underway on both state and federal lands to insure adequate mounts of breeding habitat in the 1990's and beyond.

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PERSPECTIVE ON THE KIRTLAND'S WARBLER

Harold F. Mayfield

Kirtland's Warbler Recovery Team Member 1162 Nannette Drive Toledo, OH 43614

For nearly 400 years our language has had a phrase to describe anything of special interest because of its rarity. We call it a <u>rara avis</u> or rare bird. The epitome of this term in America for more than 100 years has been the Kirtland's warbler.

Its rarity attracts attention. Every year hundreds of birders travel to northern Michigan to see it. Even scientists are not immune to its appeal, and for an additional reason. While the problems of survival in an abundant species may be almost hopelessly complex, these problems are brought into sharper focus when the subject consists of a few individuals in one place. The setting is almost like a laboratory. As a result, the Kirtland's warbler is one of the best-studied birds in America. Three books and hundreds of articles have been written on it. Kristina Huber's 1982 annotated bibliography listed 800 titles, and Amy Stone's 1986 unpublished bibliography listed 291 on migration and wintering alone.

Yet, the bird continues to baffle us. Why is it so rare and difficult to predict and manage? For perspective on these problems, let's look at its history.

Prehistory

The nesting habitat is distinctive but transitory. The warbler nests only on sandy soil in level or gently rolling terrain among extensive stands of young jack pines 2-4 m tall (8-20 years old). These conditions occur naturally only after major forest fires in pinelands of a special kind, and they last only a few years at any spot. These narrow requirements ultimately limit the bird's population and range, and virtually assure us it has been rare for a very long time.

The present jack pine plains of Michigan have existed only since the retreat of the Wisconsin Glacier. Until recently we had assumed that the Kirtland's warbler in former times had found suitable habitat broadly on the sandy outwash plains beyond the foot of the glacier as it advanced and retreated across Ohio and the Prairie states. However, recent pollen analysis has forced us to revise those views. At the height of the last glaciation 18,000 years ago jack pine was virtually absent from the Midwest, and it did not re-enter this region until about 10,000 years ago. However, during this whole glacial period jack pine was abundant in the southern Appalachians and the Southeast coastal plain. Therefore, unless the bird has changed its habitat in recent geologic times, it nested only in a limited portion of the Southeastern coast for about 70,000 years before the present inter-glacial period, migrating in winter to the nearby Bahama Islands, which were vastly larger in extent than at present with the sea level 400 feet lower.

Here again, the Kirtland's warbler may shed light on the history of other songbirds nesting in the North and wintering in the West Indies or beyond (Mayfield, 1988a).

Early Historical Record

This species was first described from a specimen, a male, taken on May 13, 1851, 138 years ago, in the orchard of the distinguished physician and naturalist, Dr. Jared P. Kirtland, on the western outskirts of Cleveland, Ohio. This was at the height of the spring migration of warblers, and the presumption was that it was bound for its nesting grounds somewhere in the Northern forests. But where?

In the next 50 years other individuals were collected at scattered locations in the Midwest and Southeast, and the bird was found repeatedly in winter in the Bahama Islands. The breeding grounds remained a mystery until 1903 when two graduate students from the University of Michigan, fishing on the AuSable River, heard and saw a strange bird and brought it back to Ann Arbor. There Norman Wood, the museum curator, instantly recognized it and hurriedly traveled north to the location. After a search of 7 days he found the first nest on July 8 (Wood, 1904). A monument now marks the spot. Fully 90 per cent of the nests found since that time have been in the drainage of that same stream.

This first eyewitness to the Kirtland's warbler on its nesting ground found it scarce at that time. He said, "It is not, however, every jack pine plain that is the home of a colony, as I examined hundreds of acres where the conditions seemed all right, and found none" (Wood, 1904:10). He continued searching for more than two decades and found other colonies within the same general range, but as late as 1926, in accordance with the views of the day, he saw fire as a threat to the bird rather than its salvation (Wood, 1926:12).

Yet, a little earlier, in the 1880's and 1890's, we have reason to suspect there may have been a temporary surge in the population. At that time specimens turned up in Illinois, Missouri, and Minnesota, well to the west of the normal migration route, where it has not appeared since. Also collectors found it with ease in the Bahama Islands, accumulating 66 specimens in those two decades, but only an occasional specimen before or since that time (Mayfield, 1960:35). Charles J. Maynard took 24 in a few weeks near Nassau in 1884, but no one has seen more than one or two in modern times.

It may be significant that this apparent upsurge in population coincided with the regrowth of jack pines following the wholesale lumbering and burning of the forests of northern Lower Michigan. Without doubt, there was more nesting habitat for the warbler in that period than before or since in historic times.

Cowbird

When the lumberman and the farmer who accompanied him opened the forest, they brought a new threat to the warbler. The Brown-headed

Cowbird, a creature of the central grasslands of the midcontinent, thrived in the newly cleared semi-open country. It spread eastward and northward with the clearing of the land, finding the horses and cows of the farmer good substitutes for the bison it had followed from time immemorial. It probably reached the Kirtland's warbler about 1880.

The cowbird builds no nest of its own but uses the nests of other birds, usually smaller species, laying its eggs in their nests and removing an equivalent number of their eggs. In addition, the cowbird eggs usually hatch first and trample or crowd out many host young. The cowbird found the Kirtland's warbler a perfect host while continuing to use other species nearby. Thus, the warbler could sink to zero without serious detriment to the cowbird. This is a rare example in nature where predatory pressure does not relent when the prey becomes scarce; that is, the pressure is not density-dependent, in the language of ecology.

In the face of this new threat, the Kirtland's warbler is almost defenseless. The longtime associates of the cowbird in the West have developed defenses against it, but many small songbirds of the East like the Kirtland's warbler are highly vulnerable (Mayfield, 1977). Since its arrival in this region the cowbird has steadily increased, putting ever heavier burdens on its hosts. In the 1940's and 1950's the cowbird was depressing the production of fledgling Kirtland's warblers by 50 per cent, but in the late 1960's the toll had arisen to about 70 per cent (Walkinshaw, 1972), an intolerable loss to sustain.

Accordingly, the population of warblers, which had been about 1,000 adults in 1951 and 1961 slipped to 400 in 1971. Immediately, measures to control the cowbirds were initiated on the warbler nesting grounds, and the decline was arrested. The way to remove cowbirds efficiently with little damage to other birds had been discovered by Nicholas L. Cuthbert, using a trap devised by the U.S. Fish and Wildlife Service to control blackbirds where they are pests in farmers' fields. Cowbird trapping was remarkably successful and this enemy was almost completely eliminated from the warbler nesting areas. In 1975 I made calculations based on the Kirtland reproduction rate under recent cowbird pressure and concluded that without protection the last Kirtland's warbler would disappear in 1978. We did not allow that to happen, but the population has not spurted as we had hoped.

Other Problems of Survival

Viewed over the long pull, the population of Kirtland's warblers in the 1970's and 1980's has been remarkably stable. In 18 years through 1988 the mean count of singing males has been 206, with a range of 167 to 242 (Weinrich, 1988). In years of gain, the mean has been 16.8 males or 8 per cent of the mean population, and in years of losses, the mean has been 19.5 or 9 per cent of the mean population. Thus, the mean variance has been less than the probable error of the census method, which has been estimated to be at least 10 per cent of each count.

Rarity itself brings a special set of problems. At some point we would expect a decline in fertility as a result of inbreeding. But if

this has occurred in Kirtland's warblers, it has not showed up in field studies. On the contrary, the bird has continued to show excellent production of eggs and fledglings. For example, the production of fledglings in the first 6 years after cowbird control was 3.11 per pair of adults per year (Walkinshaw, 1983:152). This far exceeds the production of Prairie Warblers, a well-studied, widespread, and successful species, which produces 2.2 fledglings per pair per year (Nolan, 1978:419). Also the survival rates for adults from one June to the next is typical for a small songbird with a long migration. The survival rates for adult Kirtland's warblers is about 65 per cent of the previous year's population, exactly the same rate reported for the Prairie Warbler (Nolan, 1978:469). Therefore, if Kirtland's warblers are less successful than other warblers, the reasons must lie with some selective pressure against the young in their first year of life. Here we have little exact information.

In a stable population where the annual survival rate of adults is about 65 per cent and the production of young is 3.11 fledglings per pair per year, the recruitment of yearlings calculates to be about 22 per cent per year, somewhat lower than for comparable birds. This calculation, however, could be astray if a substantial number of males on the breeding grounds are unmated, as has been suggested lately (Probst, 1986). But this idea runs against the experience of a series of past observers who worked intensively for successive years in single colonies and rarely failed to find a female with each male.

Losses of unknown magnitude occur at every stage of the annual cycle: (1) late summer on the nesting ground, (2) fall migration, (3) wintering from October to April in the Bahama Islands, and (4) spring migration. These problems beset all small migrant songbirds, of course, and our puzzle is to discover how Kirtland's warblers are different.

Our field work to date has not detected any special hazards in the summer and winter places of residence, and the adults obviously cope well with vicissitudes of migration, but the migration of birds making their first long-distance trip may present more than ordinary difficulties in this species.

The migration south ought to be relatively easy. The route is mostly over land, and a little straying ought not to be disastrous. Also the target consists of a string of islands almost 700 miles long, with each island in sight of one or more of the others. In the northward migration, on the other hand, the target is small, in recent years shrinking, and perhaps reached by one long nonstop flight (Mayfield, 1988a). If a bird misses it, the individual may find vast expanses of pinewoods beguilingly similar to what it is seeking but devoid of other Kirtland's warblers. Our experience shows that such birds may take up summer residence there but not find a mate. If so, they are wasted, victims of their own rarity (Mayfield, 1983).

Less rare birds do not have this problem. Most long-distance migrants may miss their destinations by hundreds of miles without serious consequences. If they are displaced to left or right by the width of several states, they may still find suitable habitat and mates

at the same latitude elsewhere. If the Kirtland's warbler misses by the width of two counties, its nesting potential is lost. Indeed, we know that some miss. In recent years we have found several of these, all of them males and all of them without mates. We have no idea how many are lost by straying, but it is apparent the number is larger than we would have supposed a few decades ago. Determined effort in recent years in the pinelands of Wisconsin and Ontario have turned up examples. The number found may reflect the skill and effort of the observers more than the true number of birds. In 1988, Wesley Jones, a man thoroughly familiar with the bird and its habitat, discovered 8 individuals in Wisconsin alone. It is reasonable to suppose that these strays are mainly yearlings. It is also probable that many strays are females, but being silent, are never found. In any case, the total loss from this cause must be far larger than the number of strays actually counted. Dispersal may have survival value in a widespread species, but it can be costly to a species with narrow habitat requirements.

The warblers traverse the hurricane zone spring and fall, and some people have wondered if storms might jeopardize the species in migration, but we have found no relationship between severe storms in migration season and subsequent counts of the population in Michigan (Ryel, 1981:79-81).

Since the bird seems to be doing so well on the breeding ground, we grope for explanations on the wintering ground, where it spends the larger part of the year. Here the only clue we have is a correlation with rainfall in the Bahamas, a wetter winter presumably yielding more plant and animal food for the birds (Ryel, 1981:81-83).

Habitat

With so many aspects of this bird's life baffling us, we concentrate on what we can see readily. Obviously an ultimate limitation on the population is its nesting habitat. But precisely what are the ingredients in the habitat? From the time of the discovery of the first nest, everyone has recognized the association with the jack pine. But it is equally obvious that trees are not the whole story. Soil and ground cover are involved, although we find it hard to be precise about these. We can describe the situation where we find the bird nesting, but we strain our imaginations sometimes to explain the bird's absence from some jack pine stands, both in Michigan and in other nearby states and provinces. Remember, the jack pine stretches nearly the width of the continent and northward almost to the arctic.

I find it amusing that Norman Wood estimated the suitable habitat to cover 6,000 acres in 1925 (Wood, 1926:13), exactly the same figure I was using 50 years later with much more information. However, I do not place much confidence in such estimates, including my own, because they are based on circular reasoning; the habitat is suitable if it has warblers, and it is not suitable if it does not have warblers. We still need to know what disqualifies tracts elsewhere including Christmas-tree plantations that abound just to the west of the present Kirtland range.

The greatest event in recent Kirtland's warbler history was the Mack Lake fire of 1980, which burned nearly 30,000 acres and promises to produce more habitat for the bird than all the rest combined during the last three decades. However, this should not be regarded merely as a solitary, unrepeatable incident. One has only to drive through the sand country to see thousands of acres of mature trees waiting for conditions to be right for a devastating fire. Remember, in jack pine, fire deferred is more severe when it comes. I have counted 6 fires of more than 15,000 acres each in this region since 1920.

Plainly the warbler needs more than trees. At one time we thought the character of the ground cover might be crucial, because the bird does much of its food foraging there and conceals its nest there. But each time we think we have identified features of the ground cover that are essential, we find examples that are different. Nevertheless, it must not be tall and dense unless it consists of small pines.

The first question a novice asks is how about the warbler's food? Inquiries in this direction have led us nowhere. The warbler seems to eat whatever is abundant at the time in the trees and the ground cover. Indeed, the small amount of time the bird spends in food searching suggests that it lives in the midst of a smorgasbord of invertebrates and berries on its summer range, except perhaps during the first chilly days of May when it arrives on the nesting ground.

If the Kirtland's warbler suffers more than other small songbirds from predators and competitors, we have not seen it. On the contrary, it seems to me the bird has chosen relatively depauperate regions both for summering and wintering grounds. The jack pine barrens in Michigan are so nearly devoid of life that the prehistoric Indians avoided them. The other birds found there in nesting season all seem to do better elsewhere. Predators are rare, and observed instances of predation are few. Likewise, the Bahama Islands are the most barren of the West Indies. Hence, it appears that this unsuccessful, relict species has survived by finding a sanctuary both in winter and summer.

Habitat embraces the total environment: vegetation, soil, competitors, predators, and climate. All of these except climate have received attention for decades. Now Burton V. Barnes and his students have focused their attention on the microclimates at nest sites, finding significant differences according to soil and elevation. It appears the warbler may not nest successfully in spots where early June days bring below-freezing temperatures at ground level. This may help explain why many tracts that look right to our eyes have no nests. Also it may explain why Kirtland's warblers utilize only the southernmost of the jack pines in North America.

Conclusion

Finally, as we weigh the fate of the "Kirtland's warbler at the crossroads - extinction or survival," I think it is clear that we have a greater need for ideas than for trees.

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KRILARIS WARBLER recovery plan

KIRTLAND'S WARBLER RECOVERY PLAN

Prepared by

Kirtland's Warbler Recovery Team

1976

Updated

1985



Kirtland's Warbler Recovery Team

JOHN BYELICH, Leader Mio, MI MICHAEL E. DeCAPITA U.S. Fish and Wildlife Service East Lansing, MI GEORGE Wm. IRVINE U.S. Forest Service Cadillac, MI ROBERT E. RADTKE U.S. Forest Service Milwaukee, WI NELS I. JOHNSON Michigan Department of Natural Resources Roscommon, MI WESLEY R. JONES Shell Lake, WI HAROLD MAYFIELD Toledo, OH WILLIAM J. MAHALAK Michigan Department of Natural Resources Roscommon, MI

KIRTLAND'S WARBLER RECOVERY PLAN

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KIRTLAND'S WARBLER RECOVERY PLAN

PART I

INTRODUCTION

The Kirtland's waroler, <u>Dendroica kirtlandii</u>, was first discovered in 1851 when a spring migrant was taken near Cleveland, Ohio. Five more spring migrants (four in Ohio and one in southern Michigan) were collected before the first wintering bird was collected on January 9, 1879, on Andros Island, Bahamas. Between 1884 and 1897 there were 71 specimens collected throughout the Bahamas. Until recently this species had never been found outside the Bahamas in winter, except for an unconfirmed report of two being observed near Veracruz, Mexico, in November 1974. Recent searches, however, have expanded the known winter range to a number of other Caribbean Islands.

Over a half century after the species was first described, its nesting range was discovered. A specimen collected on June 13, 1903, near the AuSaole River in western Oscoda County, Michigan, was taken to Norman A. Wood, curator of birds at the University of Michigan Museum of Zoology, who identified it as a Kirtland's warbler. Wood promptly set out on a trip to Oscoda County, traveling by rail, rowboat, buggy and foot to search for nesting birds. Between July 2 and 7 he discovered two small groups of warblers which he described as "colonies" near Butler Bridge (now Parmalee Bridge) in "jack pine plains," but found no nests. On July 8, 1903, Wood moved to a jack pine plain further to the west, and in the western part of Section 31, T27N, R1E, Oscoda County, he found the first nest.

Singing males and migrants have been found in other parts of the Great Lakes Region, but nowhere other than Michigan has a nest been found. Searches for nesting birds were initiated in Canada in 1977 and Wisconsin in 1978 and expanded to Minnesota in 1979.

No serious attempt to estimate its numbers was made until 1951. At that time, on the hundredth anniversary of its discovery, it became the first songoird in the world to have its entire population censused. Several groups of ornithologists working in cooperation visited all the suitable nabitat within the known nesting range and counted the singing males. Four hundred thirty-two males were found. The number of females was judged to be about equal to the number of males, and so the total population was put in the neighborhood of 1,000 birds (Mayfield, 1953).

Nest observations during the 1940's and 50's showed that the production of young was so low as to raise doubts that the species could maintain itself. However, a repeat census in 1961 revealed 502 males. Hence, the total population was still in the vicinity of 1,000 birds (Mayfield, 1962).

The third decennial census, taken in 1971, confirmed the dire predictions of the previous decade. The count showed a 60 percent decline to 201 singing males (Mayfield, 1972a). The population was down from about 1,000 birds to about 400. Immediately the frequency of the censuses was stepped up to yearly, and the count from 1971 to present has been remarkably level, although with a moderate, but temporary, decline in 1974 and 1975. (Mayfield, 1973a, 1973b, 1960; Ryel, 1984).

In the decline between 1961 and 1971 the population did not simply thin out across its entire nesting range but collapsed back into the center of its range, where nesting continued at normal density. The reduction in numbers and area utilized is as follows:

Population Trend, Kirtland's Warbler 1951-1985 (No. American Totals)

Year	Males	Michigan Counties	Michigan Sections (sq. mi.)
1951	432	8	91
1961	502	9 6	86
1971	201	6	2 7
1972	200	4	27
1973	216	4	25
1974	167	5	27
1975	179	6	31
1976	200	6	47
1977	219	6	42
1978	200	6	36
1979	211	6	41
1980	243	6	42
1981	232	6	46
1982	207	7	44.
1983	215	8	48
1984	215	7	49
1985	217	7	49

Past and Present Distribution

The narrow habitat requirements of the Kirtland's warbler have always limited its range severely. Presumably, the bird nested in the conifer zone on the sandy outwash plains in the wake of the Wisconsin Ice Sheet. This conifer zone was a comparatively narrow strip across the north central states, and the amount of this specific habitat suitable to the warbler probably was small. The few specimens taken east and west of the present migration path suggest the possibility of former nesting grounds in Minnesota, Wisconsin and Ontario, but there is no hard evidence of any nesting outside Micnigan.

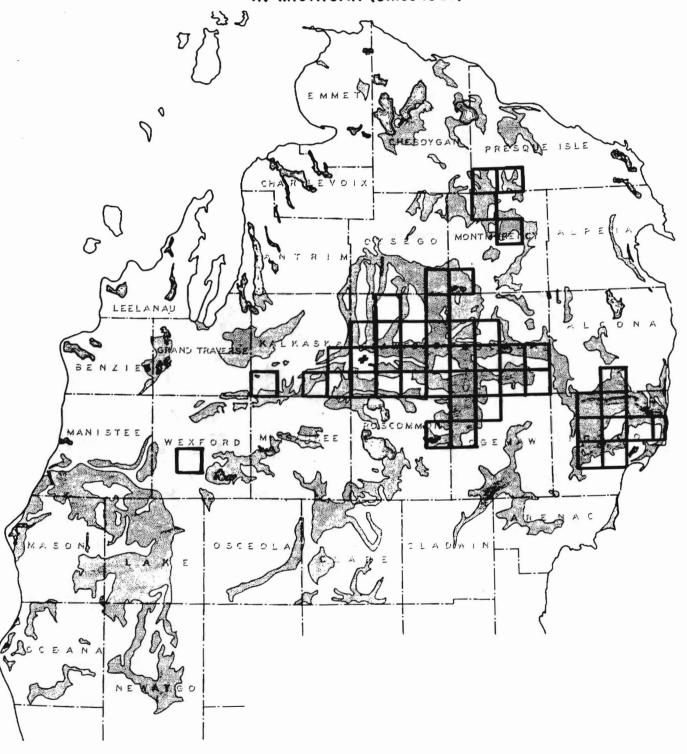
The nesting ground was discovered in 1903 near the AuSable River almost on the boundary of Crawford and Oscoda counties. Ninety percent of the nests found since that time have been located in the drainage of this stream (Mayfield, 1960). Since 1903, nests have been found in the following 13 counties but not in all of them at one time (Fig. 1):

Alcona	Crawford	Montmorency	Otsego
Alpena	Iosco	Ogemaw	Presque Isle
Clare	Kalkaska	Oscoda	Roscommon
		(4)	Wexford

In recent decades the majority of the nests have occurred in Crawford, Oscoda and Ogemaw Counties (Fig. 2).

Figure 1

FORMER STATUS OF KIRTLAND'S WARBLER NESTING RANGE IN MICHIGAN (since 1951)

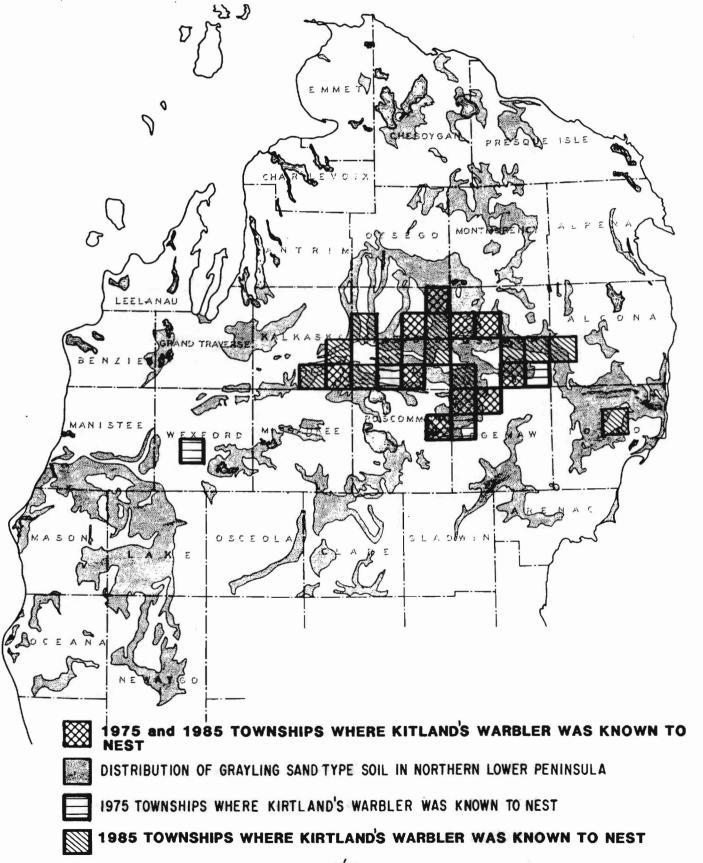


DISTRIBUTION OF GRAYLING SAND TYPE SOIL

- 1951 1984 TOWNSHIPS WHERE KIRTLAND'S WARBLER NESTED

CURRENT STATUS OF KIRTLAND'S WARBLER NESTING RANGE

Figure 2



In migration the bird travels a fairly direct route between its nesting and wintering ranges, entering and leaving the continent at the coast of North and South Carolina (Mayfield, 1960).

Until 1985 the wintering range of the Kirtland's warbler was believed to be limited to the Bahama Islands. Between September and April the bird had never been seen anywhere else, except for one uncorroborated sighting on the east coast of Mexico (Lane, 1975). In the 1880's and 1890's specimens were taken on nearly all the larger islands in the Bahama group, and there have been many subsequent chance sightings by tourists. Ongoing surveys added Grand Turk Island, South Caicos Island and Hispaniola to the lists of known locations of the Kirtland's warbler. It has been extremely difficult, nowever, to find the bird in recent years. As a result, little information about its wintering behavior and habitat requirements is available. Apparently, it occupies dry, low broad-leafed scrub which is the prevailing vegetation type on large areas of many of the islands in that region (Radabaugh, 1974; Faanes, unpublished data).

Surveys made in the Bahamas, the adjacent Grand Turk and Caicos Islands and Hispaniola (Dominican Republic) from January through April 1985, located a total of 11 Kirtland's warblers. These birds were mostly found to be associated with desert-like vegetation of deciduous shrubs. This species may also winter in similar habitats found in nearby Cuba.

History of Organized Efforts at Management

The first major effort to provide breeding habitat for the Kirtland's warbler was made in 1957. Three areas, each approximately four miles square, were established specifically as warbler management units on state forest land in Ogemaw, Crawford and Oscoda counties (Radtke and Byelich, 1963; Mayfield, 1963). Portions of two of the areas were planted with jack pine, using a special configuration to provide openings within the stand. The intention was to maintain these tracts in three age classes, seven years apart, by burning and replanting the stands when they reached an age of 21 years. Planting of the third area in Oscoda County was held in abeyance because pines on that area were approaching a commercially harvestable age. Almost one-third of this tract was burned by a wildfire in 1964. Regeneration which resulted because of that fire has provided nesting habitat for the past several years.

In 1960, the Forest Service began working on a management plan for the Kirtland's warbler. This plan was approved in 1962, and a 4,010-acre tract was dedicated in June 1963. The plan established 12 management blocks of about 320 acres each in the Mack Lake Area, Oscoda County. Ultimately, each block was to be grown on a 60-year commercial rotation with five years age difference between blocks (Mayfield, 1963).

In addition, in 1973 and 1974, the Huron National Forest cut, burned, and planted areas near Luzerne, Oscoda County, and Tawas, Iosco County, for the benefit of the warbler.

The 60 percent decline in nesting warblers indicated in the 1971 census resulted in a joint meeting of the USDA-Forest Service and Michigan Department of Natural Resources. A major result of this meeting was the formation of a Kirtland's warbler Advisory Committee whose charge was to outline needed habitat research, propose restrictions on human activity in nesting areas, initiate a cowbird control program, and locate funding. One outcome of the meeting was a program begun in the spring of 1972 to reduce cowbird parasitism by trapping and removing cowbirds from the principal nesting areas of the Kirtland's warbler. The major agency in this effort was the U.S. Fish and Wildlife Service. Other contributors were the Michigan Department of Natural Resources (MDNR), Michigan Audubon Society, and U.S. Forest Service (USFS).

Systematic cowbird trapping in 1972 was an outstanding success. Nesting studies on selected tracts showed virtually no parasitism of warbler nests and an unprecedented yield of young warblers per pair of adults. Immediately, habitat improvement was initiated by the State and Forest Service in areas outside established management areas.

In 1973 and 1974, the cowbird control program was expanded so that now virtually all nesting areas of the Kirtland's warbler receive cowbird control. Thus, the program to increase Kirtland's warbler production by reducing cowbird parasitism has been an unqualified success. While it has not, as yet, caused a substantial increase in the spring population, at least the downward slide has been checked.

Efforts on behalf of the Kirtland's waroler were given a giant thrust forward when the Endangered Species Act of 1973 became law (P.L. 93-205). This Act not only officially declared the bird "endangered", it also provided for acquisition of land to increase available habitat, funding to carry out additional management programs, provisions for state cooperation with the Federal Government and establishment of various legal protections for endangered species. While it was the most encompassing endangered species legislation to date, previous Acts in 1966 and 1969 (P.L. 89-669 and P.L. 91-135, respectively) had provided for some endangered species listings, research, and habitat acquisition.

The Federal Endangered Species Act was supplemented by the Michigan Endangered Species Act of 1974 (P.A. 203, 1974). This act provides added legal protection to listed species.

Rules promulgated under the Endangered Species Act of 1973 called for the establishment of Recovery Teams to assist the Fish and Wildlife Service in carrying out provisions in the Act. In early 1975, a Kirtland's Warbler Recovery Team was named by the Secretary of the Interior to guide efforts in aiding the warbler. As a result of efforts by the Team, a Kirtland's Warbler Recovery Plan (Byelich, et al, 1976) was prepared outlining steps designed to increase the species population.

An intensive habitat management plan was developed by the USFS and MDNR to implement the nesting habitat management phase of the Recovery Plan. In this plan, all of the potential Kirtland's warbler nesting habitat within the former range of this species was identified. Where feasible, this habitat was placed in management units where treatments were scheduled at ten-year intervals to provide sustained nesting habitat conditions within each unit. Work has been progressing at a rate slower than that called for under the Plan. Problems unforeseen when the plan was drafted, such as weak timber markets, limitation on burning, weather and equipment limitations, have inhibited progress.

Research to investigate post-fledging behavior and habitat use, as well as species biology on the wintering ground, has recently been initiated. This intensive effort is expected to provide new and important insights into these virtually unknown facets of Kirtland's warbler biology.

Nesting Habitat

It became apparent to the early observers of the Kirtland's warbler that these birds were always associated with the areas of the northern Lower Peninsula of Michigan commonly referred to as the "jack pine plains" or "barrens". Subsequent studies of the species have shown it to have an extremely close association with a particular "life community" of the jack pine type.

Jack pine is found on the North American continent from the Maritime Provinces of eastern Canada west to the upper Yukon Valley in the Northwest Territories, and from the middle of Michigan's Lower Peninsula and mid-Wisconsin north to the continent's tree line. It is in the southern extremity of the jack pine range and on the driest, most rudimentary sand soils of lower Michigan that the Kirtland's warbler has found its niche.

With one or two exceptions all nests have been found on Grayling sand soil. This very poor soil is extremely pervious to water. Thus, in addition to supporting the jack pine and the low, sparse ground cover required by the bird, the capacity of Grayling sand to quickly drain during summer downpours may be important in preventing flooding of nests set in the soil.

Grayling sand occurs in 29 counties of the Lower Peninsula, and its amount corresponds closely with the amount of naturally occurring jack pine in those counties. For example, Crawford and Oscoda Counties have large amounts of Grayling sand soil and have 95,000 acres and 90,000, respectively, of natural jack pine forest (Zimmerman, 1956). These two counties also presently have the greatest number of nesting Kirtland's warblers. A few have been found nesting adjacent to the Grayling sands on Graycalm, Deer Park, Rubicon and Croswell sands. There are also records of nesting on two isolated areas where jack and/or red pine had been planted on severely eroded Kalkaska sands.

Although the reasons are not completely understood, the burning of a jack pine site prior to its regeneration appears to be a highly significant, if not necessary, factor for the optimal use of a stand for nesting. Burning may have some subtle effects on the soil and plant community that have yet to be detected. Observations to date show that recent fire has been a factor on nearly all sites where warblers have been known to nest successfully. In recent years, Kirtland's warblers have been found nesting in jack pine stands that were regenerated without fire. However, density of nesting birds is one-half or less than found in burned habitat.

The jack pine stand is used for nesting only in a certain stage of development. Warblers will start using a stand when the height of the tree reaches 5 to 7 feet (or at an age of 6 to 13 years with the average being 8). Stands less than 80 acres in size are seldom occupied, and nesting success has been found to improve greatly where "colonies" of warblers occupy stands 200 acres and larger.

The density of the stand is usually variable, with dense patches and numerous small openings interspersed throughout. Evenly spaced plantations are used but openings appear to be important. Common associated tree species in these jack pine stands are oaks, aspen, cherry, juneberry, and other pines. It appears that the Kirtland's warbler will not use a stand where deciduous species and jack pine approach equal density.

The ground vegetation consists of plants that can survive fire, drought, and thermal extremes. These are mostly low shrubs and deep-rooted perennial herbs. The density varies from sparse areas, with bare ground exposed, to quite dense patches of vegetation. In fact, there is usually a mosaic of sedges, shrubs, grasses, and forbs. Warblers require ground cover to conceal the nest site, with mixed blueberry and grass areas being favored locations. However, nests are occasionally found where the ground cover is sparse.

The Kirtland's warbler will continue to nest in jack pine stands as long as the trees retain living branches near the ground. Depending on the density of the trees, low branches no longer exist when jack pine reaches a height from 16 to 20 feet (usually at age 21 in Michigan). When this occurs, the structure of the habitat is apparently no longer acceptable to the warbler for nesting.

Like all forest types, there are sequential changes throughout the various stages of these jack pine stands. Immediately after the old stand has been removed through cutting and/or burning, those bird species adapted to open conditions will occupy the site. Representative species include the common nighthawk, vesper and field sparrow, prairie warbler, sharp-tailed grouse (if in adjacent areas), and upland sandpiper. Where there are snags to produce cavities, the Eastern bluebird, tree swallow, northern flicker, and other open area cavity-nesters are common. As the new stand of jack pine takes form and the lower pine branches begin to touch, the "open" species decline and the "intermediate" species move in. These include the clay-colored sparrow, hermit thrush, and the Nashville and Kirtland's warblers (along with other species). As the stand continues to develop, the community changes. At about the stage where the lower branches thin out and the warbler leaves, the stand then becomes usable by other species such as the spruce grouse and whip-poor-will. When the stand moves into the "old-age" form, inhabitants include the woodpeckers, cuckoos, and other arboreal species. Of course, the more adaptive species such as the American robin, blue jay, black-capped chickadee, and brown thrasher will be found in all stages of this community.

Kirtland's warblers have occasionally been found to nest in red pine plantations. Apparently, planted red pine sometimes creates an acceptable environment. However, in most cases, the warblers have moved into the red pine from an adjacent jack pine habitat. In other circumstances where this species has used habitats such as red pine plantations, or on soils other than Grayling sand, they apparently have moved from adjacent "typical" habitats.

Wintering Grounds and Migration

Little is known of the wintering grounds or migration route of the Kirtland's warbler. Although this songbird spends approximately four months (May-August) on the nesting range and eight months on its known wintering range in the Bahamas, information about its wintering behavior and habitat requirements is very scanty. It is possible that factors on the wintering grounds at times may tend to limit the population of this species. Survival of the Kirtland's warbler may depend upon protection of its wintering range, as well as its nesting habitat.

The wintering grounds of the Kirtland's warpler were known long before the discovery of its nesting area. During the late 1800's a number of collectors took specimens of the Kirtland's warbler in the Bahama Islands (Mayfield, 1960). The first Kirtland's collected in the Bahamas was from Andros in 1879 (Mayfield, 1960).

Some 71 museum specimens are known to have been collected from the Bahama Islands. Most (66 of 71) were collected prior to 1900 from more than ten different islands (Mayfield, 1960). Radabaugh (1974) and Walkinshaw (1983) summarize the winter records of known collections and sightings in the Bahamas since 1879.

Numerous efforts have been made to learn about the wintering habitat of this species with little success. Very little is known about the ecological changes that may have occurred in the Bahamas in the last century. Most of the settlements are located along the shore, with very few areas developed inland because of poor soil and lack of fresh water. Radabaugh reports that the major land use change in the Bahamas has been the cutting of Caribbean pine in three northern islands—Grand Bahama, Great Abaco, and Andros during the period 1956 to 1974. Sightings of the Kirtland's among the Caribbean pine suggest that some portion of the population utilizes this habitat in the winter. Only four islands support Caribbean pine, and extensive logging may have an impact on the Kirtland's warbler.

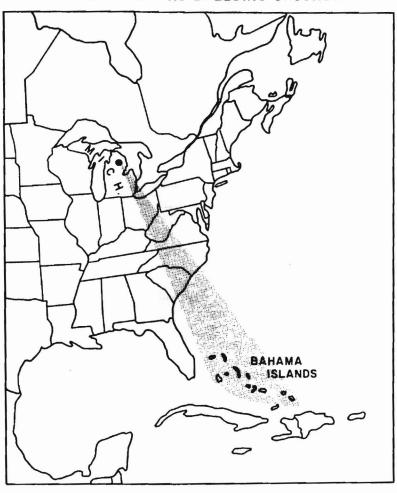
Most of the wintering records are from the scrub habitats of the Bahamas--where Caribbean pine does not exist. Even on the "pine islands" many of the Kirtland's collected have been in broad-leaved scrub. Some 24 specimens have been taken on islands which lack pine. Mayfield (1972b) concludes that, "the Kirtland's warbler usually inhabits low, broad-leaved scrub in the Bahamas ...it is significant that no one has reported them in the high scrub or coppice, trees 15 feet or more in height, that abound in these islands."

During the first year (1985) of an intensive winter habitat study conducted on a number of Caribbean Islands, eleven Kirtland's warblers were located during the January through April period. One bird was found in Caribbean pine while the remainder were found in dry coppice vegetation - all but one in low coppice. Of potentially great importance is the fact that six of these birds were located southeast of all previous signtings, considerably expanding the known winter range of the species (Faanes, unpublished data). It appears that the Kirtland's may utilize several habitats—including the Caribbean pine ecosystem and the broad-leaf scrub areas.

The Kirtland's warbler leaves its nesting grounds in late August and early September. The latest known Michigan record is September 29, in 1975 (Schempf, 1976), although Kirtland's are usually gone by mid-September. Dates of fall migration records listed by Mayfield (1960:39) range from August 28 (1902) at Oberlin, Ohio, to October 29 (1903) in South Carolina. Fall migration sightings occur mainly in southern Ontario, Ohio, and the South Atlantic states (Figure 3) -- the general direction of the Bahama Islands from central Michigan (Mayfield, 1960:39-40; Walkinshaw, 1983:26-28). The earliest recorded sighting in the Bahamas was August 20, 1970 (Robertson, 1971).

Spring migration records are more numerous and scattered (Mayfield, 1960:40-42). There have been a number of spring sightings in Ottawa County, Ohio, and at Point Pelee, Ontario, in the western Lake Erie region, but other records, some very recent, include Minnesota, Wisconsin, northern Illinois, Indiana, eastern Missouri, Ontario and Quebec (Walkinshaw, 1983:18-22). Observations (Walkinshaw, 1983) of unmated singing males during 1978, 1979, and 1980 in Jackson County, Wisconsin, one in 1977 and 1978 in Renfrew County, Ontario, one in 1978 in Quebec just north of Ottawa, and one in 1985 in southern Ontario indicate that some returning spring migrants tend to miss the primary Michigan breeding area. This may reflect faulty navigation, innate dispersal behavior, or even a return to ancestral nesting areas. The earliest arrival at the breeding ground is May 3 with an average arrival date of May 12 (Mayfield, 1960:42).

Figure 3
KIRTLAND'S WARBLER MIGRATION ROUTE BETWEEN
WINTERING AND BREEDING GROUNDS



Contributing factors to the recent Kirtland's warbler decline may be drought and hurricanes. Heavy losses among various species of warblers occurred during the spring migration of 1970-1971, due to drought conditions in the Bahamas and southern Florida.

The Kirtland's migrates north and south through the hurricane zone. During the height of migration, such storms might decimate the population, although this is unlikely since migration extends over several weeks.

Exposure to pesticides along the migration route may occur. In the United States spraying of southern agricultural lands is much more prevalent than on the northern breeding grounds (Mayfield, 1975). However, no known eggshell thinning has been detected or nest mortality attributed to chemical poisoning.

Limiting Factors

The ultimate limiting factor on the nesting population is the special habitat required. There is persuasive evidence that the amount of such habitat was at maximum during the brief lumbering period when forest fires were rampant in the pinelands during the 1880's and 1890's. The Kirtland's warbler also appears to have been at a peak at that same time. This contention is supported by the large number of specimens taken on the wintering ground during that period.

In modern times, forest fire control has reduced the total acreage burned and also the size of individual burns. These factors have worked to the disadvantage of the Kirtland's warbler. Also, practices that encourage the conversion of jack pine to other species have been detrimental.

Currently, only 4,000 to 5,000 acres are suitable for breeding birds. This is a very substantial reduction from the 10,000 to 15,000 acres available in the 1950's and 1960's and is probably the most important reason for the decline in populations of the Kirtland's warbler.

A second limiting factor is parasitism of Kirtland's warbler nests by the prown-headed cowbird, Molothrus ater. This bird of the prairies reached the Kirtland's warbler nesting range in the late 1800's with the clearing of the forests and the development of agriculture in northern Michigan. This relatively new threat is particularly ominous because the Kirtland's warbler has none of the defenses against cowbird parasitism which are exhibited by many other songoirds. Thus, the cowbird has found the Kirtland's warbler a particularly vulnerable host. Walkinshaw (1972) found that 69 percent of the Kirtland's warbler nests he examined during 1966-1971 were parasitized. Other host species nesting in the same vicinity at that time had a far lower parasitism rate.

Cowbird parasitism has, at times, reduced Kirtland's warbler production by at least 40 percent and in some years has almost completely wiped out the warbler's reproductive effort. It appears almost certain the Kirtland's warbler population cannot endure for long under this extremely heavy burden.

As previously indicated (page 6), removal of cowbirds from a nesting area is beneficial to the production of young warblers in nests. Nesting studies on selected tracts showed virtually no parasitism of warbler nests and excellent production of young warblers per pair of adults (Shake and Mattsson, 1975; Kelley and DeCapita, 1982; Walkinshaw, 1983).

Cowbird control by the Fish and Wildlife Service has continued each year since 1972. About 45,000 cowbirds were removed from 1972 through 1984. Monitoring studies of nesting birds from 1972 through 1981 showed continuing effectiveness in restoring the reproductive capability of the species to what it must have been before the cowbird arrived (Mayfield, 1975; Shake and Mattsson, 1975; Walkinshaw and Faust, 1974 and 1975; Orr, 1975; Kelley and DeCapita, 1982; Walkinshaw, 1983).

Annual censuses from 1972 through 1985 have revealed stabilization of the breeding population at approximately 200 pairs. Without cowbird control, the Kirtland's warbler population would significantly decline.

Third, although nesting Kirtland's warblers have been studied extensively, little is known of their ecology after fledging but prior to fall migration. Some limiting factors, such as excessive predation, may be in effect during this period. Research efforts should be undertaken to improve knowledge of the immediate post fledging period.

Fourth, there may be limiting factors, as yet unidentified, on the wintering ground. Since 1972, about 800-900 warblers have gone south each fall, but only about 400 have been found in the census in Michigan the next June. This could indicate that some returning birds cannot find territories because of limited breeding habitat. Also, this could indicate that one-half of the fall population is lost on the winter range or during migration, but we have no direct evidence of the cause; nor do we know if this is an excessive overwinter mortality rate for this bird. All nypotheses to explain the situation -- dry weather, increasing competition for food with other species of warblers, hurricanes and development in the Banamas -- have not been researched to date. An immediate and intensive effort should be made to investigate the ecology of the Kirtland's warbler during migration and on its winter range.

Part II

RECOVERY

A. RECOVERY PLAN OBJECTIVES

THE PRIMARY OBJECTIVE OF THE PLAN IS TO REESTABLISH A SELF-SUSTAINING KIRTLAND'S WARBLER POPULATION THROUGHOUT ITS KNOWN RANGE AT A MINIMUM LEVEL OF 1,000 PAIRS. ATTAINMENT OF THIS OBJECTIVE WILL ALLOW THE SPECIES TO BE REMOVED FROM THE ENDANGERED SPECIES LIST. SECONDARY OBJECTIVES, DESIGNED TO ACCOMPLISH THE PRIMARY OBJECTIVE, ARE AS FOLLOWS:

- 1. Manage 127,600 acres for the Kirtland's waroler. Encourage management on private lands.
- 2. Protect the Kirtland's warbler on its wintering grounds and along the migration route.
- 3. Reduce key factors adversely affecting reproduction and survival of Kirtland's warbler.
- 4. Monitor breeding populations of the Kirtland's warbler to evaluate responses to management practices and environmental changes.
- Develop and implement emergency measures to prevent extinction.

APPENDIX C

DESCRIPTION AND MAPS OF ESSENTIAL HABITAT for the KIRTLAND'S WARBLER

DESCRIPTION OF ESSENTIAL HABITAT

The Kirtland's warbler does not adapt to a variety of environmental conditions. Its requirements for breeding habitat are quite specific, so exact that its numbers will probably always be limited. The essence of its habitat is the jack pine forest. For this reason, it is often called the jack pine warbler. However, its habitat is more than just jack pine. The bird requires certain exacting conditions for nesting. Almost without exception, it is found only in extensive, nomogenous stands of young jack pine located on some of the poorest soils in Michigan.

The plant community attractive to this waroler developed in the past from repeated and extensive forest fires. Historically, wildfires have been the most important factor in the establishment of natural jack pine. These fires played an important role in past survival of the warbler since, under natural conditions, suitable habitat was produced only by forest fires. With the advent of fire protection there was a drastic decline of such suitable habitat. Nesting habitat generally consists of young jack pine stands between 5 and 20 feet in neight. Dense stands with the pines in close juxtaposition yet interspersed with small openings are best, the pattern which often results from forest fires. Such cover is not attractive to many other species of wildlife, resulting in less competition than might otherwise be expected. A breeding pair of warblers requires about 30 acres of this type for their nesting territory.

The low-growing, sparse vegetation that occurs in association with the young "Christmas tree"-size jack pine on the relatively level sandy outwash plains is an important component of the habitat necessary for the warblers. The delicate combination of conditions required exists for a relatively short period of time, lasting only 10-15 years before it is no longer acceptable.

Habitat for the Kirtland's warbler is considered essential where its destruction, disturbance, modification, or subjection to human activity might be expected to result in a further reduction in numbers of this species, or in a reduction in its potential for expansion or recovery. Essential habitat is defined to mean areas that are presently occupied by nesting pairs, and areas that can be expected to be utilized at some future time. The designation of such potential nesting areas is necessary because the birds' occupancy of any tract is temporary, extending through only one early stage of the jack pine growth cycle.

Potential habitat consists of those stands of jack pine that, through management, will provide acceptable habitat at some future date. Such stands can be managed for eventual harvest of the timber resource, with economical harvest at 45 - 50 years of age. Since the warbler occupies a tract for only about 12 years within this age span, to achieve a stable population of 1,000 pairs will require 38,000 acres of nesting habitat at all times. To meet an objective of a sustained supply of nesting habitat sufficient to support 1,000 pairs will require the designation of some 127,500 acres as essential habitat.

The criteria used for designation of essential habitat include:

- Soil type Grayling sand and closely associated soil types.
- 2. Forest cover currently in jack pine and where management for jack pine is feasible. Areas may contain a limited oak component. Habitat with significant levels of non-characteristic vegetative types (aspen, willow, cherry, etc.) was excluded.
- 3. Areas currently occupied or previously used by the species.
- 4. Tracts of about 320 acres or larger, preferably where five or more of them lie within two miles of each other. Tracts less than 320 acres, but not less than 80 acres, where they occur in close proximity to the larger tracts.
- 5. Lands preferably in public ownership (State or National Forests).
- 6. Limited development potential or where development could be controlled.
- 7. Relatively level topography.

Essential Habitat

The attached maps show the approximate location of the essential habitat. Detailed maps are available and on file with the Secretary of Interior; Director, Michigan Department of Natural Resources; and Forest Supervisor, Huron-Manistee National Forest.



U.S. Forest Service Essential Habitat

State Forest Essential Habitat

Military Area Habitat

KIRTLAND'S WARBLER HABITAT IN MICHIGAN

THE FALL MIGRATION ROUTE OF KIRTLAND'S WARBLER

MARY HEIMERDINGER CLENCH

With highly specialized habitat requirements for breeding. It has been well studied on the breeding grounds, but is little known as a migrant or on the wintering grounds. From time to time the species has been recorded during spring migration when the males may sing, drawing attention to themselves, but well documented fall migration records are exceptionally rare. In the autumn of 1971 we had the good fortune to band a migrant Kirtland's in southwestern Pennsylvania. This was an exciting event for several reasons: it was the first well documented Pennsylvania record for the species; it was the first fall banding of a migrant outside of Michigan; and the bird was rehandled at our banding station twice after it was banded, allowing us to make a limited analysis of habitat preference, weight change, and correlation of its migratory behavior with weather patterns. Perhaps most important, this Pennsylvania record may throw new light on the little known fall migration route of the species.

THE PENNSYLVANIA RECORD

On 21 September 1971 at 10:15, Robert C. Leberman captured a Kirtland's Warbler in a mist net at Carnegie Museum's Powdermill Nature Reserve, three miles south of Rector, Westmoreland County, southwestern Pennsylvania (40° 10′ N, 79° 16′ W). Realizing that this was an important record and should have verification he telephoned Kenneth C. Parkes and the author at the museum in Pittsburgh. We quickly gathered up study skins representing the various plumages of the species and drove to the Reserve. Upon seeing the bird we confirmed the identification. It was an immature individual, as indicated by the only partly pneumatized skull and heavy streaking on the breast plumage. We could not definitely determine its sex because immature Kirtland's Warblers are not known to be sexually dimorphic (Van Tyne, 1953).

After identification the warbler was measured, weighed, banded, photographed, and released. Its measurements were: unflattened wing chord, 67.5 mm; tail, 55 mm; exposed culmen, 10.7 mm; tarsus, 20 mm. It weighed 14.0 grams and had a trace of visible fat in the furcular region. To document the record color photographs were taken. Several of the pictures are now on file at Carnegie Museum and one in black and white appeared on the cover of the November, 1971, issue of Carnegie Magazine.

On 26 September, five days after it had been banded, the warbler was

Bright House

recaptured at Powdermill at 11:50; it weighed 14.9 g and had no visible fat deposits. On 2 October at 17:40 it appeared again, weighing 15.8 g and with a small amount of visible fat (index of 1 on a scale of 0-3).

When the Kirtland's originally was netted it was found in the company of several other parulids in a net lane cut through a dense old field hawthorn (Crataegus spp.)—crabapple (Pyrus coronaria) thicket. The lane is located slightly above the floor of the Ligonier Valley (elevation approximately 1,350 feet) and extends from the edge of a dirt road through the thicket for approximately 45 meters, then crosses a small open marsh and ends in another but more open old field hawthorn-crabapple thicket. The total length of the net lane is 120 meters. In the same general area of the Reserve 33 additional nets are operated, but in different types of habitat: willow thickets bordering streams and a pond; old fields in different stages of succession; second-growth forest, etc. The 45 meter stretch of the net lane in which the Kirtland's Warbler was originally found is unique within the banding area in terms of density and height of the hawthorn and crabapple trees.

When the bird was captured on 21 September it was carried to a banding office some 250 meters from the net lane; after banding it was released near the office. On the second capture the Kirtland's was transported and released near a different banding office, some 880 meters from the capture lane. Regardless of the release site it returned both times to the same 45 meter stretch of the same net lane, and was netted with other warbler species. The repeated appearance of the Kirtland's in the same hawthorn-crabapple thicket would seem to indicate a preference of this individual for this type of habitat. The region in and around Powdermill lacks any habitat similar to the jack pine scrub of the Michigan breeding grounds.

The weather records during the period the Kirtland's was at Powdermill show an interesting correlation of wind direction with the probable migration direction of the bird. According to the U.S. Weather Bureau at the Pittsburgh airport (approximately 56 airmiles WNW of the Reserve) northwest winds developed in the early evening of 20 September; during the two previous days the winds had been from the south. The northwest winds continued until the late afternoon of 21 September, several hours after the warbler had been caught and banded. For the entire eleven-day period the bird stayed at Powdermill the winds did not come from the northwest quarter except for very brief periods. Two days after the warbler was last handled the winds swung around and blew from the northwest, from the evening of 4 October until the morning of 8 October.

The Reserve banding records indicate that although the Kirtland's remained in the area from 21 September at least through 2 October, considerable numbers of migrants were passing through the region during that period.

On 21 September the capture rate at the banding station was 0.91 birds per net hour, with a total of 145 birds of 33 species (including 99 warblers of 16 species). In the following days through 2 October the capture rate remained high (for the Powdermill station): 0.48 birds per net hour, with 1,146 birds banded, or 104 birds per banding day. During the same period, 21 September-2 October, in the previous five years, with more nets open for longer periods (av. 3,062 net hours 1966-70 vs. 2,390 in 1971) the capture rate was lower: 0.29 birds per net hour, or 85.6 birds per banding day. Thus it is clear that a higher than normal amount of migratory activity occurred at Powdermill while the Kirtland's was present.

Yet with all this movement of other species, the warbler remained. It apparently had a habitat preference, and it was gaining weight (1.8 g, an increase of 13 percent over its original capture weight). The layover period was a minimum of eleven days, presumably a long time for a migrant passerine.

The most reasonable explanation for this delay is that although other birds were actively migrating (the winds were out of the northeast quarter for a total of six days, the southeast for one, and the southwest for four), the Kirtland's was waiting for a more favorable wind. It had been banded, apparently as a new arrival, during a period of northwest winds and it remained in the area at least until two days before the next northwest winds began. After that second period of northwest winds the bird was not seen again. The association of this warbler with a particular wind direction, therefore, seems fairly clear and reasonable. Powdermill lies to the southeast of the Michigan breeding grounds, hence a bird migrating from there on a northwest wind might easily come down in southwestern Pennsylvania. A second period of northwest winds would take the warbler toward the southeastern states, where it could then continue south to the wintering grounds in the Bahamas.

Support for our belief that the Powdermill bird was not an "accidental" (an individual well outside the normal migration route) comes from two other southern Pennsylvania records. On 26 September 1972, an "adult male" was watched for over an hour while it fed with other warbler species on insects in "sweet birch" growing on abandoned strip mine spoil on a hill above Wellersburg, Somerset County (McKenzie, 1973; in litt.). Wellersburg is less than 45 airmiles SE of Powdermill. Mr. McKenzie saw the bird at close range and described it well; unfortunately he was alone at the time and did not have a camera with him, but otherwise his is a convincing description of a Kirtland's Warbler. At the time he apparently was unaware of the Powdermill banding record. An earlier sight record from Lewisville, Chester County, in the southeastern corner of Pennsylvania, is similarly well

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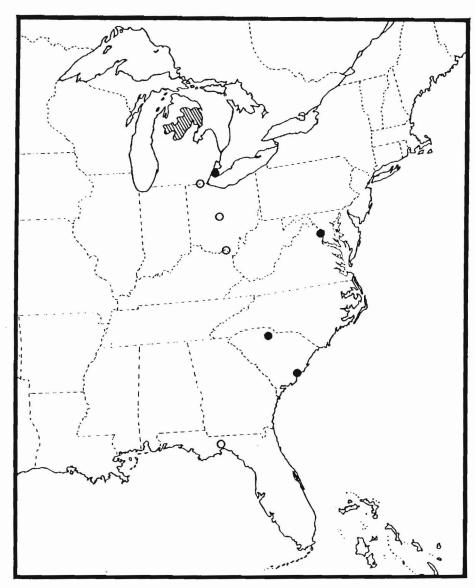


Fig. 1. Fall migration records of Kirtland's Warbler as mapped by Van Tyne. Solid circles represent specimen records; open circles, accepted sight records; hatched area, known breeding grounds. Redrawn from Van Tyne (1951).

described but undocumented. The bird was in "full breeding plumage" and recorded on 27 September 1964, by a single observer who had had previous experience with the species on the breeding grounds (B. Hurlock, D. Cutler, in litt.).

OTHER FALL RECORDS

What little is known about the fall migration route of Kirtland's Warbler was first summarized by Van Tyne (1951). Van Tyne also was almost entirely

TABLE 1
FALL MIGRATION RECORDS OF KIRTLAND'S WARBLER*

	MIGRATION KECORDS OF		
Locality	Date	Туре	Reference
Ontario			
Point Pelee	2 Oct. 1915	Specimen	Mayfield, 1960
Michigan			•
Bloomfield Hills	24 Sept. 1965	Banding	W. P. Nickell, AFN**, 20:52
Ohio			
Bowling Green	28 Sept. 1969	Sight	V. B. Platt, in litt. to Mayfield
Buckeye Lake	Sept. 1928	Sight	M. B. Trautman, in litt. to Clench
Cleveland	14 Oct. 1886	"Specimen"	Davies, 1906
Cleveland	25 Oct. 1969	Sight	J. N. Henderson, in litt.
(Hudson)			to Mayfield
Columbus	11 Sept. 1925	Sight	Thomas, 1926
(Alum Creek)			•
Ironton	28 Aug. 1902	Sight	Jones, 1903
Toledo	22 Sept. 1929	Sight	Mayfield, 1960
Pennsylvania			
Lewisville	27 Sept. 1964	Sight	B. Hurlock, AFN, 19:24
Rector	21 Sept2 Oct. 1971	Banding	This paper
Wellersburg	26 Sept. 1972	Sight	McKenzie, 1973
Virginia			
Fort Meyer	25 Sept., 2 Oct. 1887	Specimen,	Smith & Palmer, 1888
(Arlington)		sight	
North Carolina			
Rocky Mount	2-23 Sept. 1936-41	Sight (3 dates)	Mayfield, 1960
South Carolina			
Chester	11 Oct. 1888	Specimen	Loomis, 1889
Christ Church Parish	4 Oct. 1910	Sight	Wayne, 1911
(nr. Charleston)			
Mt. Pleasant (nr. Charleston)	29 Oct. 1903	Specimen	Wayne, 1904
Florida			
E. Goose Creek (20 mi. W. St. Marks)	9 Sept. 1919	Sight	Mayfield, 1960
Miami	21 Sept. 1958	Sight	R. L. Cunningham & A.
West Palm Beach	2-3 Nov. 1961	Sight	Schaffner, AFN, 13:24
Alabama	- 0 1101. 1701	Jigiit	V. I. Carmer, AFN, 16:24
Jacksonville	5 Oct. 1966	Sight	W. J. Calvert, AFN, 22:53

^{*} Accepted by Van Tyne (1951) and in the present paper ** AFN = Audubon Field Notes

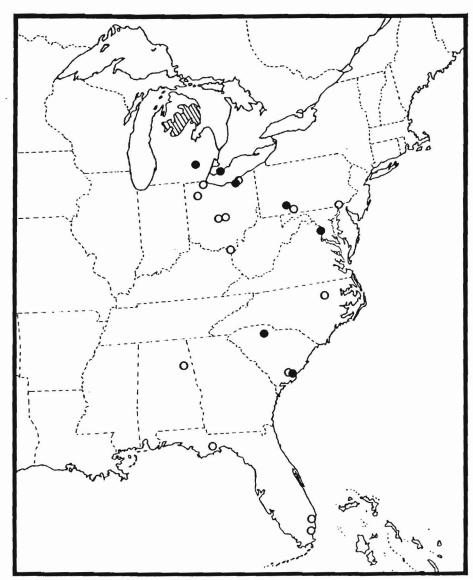


Fig. 2. Accepted fall migration records through 1972. Conventions as in Fig. 1 (banding records also shown as solid circles).

responsible. (Mayfield, in litt.) for the section on fall migration records in Mayfield's excellent monograph on the species (1960). In both publications the same map (Fig. 1) was used to illustrate the accepted fall migration records. The later publication also includes a list of localities and dates for each record. In comparing the list of records with the map I found several puzzling discrepancies: four of the listed records are not spotted on the map and three of the map spots are not listed. I then wrote to Dr. Mayfield and he kindly sent me all of his and Van Tyne's notes and correspondence on the

fall migration records. In addition to studying this material, I have also searched the literature through 1972 in an effort to gather together all the records, substantiated or otherwise, for analysis.

I found that the Van Tyne map is actually missing only two records that he accepted: one for a specimen from Cleveland, Ohio in 1886, and one for three sight records at Rocky Mount, North Carolina from 1936 through 1941. The third, apparently missing, record was erroneously listed as Oberlin, Ohio but correctly spotted on the map at Ironton on the Ohio River. The fourth, a sight record from the Charleston, South Carolina area, could have been omitted because of the specimen already marked for that locality on the map. The unlisted map spots are both valid records: one a sight record from Columbus (Alum Creek), Ohio in 1925 and the other a specimen taken in interior South Carolina (Chester) in 1888. All these previously accepted records and others made in recent years are detailed in Table 1 and mapped in Figure 2.

The following sight records (listed alphabetically by states) known or suspected to have been rejected by Van Tyne and/or rejected by me have not been included in Table 1. Arkansas: Arkansas County, 23-28 Sept. 1936 (Baerg, 1951); Harrisburg, 11 Sept. 1972 (in litt. to Mayfield). Florida: Fort Pierce, 1 Nov. 1918 (Sprunt, 1954); Chokoloskee, 11 Oct. 1915 (Sprunt, 1954); Pensacola, 26 Nov. 1953 (Sprunt, 1954); Princeton, 25 Oct. 1915 (Sprunt, 1954). Georgia: Savannah, 27 Aug. 1909 (Burleigh, 1958). Kentucky: Bowling Green, 28 Sept. pre-1922 (rejected by Mengel, 1965). Missouri: Weldon Springs, 29 Sept. 1950 (in litt. to Van Tyne). Ohio: Canton, 2 Sept. 1939 and 9 Sept. 1939 (in litt. to Van Tyne); Cleveland, eight dates between 2 Sept. and 7 Oct. 1934-46 (Williams, 1950); Zanesville (Dillon Dam), 3 Sept. 1962 (Hurley, 1963). South Carolina: Eastover, 14 Oct. 1949 and 1 Sept. 1951 (in litt. to Van Tyne). Virginia: Bristol, a specimen supposedly collected sometime in the fall, no date specified (Jones, 1931). A few other records in the Van Tyne correspondence are too inexact or fragmentary to identify. I have listed these rejected records so future workers will know which of the records have already been taken into consideration.

DISCUSSION

In assembling all the known fall migration records for Kirtland's Warbler I have found only two that were, to my mind, completely satisfactory indicators of the route the species is *presently* taking. These two records are the 1971 Powdermill banding and an individual banded by Walter Nickell at Bloomfield Hills, Michigan, in 1965. Most of the others are sight records, and although undoubtedly many are valid they are nevertheless subject to the

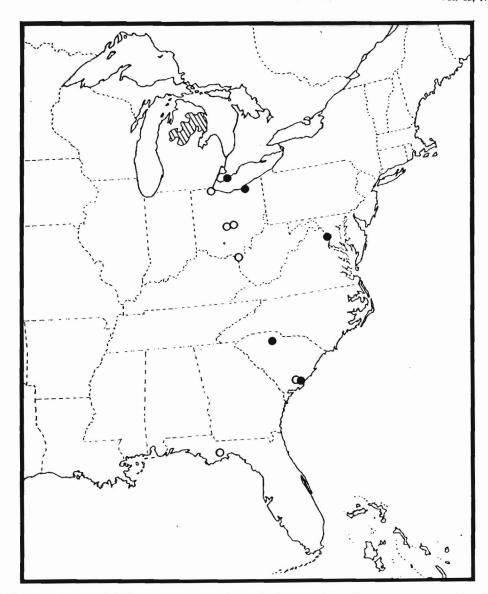


Fig. 3. Accepted fall migration records made before 1935. Conventions as in Fig. 1.

doubts that may be applied to any sight record. Specimen records are few, only five, and all over 50 years old: three from 1886 to 1888, one in 1903, and one in 1915. Of course in recent years, because of the species' low populations and official endangered status, it has been unwise or illegal to collect any birds that otherwise might have been secured for unquestioned records.

The greatest problem with the older records is that Kirtland's Warbler apparently has undergone striking changes in population and range size within the last 100 years. It is believed that the species enjoyed an expanded range

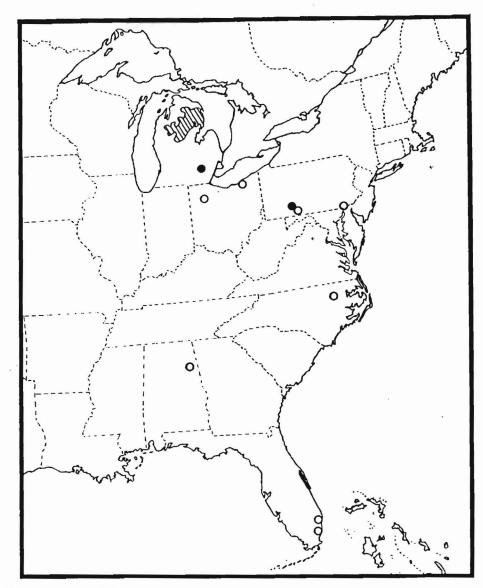


Fig. 4. Accepted fall migration records made after 1935. Conventions as in Fig. 1.

and population between 1885 and 1900. Mayfield (1960:41; legend to Fig. 5 adapted from Van Tyne, 1951) points out some of the spring migration records between 1885 and 1900 that are well "outside the normal migration route . . . when these birds are believed to have been more numerous than before or since." Van Tyne (1951:542) in the legend to the same map states "The dated records, occurring from 1885 to 1900, are those of birds which seem to have been en route to some nesting ground other than that now known." In addition, the population may have suffered a serious decline after about 1934 (Milton Trautman, in litt.; Mayfield, 1960:40) from which it

eventually at least partially recovered only to show another marked population loss in the last decade (Mayfield, 1972). All of this means that when considering fall migration records, one must take into account when the records were made and the probable state of the species' population at the time. Certainly the very early records, before 1900, must be considered as coming from a period of relative abundance and possibly representing migration routes that are no longer in use.

To see if any differences were apparent between earlier records and those made in recent years, I mapped the records made before and after 1935 (Figs. 3 and 4). As might be expected, the pre-1935 map is similar to Van Tyne's, and indicates a relatively straight-line, SSE route between the breeding and wintering grounds. The more recent records, however, suggest a more directly eastward route from Michigan, across northern Ohio and southern Pennsylvania (crossing the Appalachians at a relatively low point) and then perhaps following the Piedmont or the inner coastal plain to the southeast coast before the over-water flight to the Bahamas. I doubt that the species reaches the coast north of South Carolina. The evidence for this belief is negative: no Kirtland's Warbler has even been seen on the coast north of the Charleston region. With the many hundreds of thousands of fall migrants that have been banded in recent years by coastal stations from New Jersey to Virginia, and with the many bird watchers that frequent the middle Atlantic coast during autumn, if the species did occur there with any regularity, it probably would have been recorded at least once. One might also reasonably suppose that the "Jack Pine Warbler" would find the extensive pinelands of the Piedmont and inner coastal plain attractive habitat.

It is also possible (Fig. 2) that some individuals may travel from Michigan via the western side of the mountains. A few accepted sight records indicate this route, and a number of the rejected records are also from this western area. It is not possible to say which of these unsubstantiated records may actually be valid, but by their very numbers I suspect that at least a few of them may be true sightings.

The direct route, SSE, crossing the Appalachians in Kentucky, Virginia, Tennessee, or the Carolinas, may also be used as suggested by the records in Fig. 3. We have no knowledge of whether mountains such as those in the southern Appalachians are sufficiently high to deflect this species on migration. Perhaps these mountains are not a serious barrier to a migrating warbler, yet none of the existing records come from within the southern mountains. The Chester, South Carolina, specimen is not, as it might first appear, from the mountains, but from well within the Piedmont. This specimen was also collected after a heavy gale and the bird might have been blown into the locality from elsewhere. The only montane records of the species, therefore,

are both from southwestern Pennsylvania: the 1971 Powdermill banding and the 1972 Wellersburg sight record.

Hopefully field observers and banders from Ohio and Pennsylvania south, and especially those working in the southern mountains and Piedmont, will keep these possible additional migration routes in mind and be on the lookout for the species in the fall. Rare as Kirtland's Warblers now are (only about 200 pairs in the 1971 census) they still *must* pass through the eastern U.S. twice a year and, with luck, can be recorded.

This, then, is the existing evidence on the fall migration route of Kirtland's Warbler: a very sparse record consisting of 21 localities, only seven of which are adequately documented. Of these seven, five are specimens collected between 1886 and 1915, a period when the species is believed to have been more numerous and with a larger breeding range than is now the case; and two are bandings, both within the last decade and the only completely satisfactory modern records. The remainder are sight records which, although apparently valid, are still sight records and thus open to question. Since Van Type's compilation, however, nine records have been added to the twelve earlier ones, and the resulting picture is no longer of a straight-line, SSE route leading directly from Michigan to the Bahamas. The evidence is still too sparse to allow a definite statement on the present (or past) fall migration route of the species. It is fairly clear, however, that not all birds now follow the route suggested by the Van Tyne map. It is also probable that several routes are (or have been) used, either by different segments of the population, by different age or sex classes, or in response to varying weather conditions. How or when these various routes may be used cannot be explained by the present data. One might also hazard the (perhaps overly optimistic) guess that Kirtland's Warbler may have breeding grounds in addition to those known in Michigan, and thus in the fall is coming from regions we know nothing about.

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KIRTLAND'S WARBLERS ON THEIR WINTERING GROUNDS IN THE BAHAMA ARCHIPELAGO--A PRELIMINARY REPORT

Paul W. Sykes, Jr.

U.S. Fish & Wildlife Service Patuxent Wildlife Research Center School of Forest Resources The University of Georgia Athens, GA 30602

Surveys for the Kirtland's warbler (<u>Dendroica kirtlandii</u>) were conducted on 15 islands in the Bahama Archipelago in 1985 and 1986, and at least 6 individuals were located. Emphasis in 1986 concentrated on the island of Eleuthera to examine habitat, foraging strategies, food habits, and site tenacity. The species spends approximately 44% of the year on the wintering grounds throughout the archipelago. The warblers (N=149 records, 1878-1988) used 5 biotic communities, but appeared to favor second growth coppice 3-10 feet in height, or low virgin scrub on the more arid southern islands. Individuals (N=2) foraged over an area of approximately 15 acres and exhibited strong site tenacity.

A survey of Eleuthera revealed that at least 2% (4 square miles) of the island's uplands had high potential as winter habitat for Kirtland's warbler. If this percentage is extrapolated to the archipelago as a whole, there is a minimum of 112 square miles of available winter habitat. In reality, however, available winter habitat probably greatly exceeds this speculative figure.

Foraging behavior of two individuals studied consisted of 75% gleaning, 13% probing, 7% hover-gleaning, and 5% other foraging techniques and took place from the ground up to 12 feet. Food items (N=448 observations of 2 individuals) consisted of 59% small fruits (83% of which were of a single species), 20% arthropods, 1% seeds, and 20% undetermined. Based upon this limited work in the islands and preliminary results of banding returns in Michigan, the factor or factors suppressing the Kirtland's warbler population do not appear to be on the wintering grounds.

Çişiye de Bakısınının

KIRTLAND'S WARBLERS ON THE NESTING GROUNDS DURING THE POST-BREEDING PERIOD

PAUL W. SYKES, JR.,¹ CAMERON B. KEPLER,¹ DAVID A. JETT,¹
AND MICHAEL E. DECAPITA²

ABSTRACT. - Eighty-four Kirtland's Warblers (Dendroica kirtlandii) were caught 122 times during 8809 net-h at five study areas on the breeding grounds in northern lower peninsular Michigan during the post-breeding seasons (16 August-30 September) from 1984-1987. This more than quadruples the known number of post-breeding season records for the species at the nesting colonies. Combined with older records within and south of the breeding grounds, this information indicates that a substantial number of breeding birds remain in Michigan through September, and a few individuals probably remain into early October. Mean capture rate per 100 net-h was 1.4 warblers at the principal study area for the postbreeding period. Males were captured more frequently than females. Most hatching year (HY) birds had completed Prebasic I Molt by the end of August whereas Basic Molt occurred throughout the 16 August-30 September study period in after hatching year (AHY) birds. Subcutaneous fat deposition was low for both sexes in the two age classes prior to migration. Migration apparently consists of two waves—an early departure (mid-August to early-September) of HY birds, and late departure (late September) of AHYs. These late-season birds may face some man-induced stresses after the traditional 1 May-15 August breeding area closure. An extension of the closure through mid-September is recommended. Received 12 Jan. 1989, accepted 20 Feb. 1989.

Because the endangered Kirtland's Warbler (*Dendroica kirtlandii*) breeds within a highly restricted range centered in a six-county region in northern lower peninsular Michigan (Walkinshaw 1983), great care has been taken to protect the bird and its habitat during the period it remains in the state. The Kirtland's Warbler Recovery Team (Byelich et al. 1976, 1985) stressed the need to restrict human use of all state and federal forest lands used by the warbler for nesting (95–97% of current nesting areas; Ryel 1984, Weise 1987) from 1 May to 15 August each year, embracing the mid-May to mid-July nesting period (Mayfield 1960). These closure dates include time before and after the known nesting period to buffer the birds from undue stresses which might affect survival. The original recovery plan further indicated that a review of "all land use plans" should be made "in order to avoid conflicts which may be detrimental to the birds" (Byelich et al. 1976, p. 25).

¹ U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Southeast Research Group, School of Forest Resources, The Univ. Georgia, Athens. Georgia 30602.

² U.S. Fish and Wildlife Service, Manly Miles Building, 1405 South Harrison Road, East Lansing, Michigan 48823.

The Wood State of Section 1986

Biologists working with Kirtland's Warblers have concentrated their efforts during the breeding period, when adult males are highly vocal and conspicuous and nests are easily found. By mid-July most singing has ceased, most chicks have fledged, and the birds become more cryptic in plumage and behavior, requiring increased effort to find them (Mayfield 1960, Walkinshaw 1983). By August, the first Kirtland's Warblers have returned to the Bahamas (Hundley 1967, Wallace 1968, Robertson 1971). It has been widely assumed that most of the warblers leave the nesting areas in August (Mayfield 1960; Walkinshaw 1983; Byelich et al. 1976, 1985), as relatively few published records exist (11 for the second half of August and 13 for all of September); only one record is later than 1933 (Table 1).

In 1984 we began banding Kirtland's Warblers in the post-breeding season. We were initially surprised to capture five birds in September in a modest banding effort. Since the presence of large numbers of Kirtland's Warblers on the breeding grounds during the post-breeding season would alter our understanding of their post-breeding and migratory behavior, and also have major implications for their management, we decided to obtain information on the numbers, age, sex, and locations of these late-summer early-fall birds.

STUDY AREAS AND METHODS

Study areas in 1984 were east of Grayling in Crawford County, Michigan, and included: (1) "Bald Hill" (Sect. 20, T-27-N, R-1-W) north of North Down River Road, two net sites, 23 nets; and (2) "Bucks Crossing" (Sect. 8 and 9, T-27-N, R-2-W) along Lewiston grade on Camp Grayling Artillery Range (Michigan National Guard), three net sites, 39 nets. Study areas in 1986 included: (1) "Bald Hill," four net sites, 48 nets; and (2) "McKinley" (Oscoda County, Sect. 10, T-26-N, R-4-E); 2 net sites, 14 nets. Study areas in 1987 were in the vicinity of Grayling and Mio and included: (1) "Bald Hill," six net sites, 91 nets; (2) "Muskrat Lake" (Oscoda County, Sect. 13, T-27-N, R-1-E) north of County Road 608, three net sites, 26 nets; and (3) "Mack Lake" (Oscoda County, Sect. 21 and 22, T-25-N, R-3-E) west and east of U.S. Forest Service Road 4147 in the southcentral part of the 1980 Mack Lake Burn (Simard et al. 1983) on the Huron National Forest, two net sites, 27 nets. When a study area was used for more than one field season (Bald Hill) the same net sites and net lanes were used each year, with new net sites and lanes being added as needed.

Netting operations were conducted from 8 August-6 September 1984, 13 August-13 September 1986, and 1 July-29 September 1987. The post-breeding period in this paper refers to 16 August to 30 September. This 46-day period has been subdivided into three intervals for analysis; 16-31 August, 1-15 September, and 16-30 September. Birds were captured with black nylon ATX 4-shelf, 12 × 2.6-m tethered mist nets with 36-mm mesh stretched between two 3-m-high pieces of galvanized electrical thin-walled conduit. Each net had its own set of support poles. Net configurations, conforming to vegetative cover and topography, consisted of single nets, nets end to end in line, and in T and L configurations, right angle crosses, etc.

Netting was generally conducted during the morning, as winds and/or high temperatures

made afternoon or early evening netting impractical on most days. No netting was attempted during rainy weather. We generally did not operate the same net sites on consecutive days in an attempt to prevent birds from acclimating to the nets. Nets were checked and birds removed every 15-30 min. All Kirtland's Warblers were released at the same net where captured after being banded, aged (adult = after hatching year - AHY; immature = hatching year-HY), sexed, and checked for molt. Birds were checked for subcutaneous fat using the system developed by Helms and Drury (1960) with the following fat classes: 0 = no fat, 1 = trace of fat in furculum, 2 = furculum lined with thin layer of fat, 3 = 1/4 to 1/3 furculum full of fat, 4 = furculum full of fat but not bulging, 5 = furculum bulging and fat along sides, etc. If an individual was captured more than once, fat class for the latest date captured was the value used in this paper. Handling of the warblers was completed as quickly as possible. Birds were transported and held in soft white open mesh nylon delicate-fabric laundry bags $(36 \times 45 \text{ cm with } 4 \times 4 \text{ mm mesh})$ with zippers across one end. All birds were uniquely color banded, two bands per leg, with red, light green, light blue, or yellow plastic butt-end size I bands bonded with a drop of acetone in combination with a size I U.S. Fish and Wildlife Service band.

The sex and age ratios, and proportion of birds with fat were compared using contingency table analyses. Capture rates were assumed to follow a Poisson process and were compared among time periods using the normal approximation of Cox and Lewis (1978).

RESULTS

During the post-breeding season, 84 different Kirtland's Warblers were caught 122 times. Twenty-five of these birds were recaptured a total of 38 times. Each bird was tallied only once in each of the three time intervals used in our analysis, even if caught more frequently. This resulted in the addition of 23 recaptures to our data set (Table 2). These 107 records are comprised of 57 males, 39 females, and 11 sex-undetermined HY birds.

There was a continuing drop in the number of individuals of both age classes (HY = 38 to 0 and AHY = 25 to 11) from late August to late September, with a significantly greater decrease (χ^2 = 13.65, P < 0.0002, df = 1) for HYs than for AHYs during this period (Table 2). HY birds made up 49% (N = 52) of the total captures (includes recaptures) throughout the post-breeding season. HY birds constituted a majority (60%, N = 38) of birds netted during 16-31 August, decreasing to 42% (N = 14) from 1-15 September, and strikingly, to 0% from 16-30 September.

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The netting effort (8809 net-h for the five study areas) is summarized in Table 3. Our effort increased each year of the study. Only at Bald Hill (with 76% of the total net-h) did we net in all three years; all other areas were netted during one year. Mean capture rate per 100 net-h at Bald Hill for the 16 August-30 September period was 1.4 (Table 4). This rate was variable from year to year with 3.7, 2.2, and 1.0 birds for 1984, 1986, and 1987, respectively. The annual decline of capture rate over the years at Bald Hill reflects an annual increase in our banding effort later in the season combined with coverage in more marginal sites in an attempt to capture dispersing birds.

Date	Locality	Age*	Sexb	Type of record ^c	Collector or observer	Reference ^d
20 Aug 1903	Near junction of N. Branch Au Sable with Au Sable Riv., Craw- ford County	U	U	Sighting	J. A. Parmalee	Wood and Frothingham 1905
20 Aug 1933	Red Oak, Oscoda County	U	M	Specimen UMMZ 97791	A. D. Tinker	Wood 1951
25 Aug 1904	Roscommon County	U	M	Sighting	-	Frothingham 1906
26 Aug 1933	SE of Lovells, Crawford County	U	M	Specimen UMMZ 72366	A. D. Tinker	Wood 1951
26 Aug 1933	SE of Lovells, Crawford County	U	M	Specimen UMMZ 155,431	A. D. Tinker	Wood 1951
27 Aug 1915	Near Luzerne, Oscoda County	Α	M	Specimen UMMZ 125,703	M. M. Peet	Wood 1951
30 Aug 1916	Near Luzerne, Oscoda County	I	F	Specimen UMMZ 125,705	M. M. Peet	Wood 1951
30 Aug 1916	Near Luzerne, Oscoda County	A	F	Specimen UMMZ 125,706	M. M. Peet	Wood 1951
30 Aug 1916	Near Luzerne, Oscoda County	A	F	Specimen UMMZ 125,707	M. M. Peet	Wood 1951
30 Aug 1916	Near Luzerne, Oscoda County	Α	M	Specimen UMMZ 125,708	M. M. Peet	Wood 1951
31 Aug 1916	Near Luzerne, Oscoda County	A	M	Specimen UMMZ 125,709	M. M. Peet	Wood 1951
1 Sep 1915	Near Luzerne, Oscoda County	Α	M	Specimen UMMZ 125,704	M. M. Peet	Wood 1951
1 Sep 1930	3 mi. SE Lovells, Crawford County	Α	F	Specimen UMMZ 65993	A. D. Tinker	Wood 1951
3 Sep 1904	Near junction of N. Branch Au	U	U	Sighting	J. A. Parmalee	Wood and Frothingham 1905
	Sable with Au Sable Riv., Craw-					
	ford County					
4 Sep 1916	Near Luzerne, Oscoda County	Α	M	Specimen UMMZ 125,710	M. M. Peet	Wood 1951
5 Sep 1916	Near Luzerne, Oscoda County	A	F	Specimen UMMZ 125,711	M. M. Peet	Wood 1951
6 Sep 1916	Near Luzerne, Oscoda County	I	M	Specimen UMMZ 125,712	M. M. Peet	Wood 1951
6 Sep 1916	Near Luzerne, Oscoda County	Α	F	Specimen UMMZ 125,713	M. M. Peet	Wood 1951
7 Sep 1916	Near Luzerne, Oscoda County	Α	F	Specimen UMMZ 125,714	M. M. Peet	Wood 1951
8 Sep 1916	Near Luzerne, Oscoda County	Α	F	Specimen UMMZ 125,715	M. M. Peet	Wood 1951

Date	Locality	Age*	Sex ^b	Type of record ^c	Collector or observer	Reference ^d
8 Sep 1916	Near Luzerne, Oscoda County	A	M	Specimen UMMZ 125,716	M. M. Peet	Wood 1951
9 Sep 1916	Near Luzerne, Oscoda County	Α	M	Specimen UMMZ 125,717	M. M. Peet	Wood 1951
28 Sep 1919	7 mi. S of Houghton Lake Village, Roscommon County	A	M	Specimen UMMZ 125,718	M. M. Peet	Wood 1951
29 Sep 1975	Mack Lake Mgt. Area, Oscoda County	U	U	Sighting	P. F. Schempf	Schempf 1976

A = adult, I = immature, U = unknown.

b F = female, M = male, U = unknown.
c Specimen data at the Univ. of Michigan Museum of Zoology (UMMZ) courtesy of Janet Hinshaw.
d Complete references listed in Lit. Cit. section.

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TABLE 2
KIRTLAND'S WARBLERS CAPTURED DURING 15/16-DAY INTERVALS IN THE POST-BREEDING
SEASON 1984, 1986, AND 1987^a

	Num	eriod		
Sex/age ^b	16-31 Aug	I-15 Sep	16-30 Sep	Total
Male	30	20	7	57
HY	17	8	0	25
AHY	13	12	7	32
Female	25	• 10	4	39
HY	13	3	0	16
AHY	12	7	4	23
Sex undetermined HY	8	3	0	11
Total individuals	63	33	11	107

^{*} Individuals captured in each 15/16-day interval were counted only once for that interval (although some were captured more frequently).

b HY = hatching year bird; AHY = after hatching year bird.

Capture rates at Bald Hill for the late-breeding season (1 July–15 August) compared to the post-breeding season (16 August–30 September) are presented in Table 4. Using data for all three years, the capture rates during the late-breeding period were higher than during the post-breeding period ($Z=4.11,\ P<0.0001$). Within the post-breeding period, data from all three years were used to compare late August with early September, but only 1987 data were available to make comparisons with late September. Capture rates did not differ between late August and early September ($Z=0.51,\ P=0.6080$), but rates for both periods were higher than that of late September ($Z=3.01,\ P=0.0026$ and $Z=1.98,\ P=0.0479$). Sample sizes from other study areas in 1987 and earlier were too small for statistical analyses.

The late recaptures (1 September or later) in 1987 totalled 11 individuals (Fig. 1). These birds were assumed to be present in the vicinity continually at least until the last date shown, as all initial bandings of the 11 birds and all subsequent recaptures were within the same study areas. Some of these birds were probably present later than we recorded them. The late recaptures consisted of 18% HYs (1 male, 1 sex undetermined) and 82% AHYs (7 males, 2 females). All birds initially banded in September 1987 were subsequently recaptured in the same month. The last date on which a Kirtland's Warbler was recaptured (29 September 1987 at Bald Hill) equals the latest published record (Schempf 1976) for the species on the breeding grounds.

The sex ratio of the captures when sex was determined (89%) was 1.4 males to 1 female, but this was not significantly different from 1:1 (χ^2 =

TABLE 3

MIST NETTING EFFORTS AND KIRTLAND'S WARBLER CAPTURE RATES IN MICHIGAN DURING THE POST-BREEDING PERIOD

							Stu	dy areas								
		Bald Hill		М	ack Lake		M	uskrat Lak	e	Buo	ks Crossin	ıg	ħ	McKinley		
Period•	Total net-h	Capture rate/100 net-h	Birds (N)	Total net-h	Capture rate/100 net-h	Birds (N)	Total net-h	Capture rate/100 net-h		Total net-h	Capture rate/100 net-h	Birds (N)	Total net-h	Capture rate/100 net-h		Total net-h
1984																
(16 Aug-6 Sep)		740														
16-31 Aug	275	3.6	10							132	1.5	2				407
1-15 Sep	78	3.8	3		•					42	4.8	2				120
Total	353	3.7	13	0			0			174	2.3	4	0			527
1986																
(16 Aug-13 Sep)																
16-31 Aug	743	2.4	18										0			743
1-15 Sep	557	1.8	10										102	1.0	1	659
Total	1300	2.2	28	0			0			0			102	1.0	1	1402
1987																
(16 Aug-29 Sep)	5.3							t								
16-31 Aug	2246	1.4	31	340	0.3	1	226	0.4	1							2812
1-15 Sep	924	1.3	12	671	0.3	2	165	1.8	3							1760
16-30 Sep	1842	0.5	9	231	0.4	1	235	0.4	1							2308
Total	5012	1.0	52	1242	0.3	4	626	0.8	5	0			0			6880
Study area total	6665	1.4	93	1242	0.3	4	626	0.8	5	174	2.3	4	102	1.0	1	8809

^a Dates in parentheses are inclusive for data used in this paper.

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TABLE 4

COMPARISON OF CAPTURE RATES OF KIRTLAND'S WARBLERS BY YEARS FOR BALD HILL

STUDY AREA FOR LATE-BREEDING AND POST-BREEDING SEASONS

	Late	breeding seas	son	Pos	t-breeding seas	son
	1	July-15 Augus	st	16 Au	gust-30 Septe	mber
Year	Total net-h	No. birds captured	No. birds/100 net-h	Total net-h	No. birds captured	No. birds/100 net-h
1984	201	8	4.0	353	13	3.7
1986	119	3	2.5	1300	28	2.2
1987	1989	58	2.9	5012	52	1.0
Total	2309	69	3.0	6665	93	1.4

2.42, P = 0.1198, df = 1) (Table 2). This preponderance of males was found in both HY and AHY age classes and for each of the three post-breeding season intervals.

Our study of molt in this species during the post-breeding period has just commenced, so the results presented are preliminary. The Prebasic I Molt (Postjuvenal Molt, body plumage only; see Mayfield 1960) in HY birds (N = 37 different individuals) was generally completed by the end of August. However, there was a wide range of variability among individuals, as some had completed their Prebasic I Molt by 16 August, while others extended to the end of August (32%) and a few to 10 September. We did not observe any sign of molt in remiges and rectrices of HY birds after the end of August. The Basic Molt (Postnuptial Molt) in AHY birds (N = 38 different individuals) spanned the length of our study period, 16 August through 29 September. As with HY birds, the start and completion of molt was highly variable among individual AHYs. Two AHY males required more than 30 days, and that for an AHY female exceeded 28 days. Although the work presented in this paper does not extend long enough into the fall to encompass the entire Basic Molt, it may prove similar in length to the 39–42-day period that Nolan (1978) found for the Prairie Warbler (D. discolor).

Fat classes were determined for 26 Kirtland's Warblers (12 HYs, 14 AHYs) in 1986 and 50 warblers (25 HYs, 25 AHYs) in 1987. In 1986, the percentages of individuals for the fat classes (0 [none], 1, 2, 3, 4, and 5 [highest value]) were 31, 50, 15, 4, 0, and 0, respectively and for 1987, the percentages were 40, 4, 24, 26, 6, and 0, respectively. Combining classes 0 and 1 into a low fat group and classes 2–5 into a high fat group showed that proportionally more high fat birds were caught in 1987 than in 1986 ($\chi^2 = 9.41$, P = 0.0022, df = 1). This difference may be a result of more late captures in 1987.

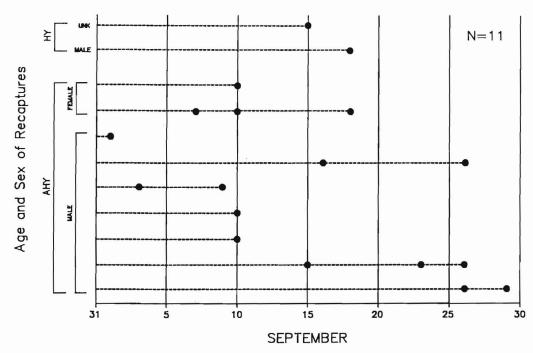


Fig. 1. Late recaptures of Kirtland's Warblers in 1987. Each solid dot represents a recapture; dashed lines indicate the birds were probably present in the vicinity.

DISCUSSION

Our study reveals that a substantial portion of the Kirtland's Warbler population remains on the breeding grounds in Michigan at least through September. Also, from 18 August–12 September 1985, biologists with the Michigan Department of Natural Resources made eight observations of 10 unmarked (4 in September) Kirtland's Warblers on the breeding grounds (E. S. Carlson and J. A. Weinrich pers. comm.). We infer that a few birds may remain to the first half of October. The published records of migrant Kirtland's Warblers (N = 15) in areas south of the breeding grounds after 1 September support this hypothesis (Table 5). Five Kirtland's Warblers (33%) were located within 310–460 km of the breeding area from 2–25 October.

HY birds appear to leave the breeding grounds earlier than adults, because proportionally fewer young of the year are found in September. This apparent decrease could result from HY birds migrating earlier than AHY birds, from higher mortality of HY birds during this period, from post-breeding dispersal by HY birds, or from temporally based changes in capture probabilities. We feel that HY birds, in general, migrate earlier than adults. Nolan (1978) found this to be true with Prairie Warblers. Also, during the post-breeding period, HY birds complete their wing and tail molt by the end of August, while in adults this extends through

TABLE 5 FALL KIRTLAND'S WARBLER RECORDS ADJACENT TO THE BREEDING GROUNDS AFTER 1 SEPTEMBER

Region	Date	Locality	Age*	Sex ^b	Type of record	Reference
Southern	24 Sep 1965	Bloomfield Hills, Oakland County	I	M	Sighting	Nickell 1965
Michigan	29 Sep 1951	Muskegon	U	U	Sighting	Whelan 1952
Southern	14 Sep 1948	Pickering, Durham County	U	U	Sighting	Walkinshaw 1983
Ontario	2 Oct 1915	Point Pelee, Essex County	I	M	Specimen	Harrington 1939
Northern	2 Sep 1948	Loves Park, Winnebago County	Α	M	2 sightings	Smith and Parmalee 1955
Illinois	4-5 Sep 1966	Chicago	U	U	Sighting	Peterson 1968
Northern Indiana						No records
Northern	2 Sep 1935	Near Hilliard Bridge, Cleveland	U	U	Sighting	McQuown 1944
Ohio	8 Sep 1940	Cleveland	U	U	Sighting	McQuown 1944
	22 Sep 1929	Springfield Township, Lucas County	U	U	Sighting	Campbell 1940
	26 Sep 1943	Rocky River Valley, Cuyahoga County	U	U	Sighting	Williams 1943a, b
	28 Sep 1969	Bowling Green	U	U	Sighting of 2 birds together	Clench 1973
	5 Oct 1941	Rocky River Valley, Cuyahoga County	U	U	2 sightings	Williams 1941a, b
	7 Oct 1934	Near Hilliard Bridge, Cleveland	U	U	2 sightings	McQuown 1944
	14 Oct 1886	Cleveland	U	U	Found dead	Davies 1906
	25 Oct 1969	Cleveland	,U	U	Sighting	Clench 1973

^a A = adult, I = immature, U = unknown. ^b M = male, U = unknown. ^c Complete reference listed in Lit. Cit. section.

September. Furthermore, Berger (1968) found migratory restlessness in captive (hand reared) HY Kirtland's Warblers (N = 9) between 25 August-8 September.

Of the August records in the Bahamas, one Kirtland's Warbler was listed as an adult female (Wallace 1968), two males and a female were listed with age unspecified (Hundley 1967), and another was listed with age and sex unspecified (Robertson 1971). Our experience with Kirtland's Warblers leads us to question the reliability of aging and sexing this species at this time of year unless examined in hand. The more subdued plumages of the two age groups in the fall made it difficult to distinguish between age/sex classes. However, a few (but not all) adult males retain some trace of black in the region of the lores, and these individuals can be aged and sexed in the field if seen at close range under good lighting conditions. Given these conditions, the age and sex for the August sight records in the Bahamas may not be reliable.

Our data suggest that Kirtland's Warblers tend to migrate alone in the fall rather than in groups. This is supported by published accounts of migrating individuals with no mention of conspecifics (Mayfield 1960, Clench 1973, Walkinshaw 1983). Hence, most HY birds probably make their first southward migration alone in the absence-of adults with prior experience.

Subcutaneous fat deposition was surprisingly low for the 76 individuals (1986 and 1987 combined) examined. Many of the birds during 16 August-29 September showed no fat deposition (31% in 1986 and 40% in 1987). There were no birds in 1986 in the two highest fat classes (4 and 5) and only 6% in fat class 4 and none in fat class 5 in 1987. This small sample suggests that most Kirtland's Warblers have not accumulated a large energy reserve by late September prior to initiating migration. Data for HY and AHY birds were similar in this regard. Migratory birds are known to build up fat just prior to migrating (Wolfson 1945, Cherry 1982, Pettersson and Hasselquist 1985, Moore and Kerlinger 1987). The apparent lack of fat accumulation in Kirtland's Warblers prior to migration needs further investigation.

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Probst and Hayes (1987) suggested the possibility of an imbalance in the sexes. Although the sex bias in favor of males that we found supports Probst and Hayes, the sex ratio is not significantly different from 1:1. Although there could be higher female mortality, due to incubating the eggs and brooding the young in ground nests, we note here that capture probabilities for males and females may have differed and led to biased sex ratios in the capture data. However, with the Kirtland's Warbler population hovering near 200 singing males for the last 17 years (Ryel 1984, Weinrich 1987), a possible skewed sex ratio in favor of males is cause for concern and should be carefully monitored in the future.

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The first posted closure of Kirtland's Warbler breeding grounds on public land was implemented in 1964 at Mack Lake (Huron National Forest), and this management procedure was followed on state forest lands several years later (G. W. Irvine, J. A. Weinrich pers. comm.). The time of closing was set to encompass the entire breeding season. An opening date in mid-August was based upon the supposition that all breeding activities were completed and that most of the warblers had left the nesting areas by late August or early September (Mayfield 1960; Walkinshaw 1983; Byelich et al. 1976, 1985). The mid-August opening date for the warbler areas was further supported by the early Bahama records (Hundley 1967, Wallace 1968, Robertson 1971). Published data would logically lead one to conclude that by late August most of the warblers would have left the Michigan breeding grounds. Aside from the unpublished Michigan DNR records, only one Kirtland's Warbler has been reported on the breeding grounds after 16 August in the last 50 years (Schempf 1976). Males sing only from early May to early July, and the birds become extremely difficult to find by the end of July; it is easy to conclude erroneously that most birds have left by this time or shortly thereafter.

We (pers. obs.) have seen five recently fledged young from three nests being actively fed between 14 and 17 August. Kirtland's Warblers generally care for their young from 29 to 44 days after they leave the nest (Mayfield 1960), so these late young would not be independent until well into September.

We have observed various potentially harmful activities in occupied Kirtland's Warbler habitats following their opening to the public on 15 August. Included were: recreational use of all-terrain vehicles (ATVs), dirt bikes, pickup trucks, and automobiles; firewood cutting and gathering; field training and conditioning of dogs for hunting; cutting, stacking, and hauling of pulpwood; seismic exploration for petroleum deposits; and, starting in mid-September, hunting of snowshoe hares (Lepus americanus) and Ruffed Grouse (Bonasa umbellus). While there may be little chance of direct harm to individual Kirtland's Warblers from these activities, mortality to the birds could occur. More serious is the threat of fire from people (discarding hot matches, smoking, open camp fires, etc.) and mechanized equipment (hot exhaust systems, sparks, etc.) in jack pine areas that are adapted to burn, particularly in dry years. As an example, in 1987 43% of the Kirtland's Warbler population was found in two areas, and loss of this habitat could have been a disaster to a species with such low numbers.

Because the Kirtland's Warbler is endangered and is a breeding species unique to Michigan, it would seem reasonable to keep the few areas occupied by them closed while the birds are present and while fire danger is still high. The total habitat occupied by the warbler (parts of 54 sections

in six counties, Weinrich 1987) is miniscule compared to the Federal and State forest lands in northern lower peninsular Michigan available for recreational activities enjoyed by the public.

Our efforts indicate that many Kirtland's Warblers remain on the breeding ground longer than previously thought, with a few birds possibly remaining into October. We recommend that all breeding areas having more than ten singing males remain closed until mid-September. This would protect the warblers from human activity as much as possible. The extension would encompass all late nesting activities, provide added protection for late hatched HY birds not yet fully independent, minimize disturbance to molting adults (AHYs), and provide added protection during the critical period when migratory energy reserves are being acquired. Since we do not know what factors are suppressing the population of this endangered species or where these factors occur in the annual cycle, this small modification to present management procedures might prove beneficial to the future survival of this unique parulid.

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PAIRING SUCCESS OF KIRTLAND'S WARBLERS IN MARGINAL VS. SUITABLE HABITAT

JOHN R. PROBST AND JACK P. HAYES1

USDA Forest Service, North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, Minnesota 55108 USA

ABSTRACT.—We compared pairing success of male Kirtland's Warblers (Dendroica kirtlandii) in different habitats to test the hypothesis that a lower proportion of males in marginal habitat are mated. Fewer than 60% of the males in marginal habitat were paired, but 95% of the males in suitable habitat were paired. We estimated the overall pairing success of the known breeding population at 85%. We could not estimate the number of females because the adult sex ratio is unknown, and an unknown proportion of Kirtland's Warblers are polygynous. The Kirtland's Warbler population was fairly constant from 1971 to 1983, despite markedly improved nest success resulting from cowbird control measures. If there are more males than females, or if many females fail to breed or must accept mated males or marginal habitat, population growth could be impeded. We combined reduced pairing success with an estimate of fledgling mortality, and revised the estimated number of fall immatures to between 369 and 471 birds—about 36% lower than the uncorrected estimate. Lower annual productivity of a static population implies higher annual survivorship of adults, yearlings, or both. Received 31 October 1985, accepted 17 October 1986.

THE known nesting range of Kirtland's Warbler (Dendroica kirtlandii) is restricted to 13 counties in the northern lower peninsula of Michigan. The first census of these birds in 1951 produced a total of 432 singing males (Mayfield 1953). A second census in 1961 found 502 males (Mayfield 1962), but by 1971 the population had declined to 201 singing males (Mayfield 1972). An average of 206 males for the next 10 years (Ryel 1981a) caused concern that the species might become extinct. The concentration of Kirtland's Warblers into a small number of breeding colonies (Probst 1986) provides a unique opportunity for comprehensive studies of population dynamics, habitat distribution, and mating system.

Research on the pairing success of male Kirtland's Warblers and other bird species is important for four reasons. First, the existence of unmated birds has implications for estimates of reproduction and other aspects of avian population dynamics. Second, researchers need an objective methodology for determining mating status of birds in densely vegetated habitats. In the case of Kirtland's Warbler, our methodology can be modified to estimate frequency of polygyny or even to ascertain the adult breeding sex ratio of an entire species. Third, the

If some males remain unpaired, population growth will be lower than expected from calculations that assume complete pairing. In a species such as Kirtland's Warbler, with a very small population and a highly transitory breeding habitat, unsuccessful pairing could derive from an unequal breeding sex ratio. Mayfield (1960), Ryel (1979), and Walkinshaw (1983) found unpaired males, but unmated birds were assumed to be insignificant to the population dynamics of the species.

We hypothesize that the pairing-success rate varies in areas of different habitat quality, and is lower in habitat that is of marginal quality. We investigated the pairing success of male Kirtland's Warblers in three classes of habitat: suitable, young marginal, and open marginal. We studied Kirtland's Warbler pairing success in three habitat types, and extrapolated our results to the known breeding population for a reanalysis of demography. More 'pecifically, we extended our results to the habitat distribution of the males within the known nesting range,

proportion of unmated males is information vital to understanding the relative quality of breeding habitats for Kirtland's Warbler and other birds. Last, pairing determinations will be necessary to test a dispersal model that estimates colonization probability and pairing success in habitat that is central, peripheral, or disjunct from the known breeding range.

¹ Present address: Department of Biology, University of California, Riverside, California 92521 USA.

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and revised published and unpublished estimates of annual fledgling production (e.g. Mayfield 1978, Walkinshaw 1983).

METHODS

We studied the pairing status of Kirtland's Warblers in three sites during June 1982 and 1983. Each study site was classified as either suitable or marginal habitat. Marginal habitat was divided further into open-marginal or young-marginal categories. Openmarginal habitats were unburned, poorly stocked areas (see below), and young-marginal habitats were adequately stocked areas that had been used by Kirtland's Warblers for less than 3 yr. This distinction between suitable and marginal habitat was derived from the affinity of these birds for areas with a high jack-pine (Pinus banksiana) density (Mayfield 1960, Walkinshaw 1983). The period of suitability of any jack-pine area for nesting by Kirtland's Warblers is limited. There is a pattern of a gradual increase in the use of an area, followed by more stable populations that then decline (Probst 1986). To account for this rapid temporal shift in habitat suitability, we classified study sites as suitable only if they had been used by birds for 3 yr or longer. We classified as open marginal all areas that were unburned, naturally regenerated (i.e. poorly stocked), with stem densities estimated to be less than 2,500/ha. Jack-pine stands that were unburned and naturally regenerated had only about one-third the tree density of fire-regenerated stands or areas planted for Kirtland's Warbler use (Probst MS). Wildfire or plantation areas with more than 2,500 stems/ha that had been used for less than 3 yr were classed as young marginal.

During 1982, we studied two Kirtland's Warbler management areas (KWMA) in Oscoda Co., Michigan. Mack Lake KWMA represented suitable habitat. McKinley KWMA represented open-marginal habitat. In 1982, we also observed one other open-marginal habitat and two young-marginal habitats. We revisited these three areas and examined three other young-marginal areas and four other open-marginal areas in 1983 (Table 1). By 1983, Rayburn had been occupied for 3 yr and was reclassified as suitable habitat for the second year of study. One area of young habitat we studied was Bald Hill Burn, a large (800 ha) site that regenerated from wildfire. Large wildfires commonly burn an area that varies with respect to topography and site quality. The mesic microsites are occupied first, and birds colonize the xeric sites with shorter trees in later years. Thus, large wildfire areas are conveniently divided by tree height and density into two or more subareas. The 1975 Bald Hill Burn was divided into the Bald Hill North subarea, with denser jack-pine regeneration, and the more open Bald Hill South subarea. This allowed us to compare the influence of tree density on pairing suc-

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cess in an area where distance from other Kirtland's Warbler colonies and other variables were similar.

We collected data mainly from open and young habitats because our data on pairing success in suitable habitats during 1982 agreed with previous experience that most, if not all, Kirtland's Warbler males there find mates (Walkinshaw 1983, Cuthbert unpubl. rept.). These previous assessments of pairing status were conducted primarily in habitat we would classify as suitable. During 1982 and 1983 we classified 27 males in young-marginal habitat, 24 in openmarginal habitat, and 19 in suitable habitat.

Pairing determinations.-Males were classified as mated if they were found with a female or fledglings. A female or fledgling was not always seen with a male during short observation periods, so we established criteria for duration of observation for pairing determinations. To determine the amount of time needed for observation before we could conclude that a male was not mated, we plotted the percentage of males classified as paired against observation time. These data initially were obtained from N. Cuthbert (unpubl. rept.). Data from the first year of our study were used to verify and improve the determination in the second year of the study (see below). As expected, the proportion of males classified as paired increased as observation time increased, but this percentage approached an asymptote below 100% at longer observation times (see Results). The sharp inflection of the curves strongly suggests that males were observed long enough for pairing determinations that compare habitats reliably.

Analysis of the 1981 data (Cuthbert unpubl. rept.) showed that mates of 89% of the Kirtland's Warbler males studied could be found in 150 min of observation per bird. Additional observation time resulted in almost no increase in the percentage of birds classified as paired. Consequently, in 1982 we assessed pairing status by observing individual males for periods of up to 150 min or until the presence of a mate was confirmed. If a bird was seen with a female or fledgling, it was classified as paired, and observation was terminated. If a bird was silent or unseen for 20 min, we stopped accruing observation time and observations were renewed later in the day or later in the season. Furthermore, the habitats we studied were more open than most of the areas Cuthbert studied, which should have made the detection of mates and fledglings easier.

The detection of pairing success may vary in different habitats (e.g. densely vegetated vs. open habitats). We developed a measure of observability based on track time for the second study year. Track time was defined as the time for which an individual bird was observed without losing visual or audible contact. By comparing the amount of track time with total observation time, we estimated observability for a particular study area or habitat type. We compared pairing success in different habitat types by estab-

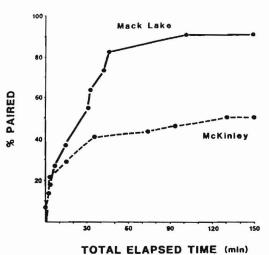


Fig. 1. The percentage of Kirtland's Warblers determined to be mated vs. total elapsed time for 1982. The curves level off after about 90 min total search time.

lishing the criterion for the required amount of observation in terms of track time alone. In 1982 all paired birds were classified as paired in less than 75 min of track time (see Results). Accordingly, in 1983 we refined our pairing determinations by observing birds for up to 90 min of track time.

Pairing determinations were made for males that were present during 5-30 June 1982, and 18-28 June 1983. Males that died, deserted, or relocated (presumably because of failure to attract or hold a mate) were excluded. If most of these males failed to attract a female at a new location, pairing success was overestimated. Because some desertions of territory were offset by immigration of new males, we assumed that few of the missing males died (see Nolan 1978). The annual mortality rate of adult male Kirtland's Warblers is about 25% (Probst 1986); hence, the mortality rate during the month of June should be no more than 2%. We assumed that seasonal survivorship is highest during the breeding season. The principal

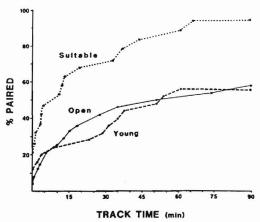


Fig. 2. The cumulative percentage of males classified as mated in 3 habitat classes in 1982 and 1983. Track time is that part of observation time for which the males actually were followed. The curves level off at about 60 min track time.

reason for low pairing-success estimates presumably was that birds we classified as unmated became paired after our observation period ended. We also may have missed a few females because of insufficient observation time.

Finally, data on male pairing success were extrapolated to the known breeding population in 1982 and 1983 (Ryel 1982, 1983) by classifying occupied habitat as marginal or suitable using the criteria described above. The data on pairing success were combined with other published demographic data to estimate upper and lower bounds of annual fledgling production.

Statistical analysis.—We used Chi-square tests with a correction for continuity to compare numbers of paired and unpaired birds in different habitat types. The 95% confidence interval for pairing success in all marginal habitat combined was calculated using a normal approximation to a binomial distribution with a correction for continuity (Snedecor and Cochran 1967). Sample sizes were too small in suitable, young,

TABLE 1. Relative observability of male Kirtland's Warblers by habitat class.

		l time elapsed• nin)	Average tr (mi		Average ratio track/elapsed	
Habitat class	All males (n)	Paired males (n)	All males	Paired males	All males	Paired males
Suitable habitat	49 (19)	41 (18)	24	24	0.62	0.61
Young marginal	90 (25)	54 (14)	48	31	0.68	0.67
Open marginal	96 (24)	59 (14)	53	25	0.59	0.59
All habitats	80 (68)	50 (46)	43	26	0.62	0.62

Total search time for female.

Actual observation time for Kirtland's Warbler male

and open habitats to use the normal approximation for pairing success, so the 95% binomial confidence intervals were used for those three habitat classes (Blyth and Still 1983).

RESULTS

We were able to classify most mated males within 90 min elapsed time (Fig. 1) or 60 min track time (Fig. 2). The percentage of track time relative to observation time (Table 1) provided a measure of the observability in each habitat.

In suitable habitat (Mack Lake 1982 and Rayburn 1983), 18 of 19 males were paired (Tables 2 and 3), confirming Cuthbert's previous conclusions about pairing success in most habitats for this species. In open-marginal habitat, however, only 14 of 24 males were paired, and in young-marginal habitat only 16 of 27 were paired. The frequency of paired males was significantly different between suitable habitat and all marginal habitats combined ($\chi^2 = 6.70$, df = 1, P < 0.01). The frequency of paired males did not differ significantly between young-marginal and open-marginal habitat ($\chi^2 = 0.086$, df = 1, P > 0.75). Moreover, habitat that was less suitable for female Kirtland's Warblers was not

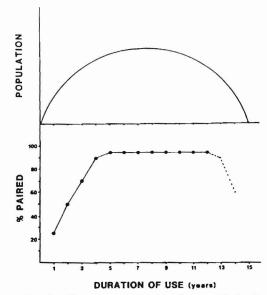


Fig. 3. Hypothetical curves of male Kirtland's Warbler population (top) and percentage of paired males for larger colonies of suitable habitat (bottom). The decrease in pairing success in older habitat is unconfirmed (dashed line) because we did not obtain data in that age of habitat.

TABLE 2. Habitat classification and pairing status of male Kirtland's Warblers.

	Year	Total males	Absent/ relocated*	Un- paired	Paired	Proportion paired
Suitable habitat	-					
Mack Lake (S.3)	1982	14	3+	1	10	10/11
Rayburn	1983	8	0	0	8	8/8
All suitable habitat		22	3+	1	18	18/19 (95%)
Marginal habitat						
Young						
Rayburn	1982	6	1	2	3	3/5
Bald Hill NW	1983	6	0	1	5	5/6
Bald Hill SE	1983	12	0	7	5	5/12
Briggs Road	1983	2	0	1	1	1/2
Lovells (S.6)	1982 and 1983	2	0	0	2	2/2
All young habitat		28	1	11	16	16/27 (59%)
Open						
McKinley	1982	17-21	3-7	7	7	7/14
Parmalee	1982 and 1983	2	0	0	2	2/2
Briggs Road	1983	1	0	0	1	1/1
Meridian	1983	4	1	1	2	2/3
Canoe	1983	2	0	1	1	1/2
Manistee	1983	2	0	1	1	1/2
All open habitat		28-32	4-8	10	14	14/24 (58%)
All marginal habitat						30/51 (59%)

^{*} Number of singing males that were absent after initial censuses; presumed to have relocated.

TABLE 3. 95% confidence intervals (CI) for pairing success in 4 habitats.

		P .	
	Paired/total	Percent- age paired	95% CI•
Suitable	(18/19)	95	0.75-1.00
Young	(16/27)	59	0.40-0.77
Open	(14/24)	58	0.37-0.77
All marginal	(30/51)	59	0.44 - 0.72

^{*}Intervals for $n \le 30$ are from table 2 in Blyth and Still (1983); for n > 30 (all marginal habitat) the normal approximation with continuity correlation was obtained from the same source.

restricted to the more open, unburned stands. The results from Rayburn 1982 and Bald Hill suggest that unmated males are more likely to occur in stands of wildfire origin if the area is small (Rayburn) or young (Bald Hill and Rayburn) or relatively isolated (Rollways). The data from recently occupied areas (Rollways, Lovells, Rayburn, Bald Hill) indicate that over 40% of the males in such areas were unpaired. The importance of tree density to pairing success also was seen within the Bald Hill burn, where 5 of 6 singing males were mated at the denser northern region, but only 5 of 12 were mated at the more open southern site. Less than 60% of the singing males in young- and open-marginal habitat were paired. We have no data to support or refute the hypothesis that males in declining habitat have a lower probability of finding mates (Fig. 3), but previous observations (Mayfield 1960) support this idea.

Male distribution among habitats.—We estimated that about 160 and 147 males were found in suitable habitat in 1982 and 1983, respectively, and about 47 and 68 males (Table 4) were found in breeding areas that were either smaller, younger, or more open (i.e. marginal habitat). We extrapolated the pairing success results from suitable habitat (95% paired) to 73% of the males, and applied the data from the marginal habitat (59% paired) to the remaining 27% of the males. This yielded an estimated average for 1982 and 1983 of 292 mated males out of 307 males in suitable habitat, and 68 mated males out of 115 males in marginal habitat. Eighty-five percent of the 422 males were paired in 1982 and 1983 combined.

The results of male pairing success were combined with other demographic factors to predict the annual reproduction of the known Kirtland's Warbler population. This analysis was facilitated by the relatively stable popula-

TABLE 4. Kirtland's Warbler males in marginal* vs. suitable habitat, 1971-1983.

	Total	No. m		
	no. males	no. Marginal Suita		
1971	201	13	188	94
1972	200	14	186	93
1973	216	45	171	79
1974	167	49	118	71
1975	179	32	147	82
1976	200	48	152	76
1977	218	48	170	78
1978	196	29	167	85
1979	210	29	181	86
1980	242	2 5	217	90
1981	232	32	200	86
1982	207	47	160	77
1983	215	68	147	68
Average	206	36.8	169.5	82

Habitat that is younger, older, or poorly stocked with trees relative to suitable habitat.

tion between 1976 and 1985. To examine the influence of reduced pairing success relative to other demographic factors, we estimated both low and high values of productivity and recruitment (Table 5). The first example assumes an operational sex ratio (OSR; Emlen and Oring 1977) of 0.90 and the second an OSR of 0.80 females per male. Fledgling production averages 2.6 fledglings per nest (Kelly and De-Capita 1982) or 3.1 fledglings per pair, which includes renestings (Walkinshaw 1983). Fledgling survivorship to independence for passerine birds ranges from 60 to 80% (e.g. Hann 1937, Walkinshaw and Faust 1975, Nolan 1978, data from Walkinshaw 1983). We used 75% survival of adults based on a 60% annual return of banded males (Mayfield 1960) plus an estimate of 15% relocations between years (Probst 1986). If we assume that our estimate of pairing success is not strongly offset by polygynous matings or late pairing by unmated males, then decreased pairing success combined with fledgling mortality reduces the estimate of fall immature Kirtland's Warblers to between 369 and 471 birds (Table 5). Uncorrected estimates ranged from 600 to 700 (Ryel 1981b, Walkinshaw 1983, Probst 1986). The number of new recruits each spring was calculated by assuming a stable population. Our data and assumptions indicated a 21-26% spring return rate of fall immature

males) males)

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DISCUSSION

The principal cause for the decline of Kirtland's Warbler between 1961 and 1971 was hypothesized to be nest parasitism by the Brownheaded Cowbird (Molothrus ater). In response, the U.S. Fish and Wildlife Service initiated an intensive cowbird trapping program in 1972. This reduced the rate of nest parasitism by cowbirds from 50-70% of the nests before the initiation of trapping (Mayfield 1960, Walkinshaw and Faust 1975) to an average of 3.4% from 1972 to 1982 (Kelly and DeCapita 1982). The number of fledglings per nest increased from 0.81 to 2.76 during the same period (Kelly and DeCapita 1982).

During 1971–1983 the Kirtland's Warbler population fluctuated between 167 and 242 singing males ($\bar{x} = 206$; Table 4). Thus, cowbird control did not promote a substantial recovery of the species. A variety of explanations for this has been offered. Ryel (1981b) suggested that the population may be limited on its wintering grounds. Probst (1986) suggested that low pairing success (ability to attract and hold mates), fledgling mortality, and yearling dispersal may account for a static situation or a slow recovery of the population.

The results on pairing success of Kirtland's Warbler may be important for revising past productivity estimates. In the period 1973-1977 an average of 23% of male Kirtland's Warblers were in either declining breeding areas or young, developing colonies (Table 4). Many of these birds may not have paired successfully, which may have contributed to the slow recovery of the population. During the years 1978-1981, 87% of the males were in larger colonies of suitable habitat; almost all of them presumably paired successfully. In 1983 the proportion of males in suitable habitat was only 68%. The trend toward a high proportion of males in marginal habitat should continue from 1984 to 1989, because most males probably will be in young or declining habitat in those years. We have not related our 1982 and 1983 estimates of pairing success to the proportion of males in marginal habitat in other years, because the distribution of females may have changed under different habitat conditions in different years. In addition, our estimate of males in marginal habitat in 1982 and 1983 may be conservative because we excluded those males that were in old marginal habitat.

BLE 5. Estimates of Kirtland's Warbler annual productivity and recruitment (1982 and 1983 average).

Adult	survivorship ^b	(402 × 0.75) (382 × 0.75)
	+	++
	[Subtotal]	[=100] [=95]
Calculated survivorship of imma-	tures	0.21 0.26
	×	××
	[Subtotal]	[=471] [=369]
Fledgling survivor-	ship	0.804)
	×	××
Fledg- lings/	pair.	3.1
	×	××
No. of	females	(190° (170°
	Estimate	High productivity Low productivity

Walkinshaw 1983.

60% return rate plus estimate of 15% relocations (Probst 1986).

"High estimate for fledgling survival (data from Walkinshaw 1983: table 39).

• 0.80 operational sex ratio (assumes that polygyny is rare and that pairing success is reduced in old, declining habitat)

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Mating system and habitat. - Polygynous mating systems are more likely to evolve in species that have minimal male parental care and in habitats where the vegetation has little vertical complexity, such as marshes or grasslands (Verner and Willson 1966). Verner and Willson argued that two-dimensional habitats are characterized by a more patchy distribution of resource productivity, and male territories of more varied quality, than habitats with greater vertical structure. Nevertheless, polygyny could evolve in more uniform habitats if males divide resources unequally (Vehrencamp and Bradbury 1984). Under such circumstances, it could be more advantageous for a female to pair with a mated male in a highly suitable territory than to choose an unmated male in an unsuitable or marginal one. Thus, polygyny could evolve in a species without a surplus of females (Verner 1964, Orians 1969; but see below). Birds with polygynous mating systems may occupy habitats with unmated, monogamous, and polygynous males present in the same stand. In some cases, the mating status of the males has been correlated with habitat variables (e.g. Verner 1964, Willson 1966, Pleszczynska 1978, Carey and Nolan 1979, Zimmerman 1982).

There are 14 published incidents of polygyny reported for Kirtland's Warbler (Mayfield 1960, Radabaugh 1972, Walkinshaw 1983). Radabaugh (1972) estimated a maximum of 12% (9/72) of the males in one subsample had two mates (a larger sample of male Kirtland's Warbler may not have been observed long enough to confirm all possible cases of polygyny).

Kirtland's Warblers differ from other examples of the evolution of polygyny in at least two respects. First, males are actively involved in nesting at all stages of the cycle. They help build the nest, feed the female during incubation, care for nestlings, and help feed fledglings (Mayfield 1960, Walkinshaw 1983). Thus, Kirtland's Warbler should have an unusually high polygyny threshold (Verner and Willson 1966, Orians 1969) for selection to favor sharing of male parental care relative to pairing with unmated males. For example, if male Seaside Sparrows (Ammodramus maritimus) are removed experimentally, reproduction suffers (Greenlaw and Post 1985), so male assistance can be significant to nesting success in species where males help regularly. Second, the jackpine habitat has more vegetative complexity vertically than marshes or grasslands, but less

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than forests. Nevertheless, the patchy distribution of trees in the Kirtland's Warbler shrubland habitat has potential for male territories of unequal quality, so it still would be advantageous for a female to pair with a mated male if her reproductive success could be higher than it would be on a poorer territory with an unmated male.

Number of breeding females and annual productivity. - Although male pairing success is a useful criterion for ranking habitat quality, reproductive estimates must be made from the number of breeding females. Polygynous matings compensate for unpaired males to an unknown degree. Similarly, successive monogamy could add to the number of females estimated from the number of males alone. The possible alternatives that would explain the existence of unmated males in marginal habitat have consequences, however, that lower the production of fledglings relative to a habitat situation where almost all pairs are monogamous in suitable habitat: (1) successive monogamy or late pairing, (2) polygynous mating, (3) unequal tertiary sex ratio, or (4) females unmated for an entire breeding season.

The Kirtland's Warbler mating system may vary with changes in habitat quantity and distribution. When suitable habitat is relatively abundant, monogamy should be more prevalent. Polygyny should become more widespread as suitable habitat becomes scarce or dispersed, a situation that probably occurred in the 1960's and early 1970's. At present, habitat is relatively scarce and scattered. This situation should favor a mix of unmated, monogamous, and polygynous males. Similar habitat conditions are occurring now, and by 1989 5 or 6 major breeding areas should have negligible populations. Most Kirtland's Warblers may be concentrated in two major wildfire areas by that time. Polygyny may become more prevalent, and scattered males may occupy a number of smaller stands where their pairing success is low. If the population is to remain constant, these declines must be offset by large numbers of breeding females in two major wildfire areas that should comprise a large part of suitable Kirtland's Warbler habitat in the future. Thus, the Kirtland's Warbler mating system may result from the species' fragmented and transitory habitat within a limited breeding range. The proportion of unmated and polygynous males may fluctuate with habitat conditions through time.

. El consideration pages

We recommended that Kirtland's Warbler habitat managers raise the tree-stocking level to 2,500-3,800 stems/ha in situations where this is not already being done. This suggestion, accepted by the USDA Forest Service, should maximize pairing success in areas managed for Kirtland's Warbler. Previously, Probst (1985) also suggested that stand rotations within Kirtland's Warbler Management Areas should be planned for more temporal overlap to increase Kirtland's Warbler colonization success and male pairing success during the early period of Kirtland's Warbler occupancy of a stand.

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A Review of Factors Limiting the Kirtland's Warbler on its Breeding Grounds

JOHN R. PROBST

North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, Minnesota 55108

ABSTRACT: Previous discussion about factors limiting the population of Kirtland's warbler has centered about nesting success and adult mortality in winter. I present a review and synthesis of published and unpublished reports on Kirtland's warbler demography which suggests that this species may also be regulated by habitat maturation and fragmentation, pairing success, fledgling mortality and breeding dispersal.

Only 85% of male Kirtland's warblers may pair successfully, though this low pairing success is offset somewhat by polygyny. Estimates of fledgling mortality (30%) and pairing success are combined with published data on Kirtland's warbler productivity (3.1 young/pair) and adult survivorship (75%) to calculate annual recruitment

of yearlings (28%) assuming a static population. *

Kirtland's warblers are concentrated into a few large breeding areas, each of which provides suitable habitat for only 10-14 years. The growth and decline of these "colonies" is described from a comprehensive, 13-year population count. For the short term, regenerating habitat may not be sufficient to replace currently occupied maturing stands, and a habitat shortfall is predicted for 1986-1987.

80 x 115 Km Introduction

The known nesting range of the Kirtland's warbler (*Dendroica kirtlandii*) is restricted to an area ca. 20 by 160 km in northern Lower Michigan. All nests have been found within 13 counties. But migrants and stray summer males have been collected and observed across a much broader range from Missouri to the SW, Minnesota to the NW and Virginia to the E (Tilghman, 1979).

The quantity of suitable breeding habitat available to the Kirtland's warbler (KW) has decreased in recent decades (Ryel, 1981b). Typically, the species occupies dense 1.7 to 5.0-m-tall jack pine (*Pinus banksiana*) stands of wildfire origin. Plantations are also used, including a few red pine (*P. resinosa*) stands, but logged, unburned jack pine stands stocked by natural regeneration from nonserotinous cones are usually not dense

enough for breeding warblers.

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In 1951, Harold Mayfield organized the first census of the entire known population of the species (Mayfield, 1953). This census counted 432 males. The second census in 1961 discovered 502 male Kirtland's warblers (Mayfield, 1962). However, the third count taken in 1971 showed a 60% decrease to 201 males (Mayfield, 1972). The principal reason for this decline appeared to be nest parasitism by the brown-headed cowbird (Molothrus ater). Mayfield (1960) estimated the parasitism rate to be 55% and Walkinshaw and Faust (1974) estimated it to be 69%. They found that less than one Kirtland's warbler fledged per nest.

In response to the dramatic population decline from 1961 to 1971, a Kirtland's warbler Recovery Team was appointed under authority of the Endangered Species Act of 1973. This team instituted the following steps to help the Kirtland's warbler: (a) annual population census: (b) cowbird control; (c) closure of breeding areas during the nesting season, and (d) an expanded habitat management program. I will address four major topics in this paper: (1) a synthesis of published and unpublished demographic data that postulates lower reproductive potential and higher rates of breeding dispersal and fledgling mortality for Kirtland's warblers than have been assumed previously; (2) the present concentration of Kirtland's warblers into only a few breeding areas, and the growth and decline of such colonies; (3) the relation between habitat quantity, decline of individual nesting areas and the total Kirtland's warbler population; (4) an overview

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evaluation of the role of habitat limitation in Kirtland's warbler population regulation and the probable future influence of habitat quantity on population size of the species.

I used the annual census results (Mayfield, 1953, 1962, 1972, 1973a and b, 1975; Ryel, 1976a and b, 1979a, 1980a and b, 1981a, 1982, 1983; Burgoyne and Ryel, 1978) in several of the analyses that follow. Population trends in individual breeding areas were compiled from unpublished reports on file with the Michigan Department of Natural Resources. I prepared an overview of Kirtland's warbler demography from published material, a literature review of related species, and unpublished data.

Estimates of winter survival of 1st-year birds were inferred from other demographic data and by assuming a static population. Thus, I calculated annual recruitment from

estimates of annual productivity, adult mortality and fledgling mortality.

HISTORICAL TRENDS

The Kirtland's warbler probably was most abundant during the logging of the virgin pine forests of Michigan (Mayfield, 1960). However, J. Weinrich (pers. comm.) has suggested it also may have been more numerous ca. 500 years ago when the Great Lakes pine forests were formed. Historically, the extent of wildfire and consequently the area of Kirtland's warbler habitat has fluctuated greatly in northern Lower Michigan. Because reproductive potential is inadequate to take advantage of a temporary abundance of habitat or food resources, the Kirtland's warbler population has likely lagged behind the quantity of habitat available. Temporary shortages of suitable wildfire habitat may have resulted in population decline because excess birds were forced into marginal habitat where reproductive success suffered. This habitat shortage probably existed at various times prior to the pine logging era when extensive areas were overmature. During the last 50 years, control of forest fires has reduced the availability of wildfire acreage.

The brown-headed cowbird was not common in Michigan until forests were cleared by early human colonists (Mayfield, 1960, 1975). As the forests were cleared, the population of cowbirds increased and so did the frequency of cowbird nest parasitism. The rate of cowbird parasitism increased from an estimated 40% before 1955 (Mayfield, 1960) to as much as 75% by the late 1960s (Walkinshaw, 1972). However, the cowbird parasitism rate varied greatly from year to year. The Kirtland's warbler population declined about 60% from 1961-1971. Ryel (1981b) reviewed the possible reasons for this decline and concluded that cowbird parasitism was the most serious limiting factor during the 1960s. Because cowbird parasitism depressed reproductive success, the Kirtland's warbler probably has not been able to fully occupy available habitat in recent decades. This may have confounded attempts to define suitable habitat for the species (Mayfield, 1953, 1960).

The Kirtland's warbler may also be limited outside of the breeding grounds. Trautman (1979) suggested that hurricanes in the Bahamas wintering grounds may have decimated birds early in this century, but we have no evidence that hurricanes damaged this species in recent decades. Winter survival may be influenced by drought on the

wintering grounds (Ryel, 1981b).

Although numerous specimens and sight records of the Kirtland's warbler exist for the Great Lakes region in the past century, there are no nesting records outside of northern Lower Michigan. However, the records from Canada, Wisconsin, Minnesota and Michigan's Upper Peninsula suggest a more extensive nesting range in the past, as Van Tyne believed (Mayfield, 1960). I speculate that the Kirtland's warbler disperses broadly because it occupies habitat that is only temporarily suitable. It is possible that the Kirtland's warbler could have formed temporary colonies in areas outside of the known nesting range during the recent past. However, these populations probably did not persist because areas outside Michigan were not large enough to maintain enough suitably aged jack pine habitat.

The area currently used by Kirtland's warblers is much smaller than that used during the past 3 decades (Mayfield, 1960, 1983; Walkinshaw, 1983). Mayfield and Walkinshaw illustrated the nesting distribution of Kirtland's warblers by mapping the townships in which birds were found. The concentration of Kirtland's warblers into a small central part of the range is more apparent than previous maps would suggest if we plot the location of individual colonies and separate them into three abundance classes (Fig. 1). Although the most peripheral areas are presently unoccupied, this is probably related to the current distribution of habitat rather than to Kirtland's warbler population biology. For example, Mayfield (1953) reported that Kirtland's warblers were in Montmorency County at the northern extreme of the nesting range, but absent in Ogemaw County to the S. By 1961 the Canada Creek wildfire in Montmorency County was too old for Kirtland's warblers, and they were not found in the 1961 census (Mayfield, 1962). However, new burns had occurred in Ogemaw County during the same period, and Kirtland's warblers have become numerous in Ogemaw County since 1965. A few have appeared to the E in Iosco County in small clear-cut stands that have been planted to jack pine or red pine. Two were found in Montmorency County in 1983 and could increase substantially there in the 1990s when a 1981 wildfire area and managed habitat both become old enough.

RECENT TERMS

Between the 1961 census and the 1971 census the number of singing Kirtland's warbler males fell from 502 to 201. This decline stimulated corrective action. Cowbird trap-

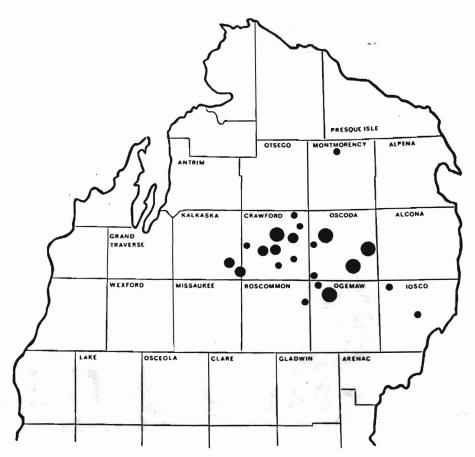


Fig. 1.—1983 Distribution of Kirtland's warbler breeding areas in three population size classes: • <6 Kirtland's warbler males; • = 6-18 Kirtland's warbler males; • >18 Kirtland's warbler males

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ping began at several breeding areas in 1972 and expanded to all Kirtland's warbler areas in 1973 under the administration of the U.S. Department of Interior Fish and Wildlife Service. As a result, cowbird nest parasitism was less than 5% from 1972-1974 (Walkinshaw and Faust, 1975), and averaged 3.4% from 1972-1981. The number of Kirtland's warbler fledglings produced per nest increased from 0.81-2.76 during the same period (Kelly and DeCapita, 1982). The production per pair per season is now estimated to be 3.1 (Walkinshaw, 1983). Predation on about one-third of the nests is the only remaining major cause of nest failure.

In the past decade, the Kirtland's warbler population has increased, but not nearly as much as first projected from higher nest success (Walkinshaw, 1972; Burgoyne and Ryel, 1978; Mayfield, 1978, 1983). Indeed, the population as measured by the annual census has declined in some years, but is most noteworthy for its remarkable stability. However, the average for the years 1976-1982 (219) is 13% higher than that for 1971-1976 (194), and the 1981 census of 232 male Kirtland's warblers shows a slight gain over the 1971 count of 201. Although the Kirtland's warbler population continued to decline after cowbird control was begun, 1974 may represent the low point from previous decades of cowbird pressure.

During the past decade, most Kirtland's warblers aggregated in a few discrete locations or clusters, termed "colonies" (Fig. 1). Burgoyne and Ryel (1978) noted that 75% of the population was in the five largest colonies. This distribution was a slight improvement over 1971 when 53% were in just two colonies and 93% were in only seven areas (Fig. 2). Such concentration is precarious to a species because the population is then vulnerable to a serious decline from events occurring in any single major nesting area.

Population trends within individual breeding areas indicate that major colonies usually increase rapidly from 3-5 years, level off for 4-7 years, and decline rapidly for 3-5 years (Fig. 3). Thus, the useful life of a stand for Kirtland's warblers is commonly from 10-14 years, with high populations for only about 7-8 years. Although Kirtland's warblers are known to shift from one colony to another, most individuals are site-tenacious (Berger and Radabaugh, 1968). Yearlings are highly unlikely to return to their natal colony, especially in mature habitat (Walkinshaw, 1983), so the decline in a single colony is almost certainly related to a failure to replace older birds with new recruits (Ryel, 1979b; Walkinshaw, 1983). The failure to colonize new areas could be due to a scarcity of potential young recruits, a shortage of suitable habitat or the geographical distribution of that habitat.

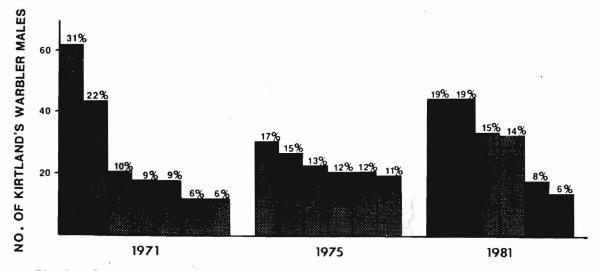


Fig. 2.—Concentration of Kirtland's warblers into major breeding colonies for 1971, 1975 and 1981. Each bar represents a discrete colony, and the percentage of the total population is above each bar

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This pattern of population buildup and decline in single colonies suggests that the annual census could be interpreted by summing the population trends from the individual colonies. Because any stand can support Kirtland's warblers only for a short time, an overall population increase can be maintained only through the formation of new colonies. Therefore, the annual census may reflect the difference between the amount of

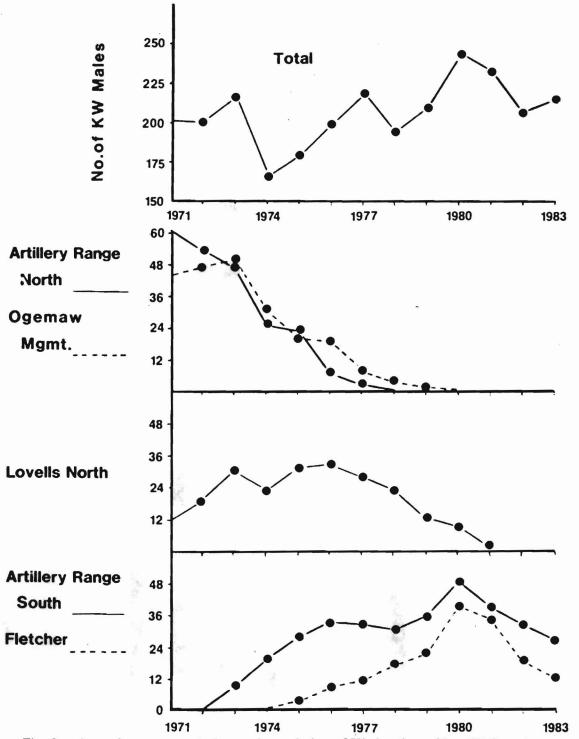


Fig. 3.—Annual census trends for total population of Kirtland's warbler (KW) males (top) and for five selected major breeding areas

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declining and the amount of developing, or optimal, habitat.

To test the hypothesis that overall population trends are not reflected in every breeding area, I combined census results of contiguous areas that had a similar date of origin. The annual population changes of these separate breeding areas were totalled for all areas showing gains and for all those showing losses (Fig. 4). The results confirm that there are partially compensating trends among individual colonies. Most losses occurred in old, declining habitat, and almost all gains were in young habitat. The losses of birds in declining habitat are somewhat trivial and circular, and follow from the definition of declining habitat. However, the results do suggest that younger birds may have an innate tendency to disperse, and that such dispersal tendencies may not be related to immediate population pressures on their natal area. Otherwise, young birds would return preferentially to the older colonies during years of general population decline, rather than disperse to new colonies where their pairing success would be lower (Table 1).

Synchronous-stand ages among breeding areas are important to Kirtland's warbler population dynamics. Large negative imbalances between total gains and losses in individual areas occurred with major declines in large colonies that were not offset by increases in younger colonies (Fig. 5). Conversely, the general increase in population from 1975-1980 coincided with the buildup of five major colonies that supported about three-fourths of the birds from 1975-1983. This suggests that the stationary warbler population during the last decade may be related to a rough balance between old habitat being

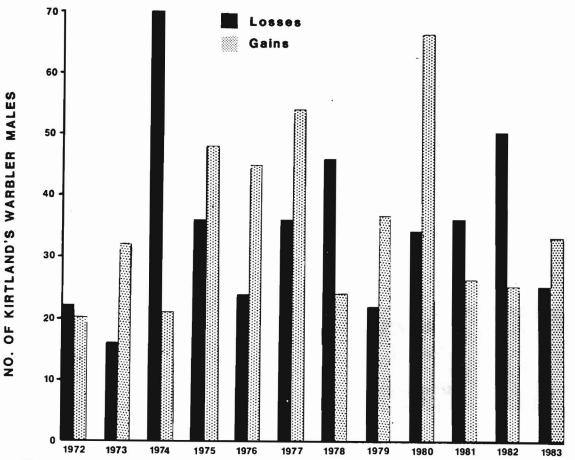


Fig. 4.—Aggregate population changes in a given year relative to the previous year combined for all breeding areas showing losses (left bar) and gains (right bar). The total annual population change for a particular year is equal to the difference between the two bars in a pair (see text)

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abandoned and new habitat being colonized, despite successful cowbird control and excellent nesting success.

REPRODUCTIVE POTENTIAL

Below I suggest that the reproductive potential of the Kirtland's warbler may be lower than previously assumed (Mayfield, 1975, 1978, 1983; Ryel, 1981b; Walkinshaw, 1983), and that the survival rates for adults and immatures off the breeding grounds

may be higher.

Walkinshaw (1983) estimated that the reproductive rate of the Kirtland's warbler is. 2.76 fledglings per nest and that the production per pair (including renesting) is 3.11: The number of fledglings produced by each pair could be higher because of double broods (Radabaugh, 1972a), but Walkinshaw found that almost none of the young from second broods return in the spring. Thus, I discount the production of fledglings from second broods.] Ryel (1981b) and Walkinshaw (1983) extrapolated these reproductive rates to the known population of males in the Lower Michigan breeding grounds. However, these rates could be lower if a significant number of Kirtland's warbler males are unpaired. Mayfield (1962), Ryel (1979b) and Walkinshaw (1983) described one or more. males that appeared to be unpaired. Cuthbert recorded the time necessary to locate mates for male Kirtland's warblers in a number of breeding areas and concluded that most males were paired, at least in suitable habitat. I propose that pairing success could be lower in habitat that is of marginal quality for Kirtland's warblers in respect to stand age, tree density or location relative to the known breeding range. Probst and Hayes found more unmated males in habitat that was too young or too open to be classified as suitable (Table 1). We estimated that at least 15% of the males may be unpaired and most unmated males are in young, or more open, habitat. However, we have insufficient data to reach conclusions about pairing success in older, declining habitat or areas peripheral to the breeding range. Although the estimate of 15% unmated males is probably conservative, it is offset to an unknown degree by polygynous matings (Radabaugh, 1982b). I do not assume that all unmated males are balanced by polygynous matings because the sex ratio could be unequal (Orians, 1969; Murray, 1984) and . skewed toward males:

MORTALITY

Fledglings. — Postfledging mortality reduces the number of young birds that survive until autumn migration. Walkinshaw and Faust (1975) were able to find only 67% of the young fledglings after but a few may have escaped detection. Nolan (1978) estimated that fledgling mortality of the closely related prairie warbler was 18%. The combined effect of reduced pairing success (about 85%) and postfledging mortality (18-35%) reduces the number of young available for autumn migration to less than 400 from the 600-800 assumed in the past (see below).

Winter mortality. — The major loss of both adult and young birds probably occurs during migration and winter. Although a long-term trend of winter habitat degradation could be occurring, Mayfield (1975) argued that winter habitat has not been significantly altered. Ryel (1981b) developed a model that strongly suggests that recent

TABLE 1. - Pairing success of male Kirtland's warblers

Habitat type	Paired (No.)	Total (No.)	% Paired
Suitable	18	19	95
All marginal	30	51	59
Young marginal	16	27	59
Open marginal	14	24	58

ESCHARACIONES CONTRA

Kirtland's warbler population fluctuations may be related to winter precipitation in the Bahamas. Mayfield (1960) has estimated 60% annual survival of Kirtland's warbler adults, based on returns of banded birds. This estimate is minimal because it assumes that all adults surviving from year to year return to the original banding area (May-

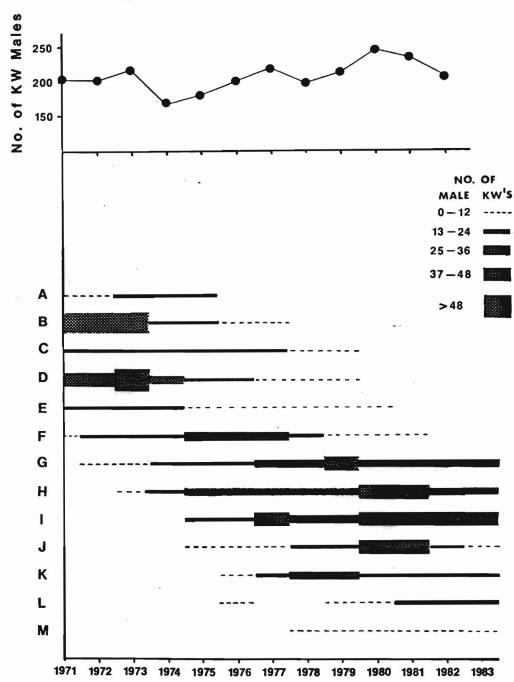


Fig. 5.—Overlap and synchrony among major breeding areas. Increases and decreases in total population (top) are related to buildup and declines of individual colonies, especially when major colonies are synchronous.

A. Luzerne; B. Artillery South; C. Mack Red Pine; D. Ogemaw Management; E. Pere Cheney; F. Lovells North; G. Muskrat Lake; H. Artillery North; I. Damon Burn; J. Fletcher Burn; K. Mack Lake Management; L. McKinley; M. Lovells South

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field, 1983). Annual survival estimates can be revised by adding a percentage equal to the proportion of adults known to have relocated between or within breeding seasons. Unfortunately, an accurate estimate of between-season relocation requires checking for marked birds at all known breeding areas. Because all breeding areas have not been checked for relocating banded males, we can only apply minimal corrections to the mortality rates based on assumptions of site fidelity. Of 39 adult males that Walkinshaw (1983) found in subsequent years, five had relocated to another breeding area (one male switched sites twice) and I found another of his color-banded males 14 km away as a breeding adult. The relocation of six out of 40 male returns is evidence that another 15% of the males may actually have survived during previous survivorship estimates, but more data are needed to determine what proportion of the adult birds change breeding sites.

FATE OF SPRING RETURNS

Floating population. —A floating population of nonsinging males could lower annual population counts and decrease survival estimates, especially if the proportion of floaters increased with higher population levels and/or less available habitat. The presence of uncounted birds would help explain the stationary Kirtland's warbler annual censuses. Presumed "floaters" have been observed for the Kirtland's warbler (Mayfield, 1962; Orr, pers. comm.) including males presumed to be floaters on territories in colonies where most birds were color-marked (Walkinshaw, 1983). In a study of the prairie warbler, Nolan (1978) found no evidence of a floating surplus of males, but did find that territorial males extensively explored surrounding habitat. Such behavior could be an attempt to attract additional mates because prairie warblers, like Kirtland's warblers, can be polygynous (Radabaugh, 1972b). At present it is not clear whether there is a distinction between floater male Kirtland's warblers and unmated territorial males. It seems most likely that floater males are exploring from nearby territories, relocating from remote areas, or a combination of both. It also is not known whether floaters or unmated males result from an uneven sex ratio (see above) skewed toward males. Although lower annual return rates of female Kirtland's warblers relative to males have been documented (Mayfield, 1960, Berger and Radabaugh, 1968; Walkinshaw, 1983), much or all of this difference could be due to the lower detectability of females in the field.

Dispersal. — Some Kirtland's warblers may not have been included in the census because they dispersed to areas outside the traditional nesting grounds, including areas outside Lower Michigan (Mayfield, 1983). This view is supported by the fact that single birds or groups have been found in marginal habitat, often many miles from the nearest colony. In addition, from 1977-1983, nine males were found during the breeding season outside the nesting range—four in Wisconsin, two in Ontario, one in Quebec (Ryel, 1981a) and two in Michigan's Upper Peninsula (Probst, in press). However, some of these could have been the same bird in different years. In the past, specimens were also taken outside the presumed migration route: one in Ontario, three in Illinois, one in Missouri, one in Minnesota and one in Virginia (Walkinshaw, 1983). Harrington (1939) described a loose cluster of Kirtland's warbler males found in Ontario in 1916 that could have been a colony, but no nests were found. Tilghman (1979) also reported nine verified sight records of migrants in Wisconsin during the past 125 years.

Any species that occupies ephemeral habitat should have extensive dispersal tendencies. This seems true of the Kirtland's warbler because it has regularly found appropriate habitat in widely scattered localities in northern lower Michigan and has been found repeatedly in adjoining states and Canada. It seems unlikely that searchers have found many of the birds that dispersed to remote locations, because isolated males may sing weakly or not at all. Also the chance of discovering birds over a vast area is poor. Similarly, it is unlikely that females would be discovered unless paired with a singing male. These isolated birds seldom contribute to the annual census and would only rarely pair with a female. These extralimital birds could have formed colonies in the past but their

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populations probably did not persist due to insufficient suitably aged habitat.

Annual Recruitment

The demographic data discussed above provide provisional estimates of reproductive potential and recruitment based on studies of nesting success, pairing success, fledgling survival and mortality of the breeding grounds (Table 2). Previous estimates of annual productivity and recruitment (Ryel, 1981b, Walkinshaw, 1983) did not separate fledgling mortality from overwinter mortality or consider possible reduced pairing success. These corrections to productivity could be large. Nesting productivity averages 2.6 per nest or 3.1 per pair (the latter number includes renestings). The estimate of 85% pairing success of Kirtland's warbler males is probably maximal, but is offset by polygyny to an unknown extent. These corrections to annual productivity reduce the estimate of autumn immatures to 391, a 40% decrease from the 654 previously estimated.

I estimate 75% survival of adults based on a 60% return of banded males plus 15% relocations between years (see above). The number of new recruits is calculated by assuming a stable population, and the corrections from pairing success and fledgling mortality raise the calculated return rate of yearlings to 28% from previous calculations of 23%. In past years the population decreased when pairing success was low, migration and winter mortality were high, or breeding dispersal was substantial. Conversely, the population has the potential to increase in years when reproduction is higher than average and mortality and dispersal are moderate.

Habitat Limitation

The decline in Kirtland's warbler numbers between 1961 and 1971 coincided with a decrease in suitably aged jack pine habitat in the known nesting range (Table 3). However, the quantity of habitat has increased since 1971 with no corresponding increase in the Kirtland's warbler population, so any possible effects of habitat limitation are not direct or immediate. Alternatively, the population trends could indicate a decrease in relative habitat quality that offsets any gains in habitat quantity. Much of the habitat regenerated since 1970 results from tree harvesting rather than from wildfire. At present, Kirtland's warblers are distributed very unevenly among occupied stands (Table 4). The average density of Kirtland's warblers in all occupied habitat in 1981 is very close to the average density in 1961 for all available habitat. This suggests that either the habitat quality was better in 1961 or that the density of Kirtland's warblers was greater in either suitable or less suitable habitat in 1961 than at the present. Because the occurrence of unburned stands with lower density of pine trees is recent, I favor the argument that stresses a general degradation of habitat quality since 1961.

In 1981, Kirtland's warblers were located on 2800-3000 ha of a possible 6400 ha of pine stands in the 8- to 20-year age range generally selected by the species. The overall density in occupied habitat was 3.2 males per 40 ha (Table 4). In the 1980 and 1981 censuses, three-fourths of the population (ca. 175-180 males) were located in five major breeding areas (Fig. 2) that totalled ca. 1450 ha (4.8 males per 40 ha). At the other extreme, an aggregate area of more than 1200 ha supported only about 32 male Kirtland's warblers (1.3 males per 40 ha). The very low Kirtland's warbler densities in marginal habitat could be viewed as evidence that habitat is not limiting at current population levels (Mayfield, 1983). Alternatively, this could be interpreted to mean that primary habitat was fully occupied and extra birds moved into marginal habitat (i.e., small

colonies or single birds in less dense stands that were usually unburned).

Population density is not the only means to evaluate relative habitat suitability. Pairing success, nest density and nest success may also be used to rank habitat quality. Fretwell and Lucas (1969) have developed a habitat utilization model that postulates a distribution of birds among habitats that results in near-equal nesting success. For example, dickcissels (Zimmerman, 1982) and indigo buntings (Carey and Nolan, 1979)

TABLE 2. - Kirtland's warbler annual recruitment for a population of 211 singing males

Estimates	Number pairs	Fledglings per pair	Fledgling survivor- ship	Autumn imma- tures	Spring return rate	Adults (422)	Spring return rate	Breeding population	Number males
Previous	211° x	3.1 ^b x	1.0	= (654	x 0.23°) +	(422 x	0.65°)	= 423 ÷ 2	= 212
Current	180 ^d x	3.1 x	0.70	= (391	x 0.28') +	(422 x	0.75^{2})	$= 426 \div 2$	= 213

^{41982 + 1983} average

^b3.1 per pair (Walkinshaw, 1983)

^{60.65} adults (Mayfield, 1983), 23% inferred rate for yearlings (Mayfield, 1960, 1978)

^{485%} pairing success

^{*0.70} fledgling survivorship until independence (modified from Walkinshaw and Faust, 1975)

Calculated from other demographic data and an assumption of a static population (see text) Estimates 15% relocations of adults (previously assumed to have died)

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in less preferred habitat and lower nesting density but similar nest success compared to birds in more preferred habitat.

Although we had no evidence to support lower fledgling rates in Kirtland's warbler marginal habitat, a few nest studies have been conducted in such areas. I have suggested above that the main disadvantage of marginal habitat might be low pairing success. This fact suggests that the Kirtland's warbler habit of forming clusters or "colonies" of birds could function to attract mates more easily. If such is the case, Kirtland's warblers could have lower productivity as well as lower densities in marginal habitat.

FUTURE PROSPECTS FOR THE KIRTLAND'S WARBLER

The success of the cowbird control program may allow the Kirtland's warbler population to increase slowly if no severe losses occur off the nesting grounds. However, five of the six major Kirtland's warbler breeding areas currently in use could decline significantly by 1985, when they will be 16-20 years old and will have been used for 8-12 years by Kirtland's warblers. Therefore, I predict that none of these five major breeding areas will be major colonies (more than 15 males) after 1986, though four of these areas have younger habitat patches that could carry a small colony beyond the normal duration of use. Because these colonies will not support many Kirtland's warblers through the end of the decade, new colonies must be formed in suitable habitat of adequate extent to replace those that decline (Fig. 5). The quantity of suitable habitat has remained roughly constant since 1971. It would have declined to ½ to ¾ of the present area ca. 1987 if a prescribed burn in 1980 had not gone out of control and burned almost 10,000 ha of forest (including 100 ha of current warbler habitat). This Mack Lake Burn has the potential to regenerate more habitat between 1988 and 1995 than exists at the present time. It appears that jack pine regeneration within the area will be sufficient to

TABLE 3. - Kirtland's warbler habitat quantity^a

Year	Area ^b (ha)	Population (Census of male)	Overall density (Males per 40 ha)	
1961	7280	532	2.9	
1971	4100	201	2.0	
1979	7206	210	1.2	
1984	8790	215	1.0	

"Suitably aged habitat in 11-county nesting region (8-20 years old for wildfires, 10-20 years old for plantations)

^bSources: Unpublished reports by J. Weinrich, Michigan Department of Natural Resources, Roscommon, Mich., 19 Dec. 1979, and D. Sorenson, Huron-Manistee National Forest, Cadillac, Mich., 3 Dec. 1979

TABLE 4. - Local distribution of Kirtland's warbler male in occupied habitat 1981

Colony size (No. per stand)	KW Males (No.)	Area of occupied stands ^a (ha)	Average density (No./40 ha)	
Primary (18-45 males)	175	1450 (5) ^b	4.8	
Secondary (10-18 males)	25	445 (2)	2.2	
Tertiary (<10 males)	32	1010 (11)	1.3	
Total	232	2905 ha (18)	3.2	

"Modified from data sources in Table 3

^bNumber in parentheses indicates number of stands

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produce thousands of hectares of Kirtland's warbler habitat. Thus, we will have an opportunity to observe any population regulation of Kirtland's warbler relative to habitat quantity as the supply of suitable habitat first decreases in the near future and then substantially increases.

Research Needs. —Additional research is needed in three broad areas. First, more studies should be conducted to determine what proportion of Kirtland's warbler males are unmated, monogamous or polygynous. Such studies may develop evidence for or against a balanced sex ratio. Second, more color-banding should be done in conjunction with systematic searches for relocating birds in subsequent years. Knowledge of relocations is important to modify survival estimates for Kirtland's warblers and other species. Third, research on postbreeding ecology is needed to obtain better estimates of fledgling mortality, and to understand the significance of postnatal dispersal. With improved knowledge of reproductive potential, survivorship, dispersal and recruitment we should have a reasonable understanding of Kirtland's warbler demography. The Kirtland's warbler is particularly well-suited to research on annual survivorship, tertiary sex ratio and postnatal dispersal because of its restricted breeding range.

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AREA REQUIREMENTS OF BREEDING KIRTLAND'S WARBLERS IN MICHIGAN

John R. $Probst^1$ and $Jerry Weinrich^2$

USDA Forest Service, North Central Forest Experiment Station, ${\rm Rhinelander,\;WI\;\;54501}^{1}$

Michigan Department of Natural Resources, Houghton Lake, MI, 48629^2

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Abstract

The population of male Kirtland's warblers (Dendroica kirtlandii) in the breeding season has averaged 206 from 1971 to 1987. The Kirtland's warbler occupies dense jack pine (Pinus banksiana) stands from 5 to 23 years old and from 1.4 to 5.0 m high, which historically were of wildfire origin. In 1984, 73% of the males censused were found in habitat naturally regenerated from wildfire or prescribed burning. The rest were in plantations (15%) or in harvested, unburned jack pine stands stocked by natural regeneration (12%). Twenty-two percent (630 of 2,886) of the Kirtland's warbler males counted in the annual censuses from 1971 through 1984 were found in 26 stands that were unburned and naturally regenerated following harvest. Kirtland's warblers withdrew almost entirely from the unburned, unplanted habitat by 1989, as predicted earlier by its lesser suitability. Thus, predictions of future carrying capacity were based on acreage of wildfire and plantation habitat only. From 1982 to 1987, suitable regenerating habitat was barely sufficient to replace currently occupied maturing stands, so population growth was impeded. An increase in suitable habitat (wildfire and plantation) was projected from 1987 through 1993. Minimum (290 males) and maximum (430 males) populations for 1993 were calculated using 1984 average density (1.9 males per 40 ha) and peak wildfire habitat populations (2.8 males per 40 ha).

Introduction

The known nesting range of the Kirtland's warbler (Dendroica kirtlandii) is restricted to an area about 120 by 160 km in northern Lower Michigan. In 1951, Harold Mayfield (1953) organized the first census of the entire known population of males within the Michigan nesting range, which totaled 432 singing males. In the second decennial census, 502 male Kirtland's warblers were counted (Mayfield 1962). By 1971, the population decreased to 201 (Mayfield 1972). As a result, the Kirtland's warbler was classified as an endangered species under the Endangered Species Act of 1973. The principal reason for this population decrease appeared to have been nest parasitism by the brown-headed cowbird (Molothrus ater) (Ryel 1981a). Since cowbird control was initiated (Kelly and DeCapita 1982), the warbler population has stabilized. Winter mortality (Ryel 1981a), habitat maturation, pairing success, fledgling mortality, and yearling dispersal (Probst 1986) may now limit population growth. Habitat area may have been a second limiting factor in recent times because suitable breeding habitat available to the Kirtland's warbler has decreased since 1961 (Ryel 1981b, Probst 1986). In recent years, Kirtland's warblers have occupied only 5 to 6 major breeding areas, each of which provides habitat for only 10 to 16 years.

Typically, the species occupies dense, 1.7- to 5.0-m high jack pine (Pinus banksiana) stands established after wildfire (Mayfield 1960, Walkinshaw 1983). Kirtland's warbler populations in jack pine burns generally build for 3 to 5 years, level off for 5 to 7 years, and then decline rapidly (Probst 1986). The vegetation in 5 active nesting areas has been described (Smith 1979, Buech 1980), but no data have been published for the complete range of stand ages, tree heights, and tree stocking densities within 3 major habitat classes

(wildfire, plantation, unburned-natural regeneration) at ages (5 to 23 years) when stands are occupied by Kirtland's warblers.

Traditional wildlife habitat evaluations have related local populations to local, multi-variate habitat characteristics. More recently, biologists have taken the broader view of regional/local population interactions (e.g. Askins & Philbrick 1987, Probst 1988, Pulliam 1988) that emphasizes distribution among habitat classes of variable quality (Fretwell 1969). This paper takes a broader view of regional habitat and its dynamic utilization as: 1) The relative area of 3 general classes of habitats utilized by Kirtland's warbler changes; 2) the breeding habitat distribution of Kirtland's warbler changes, as well as their breeding densities; and 3) the regional population increases as hypothesized by the habitat and breeding distribution. Kirtland's warblers are highly suited to studies of population regulation by habitat limitation because of their restricted breeding range, their concentration into 16 to 30 stands within any 1 year as observed between 1971 and 1989, and the ease with which the entire known male population may be censused each year.

An analysis of regional habitat available to a species must first define and assess the full range or bounds of habitat, before conducting detailed sampling within habitat categories or gradients. Aerial photographs and aerial surveys revealed a striking difference in tree cover between occupied and unoccupied Kirtland's warbler habitat. Thus, we defined suitable habitat by the bivariate limits of tree height and tree percent cover on stands below site index 55. Data reported here integrate the tree cover hypothesis with a quantification of the stand age and tree height factors identified by previous researchers (see above). The hypothesis was tested indirectly here by predicting total Kirtland's warbler populations for the near-term based on total habitat area in 3 habitat classes. A tree cover and tree density

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hypothesis was tested directly at the local, site-specific level (M. Nelson, unpubl. data) and in experimental plantations. When a sufficient sample of Kirtland's warber plantations (there have been only four currently) have progressed through the full stand age range, then local-scale multivariate analysis may be appropriate to supplement the current bivariate explanation of Kirtland's warbler habitat suitability.

Limits to Population Projections Based on Habitat

Population projections based on both declining and developing habitat assume predictable densities that are applicable when habitat is at or near carrying capacity. However, if habitat is limiting the population of Kirtland's warblers appreciably, increased habitat supply should increase the number of Kirtland's warblers until a point is reached where the amount of habitat exceeds the number of returning birds and new recruits. In such a situation, carrying capacity cannot be realized by population growth. Some evidence suggests that habitat limits Kirtland's warblers (Probst 1986). From 1982 to 1986 the proportion of males increased in marginal habitat where their density (see Results) and pairing success were lower than in more suitable habitat (Probst and Hayes 1987).

The estimates of future habitat area and carrying capacity presented here involve predictions from commonly available forestry data. These predictions cannot be improved by analysis of vegetation measurements because we cannot apply such stand-specific data to future regenerating habitat. Thus, we use the range of conditions in broad habitat classes to predict minimum and maximum KW populations in habitat currently regenerating. However, all habitat models assume habitat limitation such that a significant increase or decrease in habitat supply will result in a population response.

We assembled both field data and unpublished government reports on habitat area and Kirtland's warbler male populations to accomplish 6 objectives: (1) describe the complete known range of habitats for the Kirtland's warbler as determined by past distribution data, (2) document Kirtland's warbler utilization of unburned stands and evaluate general characteristics influencing utilization of such stands, (3) tabulate the past and current area of suitably-aged jack pine habitat on appropriate sites available to the species, (4) infer relative suitability of 3 habitat classes from differences in 1984 Kirtland's warbler distribution and density, as well as tests of hypotheses about changes in distribution of birds in 1989 relative to 1984, (5) predict future area of wildfire and plantation habitat available during 1989-1993, (6) forecast a range of Kirtland's warbler carrying capacity based on the historical range of density for suitable habitat, and (7) briefly evaluate the Kirtland's warbler habitat management goals.

Methods

We used the annual Kirtland's warbler overall census results of Mayfield (1953, 1962, 1972, 1973a, 1973b, 1975); Ryel (1976a, 1976b, 1979a, 1980a, 1980b, 1981b, 1982, 1983, 1984); Burgoyne and Ryel (1978); Weise (1987); and Weinrich (1988a, 1988b, 1989, 1991a, 1991b). For individual breeding areas, habitat area data and population trends were compiled from unpublished reports on file with the Michigan Department of Natural Resources (DNR) and the Huron-Manistee National Forest. Habitat was classified as "suitably-aged" if it was jack pine habitat 8 to 20 years old in wildfire or 10 to 20 years old in plantation or unburned, unplanted habitat. Subsets of suitably-aged habitat actually utilized were defined as "occupied habitat". Within occupied habitat, wildfire and plantation areas were classified as suitable habitat (see

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Results), and unburned, unplanted habitat as less suitable habitat. Density of Kirtland's warblers was calculated by estimating stand area from maps used for the Kirtland's warbler annual census or cover type maps from the Michigan DNR. Significant differences among the proportions of habitat classes over time, or their utilization by Kirtland's warblers, were compared with Chi-Square Tests.

Vegetation sampling was designed to represent the range of conditions existing in 7,000 to 8,000 ha of suitably aged jack pine habitat, rather than a current, but temporary distribution of conditions. Vegetation was measured in 35 subareas within 21 breeding areas occupied by Kirtland's warblers. Kirtland's warbler habitat was divided into 3 habitat classes: natural regeneration from fire (N = 19) (including one prescribed burn) referred to as "wildfire" habitat; plantations (N = 8); and harvested, unburned, naturally regenerated stands (N - 8). Twelve breeding areas were measured during the first 2 years of utilization, and 3 areas during the last 2 years of occupation to define the lower and upper bounds of acceptable stand maturity. All wildfire and plantation stands occupied between 1979 and 1985 were censused and measured as described below. We measured vegetation from 1979 to 1985 between 15 April and 30 April and between 15 August and 20 September. Vegetation measurements for tree crown cover were made using the line transect method (Lindsay 1955) combining some adaptations of that technique as done by Buech (1980) and Probst (1976) (see below). Single 300- to 500-m transects were oriented along the long axis of a cluster of Kirtland's warbler male territories in each study area. Each transect was subdivided into 10 to 15, 30.5-m long segments. In plantation habitat, transects were oriented 45° to planting rows.

Tree crown cover was estimated by measuring the percentage of the transect line covered by the vertical, plumb line projection of tree crowns or thicket

onto the ground. The border of a tree crown or thicket was delineated by those outer branches that intersected a vertical perpendicular plane above the tape. The lower height of live jack pine foliage was measured for each tree or thicket that intersected the transect. The lower heights were weighted by cover to calculate average lower height of foliage. In thickets, crown cover and lower heights were separated by species and overlapping cover was recorded. Thus, single species calculations could be combined or separated, but only combined covers are reported here because of the almost total dominance of jack pine in all but three stands which were dominated by red pine (Pinus resinosa). Trees taller than 0.6 m were counted and measured to the nearest 0.3 m. Tree stems taller than 0.6 m were counted in rectangular sample units 1.5 x 15.3 m adjacent to the transect line at alternate 15 m segments of the transect. Stand ages and lower foliage heights of different habitat classes were compared using the Mann-Whitney test. Tree density among the three habitat classes was analyzed with a nested analysis of variance (SYSTAT). Because of unequal subplot sizes, sequential subplots within a study area were combined until an area of 93 m² was achieved. The square root transformation of number of trees in each subplot was used to normalize the data.

The minimum carrying capacity of Kirtland's warbler males was predicted by using average male densities from 1984 in all stands in the two primary habitat classes (wildfire and plantation). Estimates of habitat area within those same habitat classes were used to project future carrying capacity. The 1984 Kirtland's warbler male densities were used as a basis for predicting minimum carrying capacity because populations were more dispersed at that time (see results). Also, Kirtland's warblers (KW) use stands for 8 years or more (Probst 1986) and habitat turnover from stand maturation is low in almost all

years. Thus, the overall 1984 Kirtland's warbler densities should be representative of the period 1982 to 1985, when the birds were well-represented in all 3 major habitat classes (i.e. minimal density). Maximum carrying capacity was estimated from peak male densities (13 to 15 years stand age) in 4 major wildfire areas, which was similar to 1989 male densities (see Results). We predicted future populations for "overmature" occupied breeding areas based on published rates of mortality and population decline (Probst 1986). The predictions of population decline in specific habitats were compared with the actual populations observed through 1987. Thus, future carrying capacities were estimated using data on historical rates of population build-up and decline, after testing them in the near term. The estimates of future Kirtland's warbler populations will only be valid if populations are strongly regulated by quantity of suitable habitat and if non-habitat limiting factors remain constant.

We use range rather than confidence limits on estimates of future carrying capacity for the following reasons: (1) annual censuses of Kirtland's warbler males are comprehensive, and average male density is essentially a population mean rather than a sample within a population for a given year; (2) the future habitat distribution of Kirtland's warbler is changing markedly in the near future because of the higher proportion of more suitable habitat that is becoming available from 1988 to 1998 (see Results); (3) the distribution of habitat proportions, stand sizes and stand ages of occupied areas will change in the coming decade; and (4) it is likely the Kirtland's warbler density of specific breeding areas depends on the context and interaction of overall population size and habitat area. As a result, the application of confidence limits from one population to a very different population and set of conditions is inappropriate.

Results

Stand Suitability

Data on average tree height, tree crown cover (Table 1, Fig. 1), and pine stem density for 21 stands (including 35 subareas) occupied by Kirtland's warblers (Table 2) illustrate several patterns. In general, stands are not colonized by male Kirtland's warblers until the average tree height reaches from 1.4 to 2.3 m (Table 1), at which time populations are low (Fig. 2). The tree stocking was at least 2,000 stems per ha, which provides tree cover of at least 15% to 20% in all occupied stands. I have arbitrarily divided the stand age continuum into "young", "middle", and "declining". Breeding areas support greater male densities in the middle period of Kirtland's warbler occupancy (Fig. 2, Probst 1988). During those middle years of highest Kirtland's warbler density, stands range between 2.4 and 3.9 tree height and up to 60% tree cover (Table 1). Kirtland's warbler populations begin to decrease when tree heights reach about 3.5 m and the lower height of live foliage reaches about 1.0 m (Table 1). At this stage of regeneration tree cover typically exceeds 60%.

Tree canopy cover is more useful for evaluating habitat quality than stocking frequency or stem density because it integrates the stocking, spacing, and height factors. During the middle period of Kirtland's warbler stand occupancy, tree cover is between 27% and 60% (Table 1), a condition found in fire-regenerated stands which typically have more than 5,000 stems per ha (Table 2). Because trees are evenly distributed in plantations, optimal tree canopy cover (30%-60%) can be achieved with a lower tree density. However, unplanted stands with less than 2,500 stems/ha have not been used consistently (i.e. intermittent use), and unburned, unplanted areas with less than 20% canopy cover (Fig. 1) are questionable habitat for female Kirtland's warblers (Probst and Hayes, 1987). More suitable stands have more tree cover than

unburned, unplanted stands (Fig. 1). In any stand, the stocking should have from 20% to 25% tree cover for successful colonization (Fig. 1). Warbler populations decline rapidly after 7 to 10 years of occupancy (Fig 2) at which time average tree height reaches from 4.0 to 4.5 m (4.5 to 5.0 m in plantations) and low, live foliage is absent below about 1.2 m in height (Table 1).

Historically, Kirtland's warblers have been found in large (>32 ha), 8- to 20-year-old stands that have been regenerated by wildfire. In the past 2 decades, a different type of habitat has become available: clearcut pine stands stocked by natural, nonserotinous seeding, and rarely, by planting. Twenty-two percent (630 of 2,886) of the Kirtland's warbler males counted on the annual censuses from 1971 through 1984 were found in 26 stands (distributed among 16 surveyed sections) that were unburned following harvest (data on file). Females or nests were found in at least 18 of the 26 stands. Two of these breeding areas in unburned, unplanted habitat held more than 66% of the males in that habitat during the period 1971 to 1984 and 3 areas held 82%. These 3 stands were characterized by denser tree regeneration (stands 4, 5, 16, Fig. 1) than most other unburned jack pine areas, and one of the 3 was planted for Kirtland's warbler.

Unburned, unplanted jack pine stands are characterized by lower tree density (Table 2) and more open canopy cover than wildfire areas (Fig. 1); therefore few of them develop the characteristics of occupied stands. When unburned, unplanted stands are first colonized, they are older than plantations (p <0.01) or wildfire stands (P <0.001, Table 2 and Fig. 1) and average about 3.3 m in height at this threshold. Unburned plantation for Kirtland's warbler (stands 5, 18, and 20 in Fig. 1) can produce adequate tree cover at the usual 2

to 3 m height (Fig. 2), and planted habitat (burned or unburned) can support high (2.4 males per 40 ha) Kirtland's warbler populations (Table 3).

Habitat Availability and Distribution Among Habitats

In 1984, the known breeding population of Kirtland's warblers was located on 5,500 ha (Table 3) of 9,000 ha of suitably aged jack pine habitat within the known breeding range in northern lower Michigan (Fig. 3). From 1977 to 1983 three-fourths of the male population (from 155 to 180 birds) was located in 5 or 6 major breeding areas (Ryel 1981b, Probst 1986) whose combined total area represented about one-third the entire occupied habitat. Male Kirtland's warbler density in all suitably-aged habitat fell from 3.0 males per 40 ha in 1961 to 1.0 males per 40 ha in 1984 (Fig. 3). This decrease is probably due to a degradation in average habitat suitability because dense plantation and wildfire habitat had declined in the previous 2 decades (Probst 1986). Further, overall Kirtland's warbler densities within occupied habitat in 1984 were similar to those in 1951 (Mayfield 1953) and in 1982 (Probst 1986) -about 3 males per 40 ha. More specifically, Kirtland's warbler overall densities were from 1.9 to 2.4 males per 40 ha in wildfire and plantation habitat respectively, in 1984, and between 2.5 and 2.9 males per 40 ha in 1989 (Table 3).

These observations lead to tests for nonrandom distribution of Kirtland's warblers among the three classes of habitat within 1984, 1989 and the period 1979 to 1989 as a whole (Table 3). There were no departures from random distribution in wildfire versus plantation habitat in all time periods.

However, the distribution in unburned, unplanted habitat was much lower than expected by chance and densities were lower overall in that class of habitat. Thus, I interpreted utilization of unburned, unplanted areas to be a

consequence of saturation or overmaturity of major colonies in more suitable habitat (Probst 1986) and predicted that Kirtland's warblers would withdraw from most of the less suitable habitat as more suitable wildfire and plantation habitat became 8 to 12 years old. The Chi-Square Test of 1989 warbler distribution among suitably-aged habitat based on 1984 proportions was rejected, confirming a significant shift in habitat selection as more suitable habitat appeared.

Testing the Carrying Capabity Estimate

We tested the prediction that habitat lost in declining, more suitable habitat could be replaced by colonization in developing, more suitable habitat (wildfire and plantation). We attempted to predict the rate of decline of 5 major "source habitats" in 1980 (Table 4) based on the demography presented by Ryel (1979b), and modified by new survivorship estimates (Probst 1986). The number of males in the 5 major colonies fell from 175 in 1981 and 180 males in 1982 (Probst 1986) to 43 males (48 predicted) in 1987 (Table 4).

Because the distribution of birds among habitat types can vary (Table 3), it is not possible to predict future Kirtland's warbler populations based on projections of suitably aged habitat alone. However, if we separate current and future suitable habitat (i.e., the 2 classes of suitable habitat colonized since 1980) from less suitable habitat and apply the Kirtland's warbler density figures from 1984 to wildfires and plantations, we can calculate minimal estimates of carrying capacity (Table 5). In 1980 we predicted a maximum of 125 males would be in new suitable habitat in 1987. The number of males in new suitable habitat (first occupied after 1980) in 1987 turned out to be 117 males. Thus, the prediction of 1987 carrying capacity in declining (48 males) plus new habitat (125 males) turned out to be 160 males censused vrs. 173

predicted (less than 8% error) in wildfires and plantation habitat. (Seven males were also found in unburned, unplanted areas in 1987, bringing the total to 167 males.) For these projections of male population we assumed that all suitably stocked stands would be colonized and occupied at the same approximate male densities found in 1984, which proved to be a reasonable assumption.

DISCUSSION

Future Habitat Quantity and Carrying Capacity

Between 1957 and 1961, 4 areas totalling 4,676 ha -- one in the Huron National Forest and 3 on State land in Michigan -- were set aside specifically for preserving the Kirtland's warbler (Mayfield 1963). The state areas were to be planted, and the federal areas were to be burned and planted as necessary (Radtke and Byelich 1963). With one exception (stand #10, Fig. 1), all prescribed burning has failed to provide natural regeneration. The current area targeted for Kirtland's warbler management has increased to 51,700 ha. The Kirtland's Warbler Recovery Plan (developed under authority of the Endangered Species Act of 1973) calls for regenerating jack pine habitat through harvest followed by burning on State (30,000 ha) and Federal (21,700 ha) land so that about 10,340 ha of suitably aged habitat will be available every year. This habitat will be regenerated at the rate of about 1,030 ha per year in 17 State forest and 7 federal management areas (Fig. 4). These stands are managed on a 50-year Kirtland's warbler management and commercial timber rotation; Kirtland's warblers are the primary resource objective. Prescribed burning usually has failed to provide the dense tree stocking required by the Kirtland's warbler, primarily because jack pine regeneration has been de-emphasized as an objective of fire prescriptions. Land managers have been

seeking alternatives to burning without sacrificing any secondary habitat requirements (Probst 1988).

By 1989, the suitable acreage in the Mack Lake Burn of 1980 exceeded 1,680 ha and helped provide potential habitat for 106 male Kirtland's warblers.

Between 80 (at 1.9 males per 40 ha) and 118 (at 2.8 males per 40 ha) males were predicted. M. Aili, M. Nelson and J. Probst predicted an overall 1989 minimum carrying capacity of 169 males (255 maximum) in "new habitat" (colonized since 1980) in lower Michigan. The 1989 census turned out to be 212 males. By the early 1990's all suitably stocked Mack Lake Burn acreage was old enough to support Kirtland's warbler breeding, and 3,360 ha of State of Michigan and USDA Forest Service Kirtland's warbler plantations will be old enough to be utilized (Table 5). This new habitat will be offset by maturation of the Bald Hill Burn area, which may begin a slow decline in Kirtland's warbler numbers about 1992 and will have few birds after 1998. We estimated minimum habitat carrying capacity for 290 male Kirtland's warblers in 1993 (Table 5) based on the 1984 average male density among all wildfire and plantation stands, and a maximum of 430 males based on peak densities (2.8 males/40 ha) in wildfire habitat.

Primary Habitat Factors

Some evidence suggests that tree height and percent cover (i.e. foliage volume) is the primary factor controlling habitat suitability for Kirtland's warblers. In typical wildfire habitat, areas with dense regeneration are occupied first (Table 1) and no areas were occupied with less than 16% cover (Table 1). Stands of intermediate tree density were older than dense stands when first used (Buech 1980) and usually support fewer birds (Smith 1979 and unpublished data). Territory sizes were larger in the more open areas of a stand (Mayfield 1960, Smith 1979, and pers. obs.). The average density of male

Kirtland's warblers was higher in suitably stocked plantations (whether burned or unburned) or wildfire areas (Table 3). Only 25 to 67% of males in young or poorly stocked habitat obtain mates compared to 95% pairing success in more suitable habitat (Probst and Hayes 1987). Thus, it is a reasonable hypothesis that tree density has been more limiting to Kirtland's warblers in unburned stands than lack of fire <u>per se</u>, but the number of unburned plantations available during the study was too small for statistical comparison. At the least, unburned stands have been under-managed, and therefore under-utilized by Kirtland's warblers.

Previous explanations of Kirtland's warbler habitat suitability centered about the bird's nesting biology (Mayfield 1960, Walkinshaw 1983), and the USDI Kirtland's Warbler Recovery Team has emphasized the importance of fire influencing ground cover requirements for suitable nest sites (Byelich et al. 1976). However, it is unlikely that this ground-nesting bird is limited by nest sites. The threshold for initial occupancy may be related to minimal foliage volume necessary for Kirtland's warbler foraging requirements. The decline of habitat could be related to a lack of live lower branches for fledgling cover and for the foraging of the female Kirtland's warbler (Table 1). If tree foliage volume (on appropriate sites) is of primary importance to Kirtland's warbler habitat suitability, the occupied habitat can be described by tree height and tree cover (Fig. 1). The composition and height of ground cover (Probst, unpubl. MS) may only become limiting in more mesic sites (site index greater than 55) not considered suitable habitat for the species at present.

Habitat and Population Projections

It is possible to predict Kirtland's warbler population response to major changes in habitat quantity. We predicted that the high proportion of Kirtland's warblers in young or marginal habitat between 1984 and 1987 could impede population growth enough that the 10,000 ha Mack Lake Burn would not have high occupancy initially (Fig. 3), even within the suitably stocked habitat patches. The Kirtland's warbler population is undergoing a substantial increase (beginning in 1990 and 1991), but population growth should be moderated by declines in the Bald Hill Burn from 1993-1998. However, even if population increase is only moderate between 1989 and 1995, a higher proportion of birds were in suitable habitat between 1988-1990 than existed between 1982 and 1987. Thus, we predict that the shift in nesting habitat distribution may increase annual productivity enough to allow full occupation of new Kirtland's warbler habitat that will be of suitable maturity beginning in 1995. Kirtland's warbler numbers may increase substantially around the turn of the century in fully occupied, managed habitat equal in area to the Mack Lake Burn suitable habitat. However, for this to continue it will be necessary to keep management objectives on schedule.

We can evaluate the adequacy of the habitat designated for Kirtland's warbler management using the density estimates in Table 3 and the minimum carrying capacity estimates in Table 5. The most pessimistic prediction uses the current overall density of 1.9 males per 40 ha in wildfire and plantation habitat combined. Habitat area of 10,340 ha would only support 491 male Kirtland's warblers based on 1984 densities and habitat considerations alone. However, the quality of the managed habitat may be sufficient to allow an average of 3 or more males per 40 ha in most stands, which would yield 775 male Kirtland's warblers. As more samples of occupied plantation habitat become

available, it may be possible to confirm the hypothesis of higher Kirtland's warbler densities in plantation versus wildfire habitat, but current data are insufficient for significant conclusions. A higher average male density, of over 4 males per 40 ha would be required to achieve the goal of more than 1,000 male warblers. This goal may be attainable for the quantity of habitat set aside for management, but it will require full implementation of the management program as well as suggested improvements in habitat quality (Probst 1988) to achieve the established objectives.

Finally, biologists must understand the mechanisms determining habitat limitation if they are to estimate minimum habitat area for viable populations. In the case of the Kirtland's warbler, I have suggested that population regulation through habitat limitation may result from nonbreeding birds and dispersal among fragmented habitats of marginal quality -- not from reduced average nesting success of most breeding pairs (Probst 1988). A scarcity of quality habitat may result in more birds abandoning their territories to search for better nesting areas. In addition, habitat supply and biogeography may affect colonization success (Fritz 1979), arrival dates (Probst 1988), territorial establishment, and fledging dates. Delays in the initiation of breeding may cause birds to miss food resource peaks and sacrifice opportunities for renesting or second nesting.

It is possible to investigate the influence of variable carrying capacity on the entire known population of the Kirtland's warbler because the quantity of suitable habitat has varied substantially during the past two decades. When the regional population was at or above carrying capacity, the annual censuses were stable and males expanded their habitat selection to include less suitable habitat. The area of suitable habitat doubled by 1987 and 1988. We presumed that the Kirtland's warbler population was well below carrying capacity

beginning in 1987 and increased its overall productivity beginning about 1988-1989. Thus, we predicted a rapid population increase between 1990 and 1995 based on habitat limitation, habitat area, and stand chronology. The 1990 and 1991 census results indicate that a 63% increase has already occurred.

If the Kirtland's warbler population was at or above carrying capacity, the period from 1979 to 1986 may have been a fortuitous time to study Kirtland's warbler habitat quality. More generally, if limitation by habitat varies in intensity over time, then habitat-based, local population predictions will be inaccurate unless they are coupled to metapopulation processes. Thus, geographic and annual population variability may restrict the utility of traditional local habitat modeling in wildlife biology.

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Table 1. Pine tree heights, percent cover, and lower foliage heights of occupied Kirtland's warbler breeding areas in Michigan.

	Average tree height (ranges) (m)	% Tree cover (ranges and means)	Average lower height of of foliage (ranges and means)
Declining	3.9-5.6m	36 ^b -86%	0.7-1.5m
Use Areas			
(N=5)		$(\bar{x}=61.0%)$	(x=1.2m)
Middle-aged	2.4-3.8	21-67.5%	0.2-1.1m
Habitat			
(N=16)		$(\bar{x}=43.2\%)$	$(\bar{x}=0.6m)$
Young	1.4-2.3	15.8-38%	0.1-0.9m
Habitat			
(N=10)		(x=27.3%)	$(\overline{x}-0.3m)$

^a Weighted by tree cover.

b Includes unplanted area between planted strips at one site. Excluding unplanted space within this plantation, range = 54-86%, x = 69.8%.

Table 2. Stand age and pine stem density of three occupied Kirtland's warbler habitat classes in Michigan.

	Subarea age first year occupied	Pine density (stems/ha)
Wildfire Habitat (N=19)	(7-10) 	(1,680-43,751)
Plantation Habitat (N=8)	(7-12) 	(1,272-4,296) x=2565 B
Unburned, Natural (N=8) Regeneration	(11-15) = 12.8 B	(1,272-3,705) x=2131.5 B

a Significant differences (P<0.01) among means (Mann-Whitney Test) in a column are indicated by different capital letters.

Table 3. Distribution and density of Kirtland's warblers among occupied habitat types in Michigan, 1984 and 1989.

	Area ha		No.	males	Density (No. males per 40 ha)		
Location							
	1984	1989	1984	1989	1984	1989	
Wildfire	3,414 ^A	2,495 ^B	158 ^E	156 ^G	1.9	2.5	
(N)	(19) ^A	(14) ^B					
Plantation (Burned and		765 ^B	23 ^E	55 ^G	2.4	2.9	
(N) unburned) Subtotal	3,795 ^A		181 ^E	211 ^G	1.9	2.6	
Unburned, Natural Regeneration (N)	1,657 ^C	125 ^D	34 ^F	1 ^H	0.8	0.3	
•					_	_	
Total	5,452	3,385	215	212	1.6	2.5	

Chi-Square Tests were used for significant differences (P<.005) in proportions of occupied stands, total acres, or males in a habitat class relative to the proportion of suitably-aged habitat available in that class. There were no significant differences (P>0.75) between stands or acres occupied for wildfire vs. plantation habitat within 1984 or 1989, or for 1979-1989 as a group.

Table 4. Observed and projected populations (males per 40 ha) in declining major Kirtland's warbler colonies in Michigan.

	Observed						
Year of Origin	1984	1985	1986	1987	1988		
1968	12	17	9	6(5) ^a	0		
1964	28	24	11	10(12)	4		
1966	38	32	16	14(15)	3		
1966	35	15	11	6(15)	5		
1967	_17	100	14	7(6)	_1		
	130	100	61	43(53)	13		
	Origin 1968 1964 1966 1966	Origin 1984 1968 12 1964 28 1966 38 1966 35 1967 17	Origin 1984 1985 1968 12 17 1964 28 24 1966 38 32 1966 35 15 1967 17 100	Year of Origin 1984 1985 1986 1968 12 17 9 1964 28 24 11 1966 38 32 16 1966 35 15 11 1967 17 100 14	Year of Origin 1984 1985 1986 1987 1968 12 17 9 6(5) ^a 1964 28 24 11 10(12) 1966 38 32 16 14(15) 1966 35 15 11 6(15) 1967 17 100 14 7(6)		

 $^{^{\}mathrm{a}}$ #1980 prediction based on 0.75 survivorship (Probst 1986).

Table 5. Carrying capacity for 1987, 1989, and 1993 or suitably stocked plantation and wildfire stands $^{\rm a}$ for Kirtland's warbler in Michigan.

		1987	198	39]	1993
Habitat	Area	Carrying	Area (Carrying	Area	Carrying
category	(ha)	$capacity^{b}$	(ha) ca	pacityb	(ha)	capacityb
Federal ^c						
Wildfire	810	38	1,744	83	1,744	83
Plantation $^{ m d}$	332	16	433	21	1,760	84
		_			2 504	167
Subtotal	1,142	54	2,177	104	3,504	167
State ^e						
Wildfire	1,133	54	1,133	54	1,052	50
Plantation ^d	304	14	304	14	1,599	76
		_				
Subtotal	1,437	68	1,437	68	2,651	126
Total	2,579	122	3,614	172	6,155	293
Iocal	2,373	122	5,014	112	0,133	2,3

a Colonized since 1980.

b Calculated from 1984 densities 1.9 males per 40 ha 8 to 20 years age (wildfire stands), or from 10 to 18 years age (plantations).

^c Source: G. W. Irvine & W. Jarvis, personal communication.

 $^{^{}m d}$ Suitably-stocked plantations (>2500 stems per ha) managed for Kirtland's warbler.

e Source: J. Weinrich, personal communication.

Figure 1. Ranges of average tree height and percent tree canopy of stands sampled within habitat occupied by Kirtland's warblers in Michigan. Classification of habitats into marginal or suitable follows the categories defined for contrasting pairing success (Probst and Hayes, 1987). (Young marginal habitat matures into suitable.)

- 1. Artillery South
- 2. Mack L. Red Pine #1
- 3. Pere Cheney
- 4. Ogemaw Management^a
- 5. Lovells N. (S.5)
- 6. Muskrat Lake
 - -S.7
 - -S.13N
 - -S.13S
- 7. Artillery North
 - -S.8 and 9
 - -S.9 South
- 8. Damon^a
 - -North
 - -South
- 9. Fletcher Burn
- 10. Mack L. Prescribed Burn
 - -1978
 - -1983
- 11. Mack L. Unburned
 - -1980
 - -1983

- 12. Mack L. Plantation (S.3)
 - -Jack Pine
 - -Red Pine
- 13. Lovells South
- 14. Monument
- 15. McKinley #1
- 16. McKinley
 - -Area #2
 - -Area #3
 - -Area #4
- 17. Rayburn
- 18. Lovells North #2 (S.6)
- 19. Bald Hill
 - -1982 S.20
 - -1983 S.20
 - -1983 S.14
- 20. Mack Lake, Red Pine #2
- 21. McKinley #5 ('77 Plantation)

^a Data from Smith (1979)

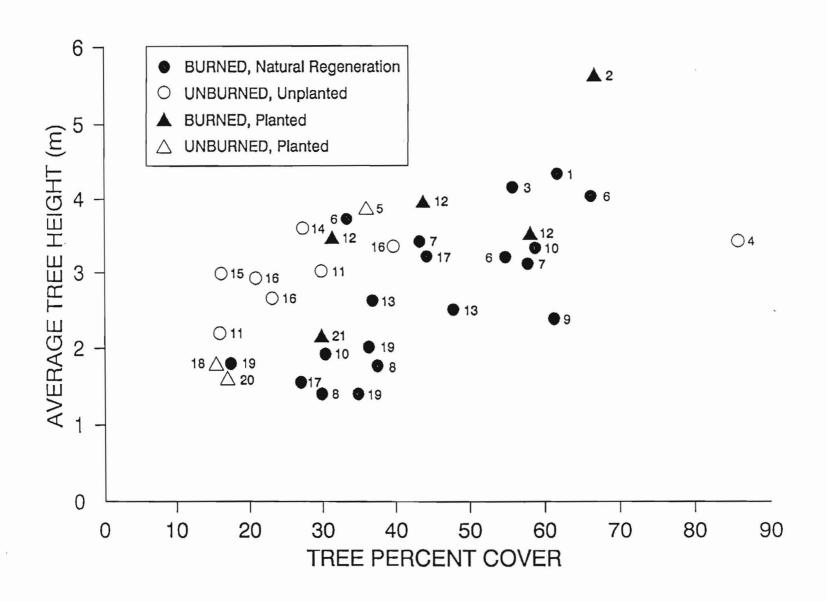


Figure 2. Stand age population trends of Kirtland's warbler males in four wildfire-regenerated breeding areas in Michigan.

NO. KIRTLAND'S WARBLERS (Four Wildfire Stands)

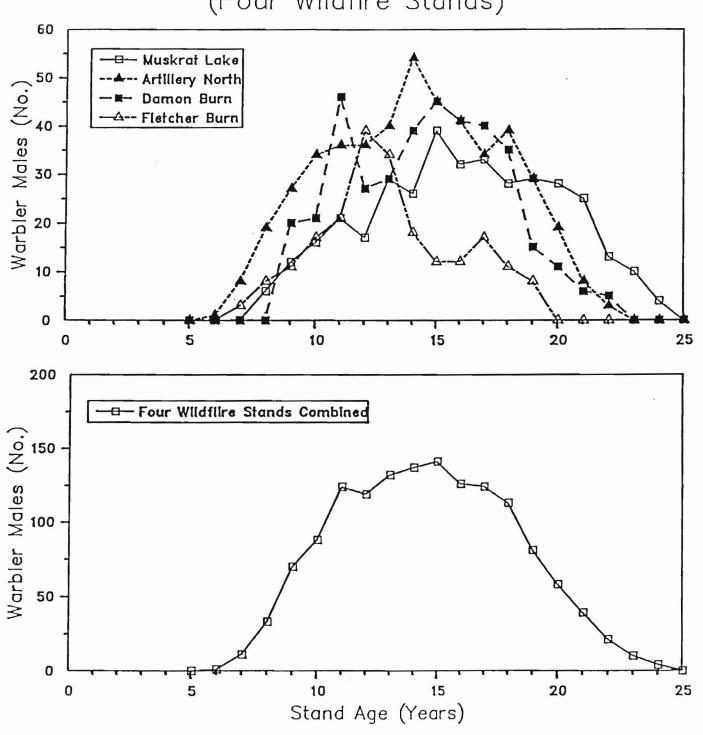


Figure 3. Area of jack pine habitat in lower Michigan suitably aged (see Table 5) for Kirtland's warbler and overall density of males between 1960 and 1990. Sources: Data from unpublished reports by J. Weinrich (Michigan DNR) and D. Sorenson (USDA Forest Service).

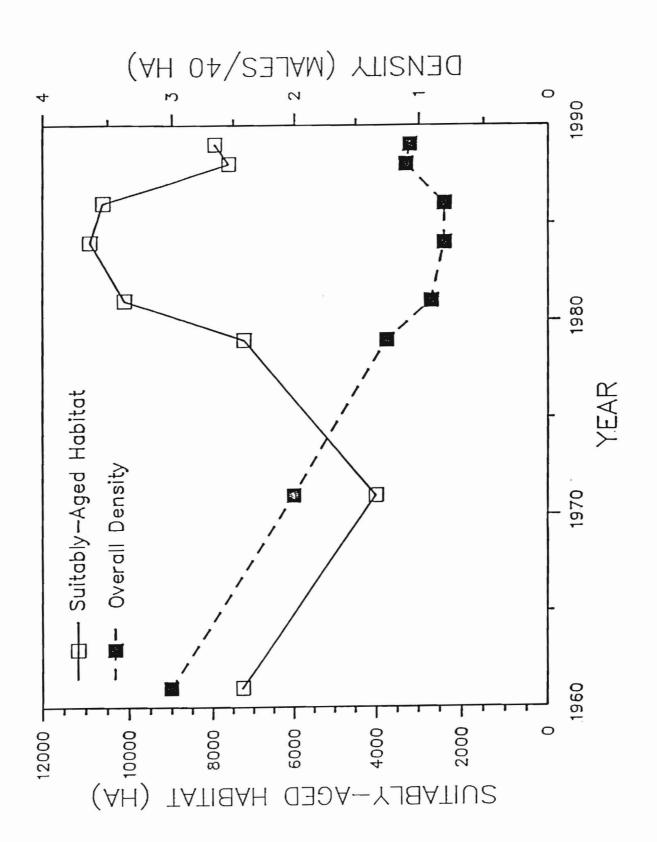


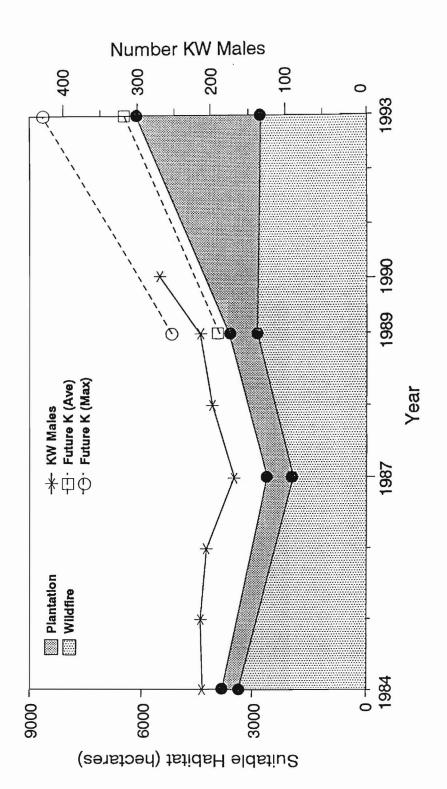
Figure 4. State and Federal Kirtland's Warbler Management Areas in Michigan.



U.S. Forest Service Kirtland's Warbler Management Areas

State Kirtland's Warbler Management Areas

Figure 5. Quantity of suitably-stocked plantation and wildfire habitat for Kirtland's warbler in Michigan (1981-1993). Past populations (1984-1988) and estimated carrying capacity (1991-1993) of male Kirtland's warblers are also shown. The lower carrying capacity estimate is based on the 1984 average male density (1.9 males per 40 ha) in wildfire plus plantation habitat. The higher estimate (2.8 males per 40 ha) was derived from peak populations during the middle years of habitat occupancy (see Fig. 2). Sources: Habitat area from unpublished reports by J. Weinrich (Michigan DNR) and D. Sorenson (USDA Forest Service).



Mich Greeking Bird Atlas KIRTLAND'S WARBLER

DR. JOHN R. PROBST NO. CENT. FOREST EXPER, STAL US FOREST SERVICE BOX 898 HWY. K RHINELANDER, WI 54501

KIRTLAND'S WARBLER Dendroica kirtlandii

The Kirtland's Warbler is an endangered species that is known to breed only in an 80 × 115 km area in the northern LP of Michigan. This warbler may have bred formerly in the UP, Wisconsin, and Canada, based on past and recent sightings of nonbreeding males (Probst 1985, Aird 1989). Winter records are restricted to the Bahama archipelago plus one sight record from Mexico.

HABITAT

Known breeding locations for the Kirtland's Warbler are discrete, well-defined pine stands on poor, sandy soils where trees are from 5 to 23 years old and from 1.7 to 5.0 m tall. The occupied habitat is characterized by very dense stands (more than 1000 stems per acre, 20% to 80% canopy cover), most commonly found in jack pine regenerated naturally following wild-fire. Suitable habitat has also been created by planting trees (jack pines and occasionally red pines) at densities about twice the normal forestry density. Between 1960 and 1987, Kirtland's Warblers were found in unburned jack-pine stands that had regenerated marginally after timber harvesting, presumably because of a shortage of higher-quality primary habitat (Ryel 1979, Probst 1986, 1988). When a large area of wildfire habitat became available around 1987, Kirtland's Warblers were no longer found in unburned or unplanted habitat.

Large populations in major breeding areas increase initially, stabilize, and then decline during the 10- to 15-year period of occupancy. Average tree heights range from 2.4 to 3.9 m tall when populations peak at approximately 13 to 15 years of stand age. When trees reach 3.5 m or more in height and no live needles are present below about 1.0 m. Kirtland's Warbler populations begin to decrease. Nests are built on the ground, concealed in the low cover of grass, sweet ferns, and blueberries.

SEASONAL OCCURRENCE

Kirtland's Warblers arrive on the breeding grounds between 5 and 20 May (Mayfield 1960, orig. obs.). Male singing lasts

throughout most of June, but is reduced to sporadic bouts of song by the last week of June and ends in early July. Females incubate eggs of first nests in early June, and young fledge beginning 15 June (Mayfield 1960, Walkinshaw 1983). Few renestings or second nestings are initiated after 25 June, but nests have fledged young as late as 20 August (Walkinshaw 1983). Individuals begin to disappear in early August, but many Kirtland's Warblers (mostly adults) stay on the Michigan breeding grounds through late September (Sykes et al. 1989).

STATUS

Reports by collectors in the Bahamas between 1880 and 1900 suggest that the Kirtland's Warbler was formerly more numerous following the logging and fires in the Great Lake states' forests around the turn of the century (Mayfield 1960). The short-term distribution, such as seen in the Atlas survey, is usually more restricted than the full historical range (shown in a separate map) because the habitat is ephemeral. Still, habitat for this warbler is almost certainly less common now than at the turn of the century.

A comprehensive census of singing males throughout the known range showed a decrease from 502 to 201 males between 1961 and 1971 (Mayfield 1962, Mayfield 1972). The major reason for this population decrease appeared to be nest parasitism by the Brown-headed Cowbird (Ryel 1981). Cowbird control beginning in 1972 reduced parasitism to less than 3% (Kelley and DeCapita 1982), and the population has since stabilized. Productivity increased from fewer than 1 fledgling per pair to 3.1 after cowbirds were controlled (Walkinshaw 1983).

The factors that may now be limiting population growth are habitat maturation and fragmentation, incomplete pairing success, fledgling mortality, and yearling dispersal to less suitable habitat or places outside the known breeding range. At present, it is impossible to separate winter and migratory losses from postbreeding mortality on the breeding grounds.

Recent evidence supports the hypothesis that the availability of suitable breeding habitat has been the principal factor limiting the Kirtland's Warbler population since cowbird control was begun. Because habitat is only suitable for a 10-to 15-year period, habitat maturation forces young birds to find new breeding areas. Thus, Kirtland's Warblers can be maintained or increased only if new breeding "colonies" are established to replace existing ones. Although the total area of jack-pine habitat in the 8- to 20-year range has not decreased much since 1951, the amount of suitable breeding habitat (adequately stocked with jack pines) has declined significantly during the past 35 years (Ryel 1981, Probst 1986 and unpubl. MS).

The remarkable population stability between 1971 and 1986 may have been related to saturation of a fairly constant area of suitable habitat. The population fluctuations that have been observed during the past 19 years are related to a synchronous increase and subsequent decrease among maturing colonies (Probst 1986, Morse 1990). The recent concentration of Kirtland's Warblers into a small portion of the available habitat of suitable age is further evidence of a population affected by the low proportion of suitable wildfire and plantation habitat (Probst 1986). In the period from 1977 to 1983, three-fourths of the Kirtland's Warbler population (between 155 and 180 males) was located in five or six major breeding areas (Ryel 1981, Probst 1986) whose combined total area represented only about one-third of the entire occupied

habitat. This suggested that the Kirtland's Warbler population might have been filling most of the suitable habitat in recent years, with some overflow into the less suitable unburned, unplanted habitat. This hypothesis was supported by the absence of Kirtland's Warblers from such marginal habitat after wildfire habitat became abundant in 1988.

The area of suitable habitat doubled by 1987 and 1988 due to management and a 10,000-ha wildfire (the Mack Lake fire, Oscoda Co.) in 1980. Beginning in 1987, the Kirtland's Warbler population was probably well below carrying capacity. Total counts from censusing increased to 265 males in 1990 in response to this sudden habitat availability, but breeding densities remained lower than in wildfire habitat of the 1981-1986 period when habitat was apparently limiting. Kirtland's Warbler males decreased their utilization of marginal habitat beginning in 1987. Overall productivity of birds in marginal habitat should be lower because of territorial movements (low site tenacity) and lower pairing success (Probst and Hayes 1987, Probst 1988). A rapid population increase between 1989 and 1995 (which may have begun in 1990) based on factors such as habitat area, stand chronology, and local stand utilization will give additional support to population regulation by large "source habitats."

CONSERVATION

The area targeted for Kirtland's Warbler management is 51,700 ha. The Kirtland's Warbler Recovery Plan (developed under authority of the Federal Endangered Species Act of 1973) calls for regenerating jack-pine habitat through harvest followed by burning on state (30000 ha) and federal (21,700 ha) lands so that about 10310 ha of suitably aged habitat will be available every year. Habitat will be regenerated at the rate of about 1030 ha per year in 17 state forest management areas and in 7 areas on U.S. Department of Agriculture Forest Service land. These stands are managed on a 50-year Kirtland's Warbler management and commercial timber rotation at present; Kirtland's Warblers are the primary resource objective. A goal of 2000 breeding birds has been set. Prescribed burning usually has failed to provide the dense tree stocking required by the Kirtland's Warbler, so land managers have been planting stands both with and without burning. In addition to habitat management, large wildfires that occurred between 1988 and 1990 make it possible that some of the currently occupied wildfire habitat can be replaced at the end of the century.

John R. Probst

DRAFT SUBJECT TO REVISION

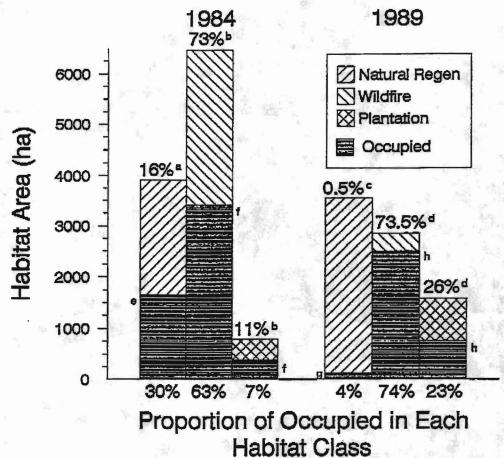


Figure 3: Changes in availability of habitat types and bird distribution between 1984 and 1989. The distribution of KW's within a year is indicated above each bar. The percentage of occupied habitat in each habitat class within a year is indicated below each bar. Chi-square Tests were used for significant differences (P<.005) in proportions of total acres or males in a habitat class relative to the proportion of suitably-aged habitat available in that class. There were no significant differences (P>0.75) between acres occupied for wildfire vrs. plantation habitat within 1984 or 1989, or for 1979 to 1989 habitat as a group.

RENCE H. WALKINSHAW
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RTLAND'S
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VVARBLER



The Natural History of

An Endangered Species

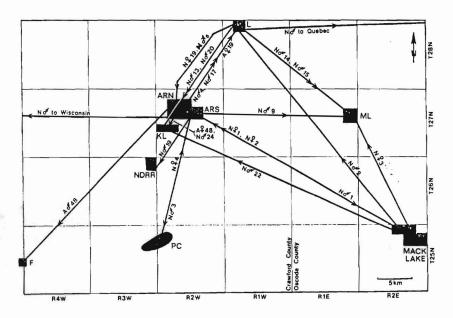


FIGURE 3. Movements in Nest Locations of Kirtland's Warblers Among Different Nesting Regions.

N = Movement from natal region to region of first nesting

A = Movement of an adult bird to a different breeding area

ML = Muskrat Lake

L = Lovells Management Area

ARN = Artillery Range North

ARS = Artillery Range South

NDRR = North Down River Road

PC = Pere Cheney

KL = Kyle Lake

F = Fletcher Burn

a strange male enters the territory of a resident male he remains in the lower jack pine branches in an alert, quiet, and watchful state. If the intruder begins singing, signifying that he is attempting to establish a territory, a confrontation with the owner ensues. Kirtland's Warblers defend their territory well into the summer, but by late July most territorial fighting ceases.

Males often defend their territories against other species of birds, especially if these birds approach a nest. Even the female Kirtland's Warbler will exhibit defensive behavior and will chase such intruders as other Kirtland's Warblers, Chipping Sparrows (Spizella passerina), Vesper Sparrows (Pooecetes gramineus), Black-capped Chickadees (Parus atricapillus), and

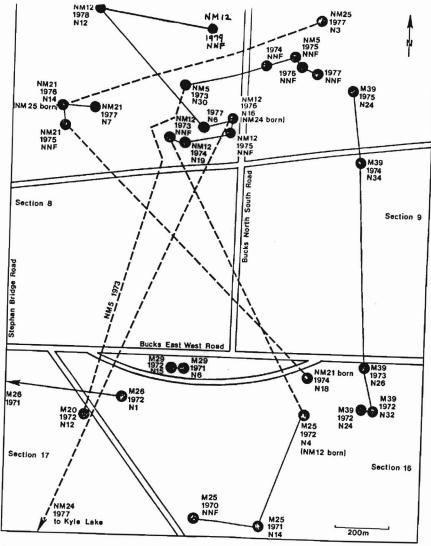


FIGURE 4. Nest Locations of Male Kirtland's Warblers on the Artillery Range and Nest Locations of Their Male Offsprings.

Black circle = Nest location

M = Males banded as adults

NM = Males banded as nestlings

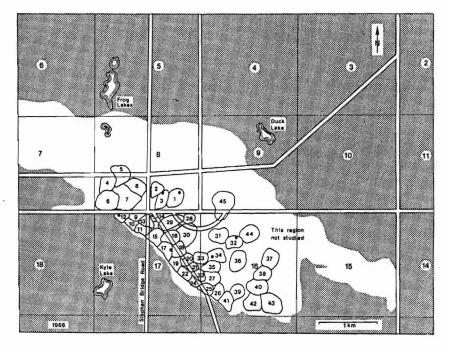
Code numbers = Birds described in Table 13

Dashed line = Distance between natal nest and first nesting site

Solid line = Distance between nest sites of adult males

Transcripe (Artillery Range South, T27N, R2W, Crawford County, Michigan)	Average Size of	Territory Complete Mean Size Region Aerial (ha)' Photograph (ha)
sies (Artillery Range South, T2	les (Aimes) ser	Number of Singing Males Observed 4 44 33 21 49 49 25 25 25 7 4 4 0
1.1 - Townstor	rbier Territor	Study Area Area (ha) (ha) 348 227 202 202 267 486 486 486 486 324 324 324 324 324 328
:	Kirtland's Wa	Size of 933 933 933 933 933 933 934 86 486 486 486 486 486 486 486 486 486
	Siz	Usable Size of Area (ha) Burn (ha) 1961 647 933 1966 728 933 1966 486 486 486 1970 486 486 1971 486 1972 486 1972 486 1975 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1977 324 486 1978 324 486 1978 324 486 1978 1978 324 486 1978 1978 324 486 1978 1978 324 486 1978 1978 324 486 1978 1978 324 486 1978 1978 324 486 1978 1978 1978 1978 1978 1978 1978 1978
	TABLE 15.	Year 1961 1966 1966 1969 1970 1971 1973 1974 1975 1974 1976 1976 1976

rarely used the extreme borders of their territories. Field observations seem to indicate that Kirtland's Warblers prefer to nest in close proximity to each other forming a colony of sorts. Extensive regions of suitable habitat observed in the field are devoid of warblers. Yet other areas of suitable habitat may support a dense population of warblers e.g. the Artillery Range South during the period 1966-1973. As the jack pines increase in height, the lower branches die and the ground cover disappears. When the trees reach this stage, fewer warblers establish territories in the area. They prefer to nest



FIGURES 10-21. Kirtland's Warbler Territories on the Artillery Range. These figures show the gradual movement of warblers into the Artillery Range North which burned in 1967 and a concomitant decrease of warblers on the Artillery Range South which burned in 1955. Clear portions of the maps outline the original August 1955 burn. The clear area north of the dashed line (after 1966) was burned again in May 1967. Territories, which are approximate, were defined by observing the activities of singing males. Stippling indicates mature jack pine forest that did not burn in either 1955 or 1967.

Black circles = Nest locations Open circle with dot = Active cowbird trap (1972-1978) portion of a nearby grove of jack pines. I crawled along the ground in that direction (to approximately 6 m from the nest site) and soon saw her again with another bill full of grass. She seemed agitated and began wagging her tail. Then she disappeared into a thick growth of blueberry and bearberry, emerging one minute later with an empty bill. Since she flew some distance away, I took this opportunity to inspect the nest site. The pit had been dug, but was only partially filled with nesting materials. Every few minutes the female would return with nesting materials and deposit them in the depression. She worked her way back and forth through the jack pines between the nest site and the place where she gathered the nesting materials (a distance of about 60 m). On each of the trips, the female was accompanied by her mate who followed a meter or more behind her, singing as he flew. This pair was first located at 0900 hrs EST and the female was still working on the nest at 1130 hrs EST when the observation was discontinued.

A second female was observed building a nest on the Artillery Range South on 18 June 1972. As the nest neared completion, she became aware of a root extending through the center of the nest. She tugged repeatedly at the root and finally succeeded in removing the outer covering. However, she could not dislodge the root itself and as a result she abandoned this nest site for another.

CHAPTER 9

EGGS

Description

Kirtland's Warbler eggs are ovoid, have a whitish or pinkish ground color, and are covered with varying numbers of brownish spots which are often concentrated in a cap or wreath at the larger end. Some eggs are nearly elliptical in shape with both ends of uniform size. Some have spots distributed over the entire surface. A few eggs have spots concentrated only at the smaller end. The average length of 253 eggs measured in the field (1938–1978) was 18.3 ± 0.7 mm (range, 15.5 mm to 19.9 mm), and the average width (at the widest point) was 14.2 ± 0.6 mm (range, 10.8 mm to 16.0 mm). The average elongation ratio of these eggs (length divided by width) was 1.29 mm.

Forty-five eggs had an average weight of 1.8 g. Weights were determined by weighing the entire clutch at one time. Only abandoned or infertile eggs were measured and no eggs were weighed after 1973 in order to minimize disturbance of nesting birds. This fact introduces a possible source of bias to the data. However, these measurements are very close to those reported

TABLE 18. Number of Kirtland's Warbler Eggs per Nest, 1957-1971.

Year	0	No.	Eggs	Per 1	Nest 4	5	Total Nests	Total Eggs	Mean Number of Eggs Observed
1957			2	3	4	2	11	39	3.45
1966	5	1	_	1	7	_	7	4	0.57
1967	2	•	1	1	2		6	13	2.17
1968					1		1	4	4.00
1969	1	1	2	2	2	1	9	24	2.67
1970		3	1	6	5	1	16	48	3.00
1971	1		9	2		1	13	29	2.23
TOTAL	9	5	15	15	14	5	63	161	2.56

Both parasitized and unparasitized nests are included.

by Mayfield (1960) and this indicates that the amount of bias was probably negligible.

Four eggs in a first clutch laid by a one-year-old female averaged 18.7 mm \times 13.9 mm in size. This same female laid eggs the following summer that averaged 19.0 mm \times 14.5 mm in size. Another female of unknown age laid an egg in 1969 that measured 17.8 mm \times 13.7 mm and a clutch of four eggs in 1970 that averaged 17.7 mm \times 14.3 mm. A third female laid a clutch of four eggs in 1969 that averaged 17.1 mm \times 14.5 mm and a clutch of five eggs in 1973 that averaged 16.8 mm \times 14.0 mm. A fourth female laid a clutch of four eggs in 1970 that averaged 18.1 mm \times 14.4 mm. This same female laid a clutch of five eggs in 1971 that averaged 17.8 mm \times 14.6 mm.

Clutch Size

Between 1931 and 1955, I observed 17 nests of Kirtland's Warbler with completed first clutches (eggs laid in late May or early June). These nests contained 85 warbler eggs and no cowbird eggs or an average of 5 warbler eggs per clutch. One known second clutch contained four eggs. During the period of most active cowbird parasitism (1957–1971), 16 of 63 warbler nests were unparasitized, but five of these contained only two eggs or nestlings indicating their clutches were incomplete. The other 11 unparasitized first clutches contained 41 warbler eggs or 3.73 eggs per clutch (Table 18).

During the period when adult Brown-headed Cowbirds were removed from warbler regions (1972–1978), 817 eggs were found in 171 nests or an average of 4.78 eggs per clutch (Table 19). Thirty-six second unparasitized clutches from the years 1972 through 1977 had an average clutch size of four eggs (Table 20). A decrease in clutch size was recorded as the summer advanced (Table 21). Most unparasitized first clutches had five eggs, while most unparasitized second clutches had four eggs. The data show that clutch size was definitely affected by cowbird parasitism. Even when eggs were not removed or nests parasitized, the clutch size was smaller in unparasitized first clutches during the years of active cowbird parasitism (1957–1971) (Tables 22, 23, and 24).

During the years 1931 through 1955, the average clutch size was five eggs, but the average clutch size declined to 3.73 eggs during the years 1957 through 1971 when cowbird parasitism was most severe. The average clutch size increased to 4.78 eggs during the years 1972 through 1978, after cowbird removal was instituted. None of the nests utilized to derive these figures was parasitized. The size of observed clutches (after cowbirds had removed all or part of the original clutch) in parasitized nests was two eggs (range, 0–5 KW eggs). One nest held five warbler eggs and two cowbird eggs, while another held four warbler eggs and three cowbird eggs. During the

Sizes of Unparasitized First and Second Clutches. TABLE 20.

									2	ľ	
Mean	Clutch	Size	4.55	4.71	4.59	4.67	4.62	4.52	I	4.61	4.64
	Total	Eggs	132	146	225	154	120	122	١	668	196
	Total	Nests	29	31	49	33	56	27	i	195	207
		9			_						4
4	hes	5 6	19	23	28	23	17	17	1	127	135
Both	\lntc	4	7	7	19	6	∞	7	1	57	28
		3	3	_	_	-	-	3			10
ean	ıtch	Size	19	40	22	50	83	20		4.00	
Ž	์ อี	S	3.	4	4	4	3.	3.	•	4	
	Total	Eggs	22	22	38	18	23	21	1	4	
	Total	Nests	9	2	6	4	9	9	1	36	
		2		3	3	7			1	8	
2nd	utch	4	4	-	2	7	2	3	1	20	
	ַ	3 4 5	7	_	_		_	3	1	∞	
	Mean	Clutch	4.78	4.77	4.68	4.69	4.85	4.81	5.17	4.78	
	Total	Eggs	110	124	187	136	26	101	62	817	
	Total	Nests	23	56	9	53	20	21	12	171	
		9			-				3	4	
	utch	2	19	20	25	21	17	17	8	127	
	1st Clutch	4	3	9	14	7	3	4	_	38	
	1	3	_		0.0	_				2	
		Year	1972	1973	1974	1975	9261	1977	8/61	Totals	

SUCCESS

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TABLE 35. Survival of Kirtland's Warblers, 1964-1982.

Age When Banded,	_ Y	ears"	Foi	ınd .	Afte	er I	Ban	din	g	T	otal	Estimated Age and Standard
Sex	1	2	3	4	5	6	7	8	9	Birds	Years	Deviation
AHY, & &	26	7	14	5	2	4	2	3	0	63	174	2.76 ± 2.06
AHY, ♀♀	43	6	6	3	2	1	1	0	0	62	108	1.74 ± 1.38
N, 3 3	1	7	3	6	4	4	1	0	1	27	108	4.00 ± 1.90
Ν, ♀ ♀	7	6	4	0	1	0	2	0	0	20	50	2.50 ± 1.85
Total	77	26	27	14	9	9	6	3	1	172	440	2.56 ± 1.93

AHY = Birds of unknown age, at least one year old when banded.

N = Birds banded as nestlings.

ond location several crows had been seen. However, there is no proof that any of these animals actually destroyed the nests.

There are two documented cases of Blue Jay predation on Kirtland's Warblers. In the first, a Blue Jay was observed beating the head of an eightday-old warbler nestling with its beak. Three nest mates of the victim had rapidly scattered into the surrounding vegetation and the parents and a pair of Chipping Sparrows were hanging in midair 30 cm above the nest location, beating their wings rapidly. The nestling which was attacked by the Blue Jay died within several minutes of the assault. The remaining three nestlings escaped harm. On 1 July 1967 at 1200 hrs EST, two nestling cowbirds were observed in Nest 1. The parents were feeding them regularly. Fifteen minutes later a Blue Jay was observed sitting on the edge of the nest eating the last cowbird nestling. The Blue Jay flew off into the forest leaving the nest empty. Since Brown-headed Cowbirds have been removed from Kirtland's Warbler nesting regions, the Blue Jay has become the warbler's worst predator, found on nearly all warbler territories. An investigation of other species of birds and mammals found on 100 different warbler territories showed the Blue Jay to be the single most prevalent species. It was found on 86 of the 100 territories studied (Table 36).

The thirteen-lined ground squirrel is probably the next most serious predator of the Kirtland's Warbler. William Freeman (personal communication) and Leighton Smith (verbal communication) both observed this mammal dragging nestlings from the nest. Although they interfered with this predation, the nests were empty on the following day. Field observations indicate that ground squirrels do not take all of the nest contents at one time. Part of a clutch or several nestlings usually disappear one day, and the remainder are taken on a future day.

Red squirrels are also suspected of preying on Kirtland's Warblers. On

10 July 1970 at Nest 18, a red squirrel was seen within 1 m of the nest. This sighting occurred at 0500 hrs EST and the nest contents were intact; at 0600 hrs EST the two nestling cowbirds had vanished. A small burrow could be seen in the bottom of the nest. On 21 June 1975 at Nest 3, four small nestlings were observed. On 23 June only one nestling remained and a pine cone had been added. The next day only the pine cone remained. This case of predation was probably also the work of a red squirrel.

One documented case of garter snake predation on Kirtland's Warblers is also recorded. On 27 June 1972 at Nest 25, a pair of Kirtland's Warblers and their five nestlings were banded. On 1 July O. S. Pettingill (personal communication) visited the region and found this pair of adult warblers in an agitated state. The nest was empty and nearby a large garter snake was found which showed several lumps in its body. Three of the banded nestlings

TABLE 36. Number of Times Other Animals Occupied the Same Territory as 100 Pairs of Kirtland's Warblers. (100 territories were included in this study)

		-) /	
Blue Jay	86	Nighthaud	
Chipping Sparrow	49	Nighthawk	5
Vesper Sparrow	34	Tree Swallow	5
Brown Thrasher	28	Black-capped Chickadee	5
Brewer's Blackbird	(0.100m)	American Robin	5
Lincoln's Sparrow	17	Eastern Bluebird	5
Nashville Warbler	17	Pine Warbler	5
Field Sparrow	15	Woodland jumping mouse	4
Thirteen lined	15	Common Flicker	4
Thirteen-lined ground		Yellow-rumped Warbler	4
squirrel	14	Clay-colored Sparrow	3
Prairie Warbler	12	Mourning Dove	2
Snowshoe hare	11	Black-backed Three-	2
Rufous-sided Towhee	10	toed Woodpecker	2
White-throated Sparrow	9	Sharp-tailed Grouse	2
Red squirrel	8	Western Palm Warbler	2
Upland Sandpiper	8	Eastern Meadowlark	2
Song Sparrow	8	Mallard	2
American Kestrel	7	101 1020010	1
American Crow	7	Spruce Grouse	1
Cedar Waxwing	7	Striped skunk	1 .
Sharp-skinned Hawk	6	Raccoon	1
Northern Junco	6	Rose-breasted Grosbeck	1
Line it t			

Whitetail deer, porcupines, and coyotes roamed most regions continuously. Marsh Hawks and Bald Eagles flew regularly over many regions and cowbirds formerly occurred on all territories. These counts were made at the Artillery Range South, the Lovells Management Area, and Muskrat Lake.

PERTE

DANGERED SPECIES

was found dead beside the nest.

rs have been observed removing I from the edge of the nest and d ant mounds are found in most they cause the birds any trouble. nd's Warbler eggs and nestlings. 32 nests were observed and 179 plers fledge from them (63.5%). ed in these nests of which 787 d (60.1%). Almost 40% of the ing stage. Eighty-five eggs failed accounted for by the 169 eggs 6).

nestlings disappeared during the s were taken and seven were dehe laying period is normally five ng the 14-day incubation period, ring the nine-day nestling period, nestlings per day. If the 9 nested to this total, then 10 nestlings ıring the period 1972-1977, 615 l nestlings. Two hundred thirtyand the date of this loss was renestlings) for which the exact date ?1 losses would have occurred at 6 eggs (5.11%) would have been 5%) during the incubation period, , and five nestlings (3.8%) would

te of adult birds, from the known present nesting success indicates plers occurs during the nine months xty-three percent of the warblers 9). The tremendous loss of warmales in 1973 as compared with een the result of a hurricane that 173.

in many regions because of dee examples of such losses are the Cincinnati, the bird that flew into her bird that flew into a lighthouse is known about the food require-

IABLE 37. Losses of Kirland's Warbler Eggs and Inesuings, 1900–1977.			-	00									
Year	1966	1961	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	Tota
Number of													
Nests	7	9	-	6	16	13	32	34	63	37	33	31	282
Number													
Successful	1	7	0	3	7	9	22	23	47	56	23	19	179
Number of KW													
Eggs Observed	4	13	4	24	48	56	135	150	258	162	134	132	1,093
KWs Hatched	7	S	0	9	27	16	106	115	200	119	104	87	787
KWs Fledged	7	S	0	9	17	12	87	92	181	102	68	2	657
Total Eggs Lost	7	∞	4	18	21	13	56	35	28	43	30	45	306
Total Nestlings										*			
Lost	0	0	0	0	10	4	19	23	19	17	15	23	130
Eggs Possibly													
Hatched					9)	ю	ю	4	7				181
Eggs Failed to													
Hatch	-	-	0	-	∞	-	12	6	16	14	10	12	851
KW Eggs & Yg.	ΙE			2E	6E	4E			17				131
Apparently													-
Taken by cowbird													
Deserted Eggs		3		4	3		7	3	9				26]
Predator Removed													
(1) Eggs		4	4	S	4	S	10	22	34	53	70	32	169
(2) Nestlings						4	14	18	17	16	6	17	95
Eggs or Young					17			1E			ΙΧ	2Y	=
Disappeared													4
Unknown				6E	9Y	3E	3Y	44	2E			1E	12
							,			•	,	,	16
Nestlings Died							2	-	-	-	n	4	14

TABLE 38. Day of Loss of Kirtland's Warbler Eggs and Nestlings, 1972-1977.

ABLE 38	•	D	ay	OI	1	788	01	K		and	3	vv ai	_	_			_							Ne	sting P	eriod				Total
			La	ying	g							Incu	batio	n Per	_	Eggs)		55C7				21	22	23	24	25	26	27	28	
Year	1	2	- 3	3	4	5	6	7	5	9	10	11	12	13	14	15	16	17	18	19	20	21		3		5	1	5		10 eggs 14 yg.
1972 1973		2										5	4	4			4		4	3	2	1	5				5	5		26 eggs 18 yg.
1974		2			4D									4			5	5	10		3				3				1	26 eggs 4D 7 yg.
1975										5		9	5						4	5	3	4				5			4	28 eggs 16 yg.
1976	1		3	3D							4			5				5	2		1			6	1	1	(5)			17 eggs 3D 9 yg. 5 died
1977												4			5		9	8		5		5			(2)	2 (2)			10	31 eggs 17 yg. 4 died
otal	1	1	4	3	4		<u> </u>	_	5	5 5	4	1 18	3 14	13	3 5	Č	18	18	20	13	9	10	5	9	4 (2)	13 (2)	6 (5)	10	15	145 eggs 9 died 81 you

D = deserted

TABLE 39. Annual Survival of Kirtland's Warbler.

		Fir	st Nesting			Seco	nd Nesting				
Year	No. of Pairs	No. of Eggs Laid $\bar{x} = 4.78$	No. of Nestlings Fledged	No. of Young One Month after Fledging	No. of Pairs	No. of Eggs Laid $\bar{x} = 4.00$	No. of Nestlings Fledged	No. of Young One Month after Fledging	Total Fall Count if No More Lost	Returns the Next Spring	Lost Durin Nine Mont
1972	200	956	605	471	100	400	253	197	1,068	432	63
1973	216	1,032	654	508	108	432	273	213	1,153	334	819
1974	167	798	505	393	83.5	334	211	164	891	358	533
1975	179	856	542	421	89.5	358	227	176	955	400	555
1976	200	956	605	471	100	400	253	197	1,068	436	632
1977 1978	218 (196)	1,042	660	513	109	436	276	215	1,164	392	772
Total	1,180	5,640	3,571	2,777	590	2,360	1,493	1,162	6,299	2,352	3,947

^{() =} young died

become chilled, and the embryos die as a result. Warbler eggs in parasitized nests frequently showed breaks in the surface. Such breaks were never found in eggs from unparasitized nests, thus it is likely that this damage was caused by adult cowbirds.

Sixty-eight parasitized Kirtland's Warbler nests contained 146 warbler eggs or 2.2 eggs per nest. Two hundred forty-one unparasitized nests contained 1,102 warbler eggs or 4.6 eggs per nest. The 68 parasitized nests should have contained a total of 313 eggs at that rate. Only one parasitized nest fledged both a cowbird (one) and warblers (two). Mayfield (1960) found that no warblers were fledged from parasitized nests which contained two or more cowbird nestlings. Four nests each contained one cowbird egg. In each instance this egg failed to hatch. Three, four, four, and two warblers, respectively, were fledged from these four nests. The nest which had the cowbird egg built into its bottom also produced two fledged warbler nestlings. In 1970 cowbird eggs were removed from three parasitized nests and six warbler nestlings were fledged (three, two, and one, respectively). A total of nine parasitized warbler nests produced 23 nestling warblers and only one cowbird. No warblers fledged from the other 59 parasitized nests. In contrast, 26 cowbird eggs hatched and could have fledged from 18 of these 59 nests. Thirty-one cowbird eggs in the remaining 41 parasitized nests were still viable at the time of my last visit. At least three of the parasitized warbler nests were destroyed by predators.

Amount of Parasitism

The 50 years during which I have studied Kirtland's Warblers can be divided into three definite periods. The first period extended from 1931 until the mid-1950s. During this period moderate parasitism of Kirtland's Warblers was observed (Table 22). Twenty-eight Kirtland's Warbler nests were studied. Three nests had incomplete clutches and seven nests were parasitized (25%). The 18 unparasitized nests contained 89 warbler eggs or 4.9 eggs per nest. The seven parasitized nests contained 14 warbler eggs (2.0 eggs per nest) and 12 cowbird eggs (1.7 eggs per nest). The second period extended from 1957 through 1971. In 1957 at Mack Lake, Oscoda County, 11 Kirtland's Warbler nests were observed. All were parasitized. These nests contained 39 warbler eggs early in the summer, but only 29 warbler eggs subsequently or 3.5 warbler eggs per nest at first sighting and 2.7 warbler eggs per nest later. These 11 nests also contained 19 cowbird eggs or 1.7 eggs per nest. From 1966 through 1971 no adult cowbirds were removed from the Artillery Range. Fifty-two Kirtland's Warbler nests were found of which 36 were parasitized (69.2%). The 36 parasitized nests contained 55 cowbird eggs (1.6 eggs per nest) and 68 warbler eggs (1.9 eggs per nest). During this period 42 pairs of warblers produced only 52 fledged warbler

nestlings (0.81 fledged nestlings per nest or per pair for the summer). Thirty-six cowbird eggs and nestlings were also removed and the data indicate that this interference allowed 15–29 warbler nestlings to fledge which would otherwise not have survived. The third period extended from 1972 through 1977 and will be discussed in a later section of this chapter.

Reduction of Parasitism

Shake and Mattsson (1975: 48) reported, "As early as 1966 Cuthbert and Radabaugh realized that parasitism posed a threat to the warbler population and undertook a study to determine whether selective cowbird trapping and shooting could reduce parasitism of warbler nests. The results showed that parasitism was reduced from 65 to 21 percent."

When the 1971 census of singing male Kirtland's Warblers was published (Mayfield 1972a) only 201 males were recorded indicating a drastic decline in population from the 1961 count. A meeting of interested persons and representatives from conservation agencies and organizations was held in Ann Arbor on 30 October 1971 and the Kirtland's Warbler Advisory Committee was formed. The organizations involved were the Michigan Audubon Society, the Michigan Department of Natural Resources, the U.S. Fish and Wildlife Service, the U.S. Forest Service, the University of Michigan, the Detroit Audubon Society, and the Pontiac Audubon Society (Shake and Mattsson 1975). During the winter of 1972, I published the results of my six year (1966–1971) study of Kirtland's Warblers at the Artillery Range, Crawford County. This study showed how severe cowbird parasitism had become and how low the reproduction rate of the warblers had fallen.

The Kirtland's Warbler Advisory Committee recommended that several actions be taken to ensure the recovery of the species (Shake and Mattsson 1975). These recommendations included:

- Encouraging state and federal agencies to manage more land for warbler nesting habitat through controlled burnings, selective cutting, and jack pine plantings.
- 2. Encouraging governmental agencies to acquire more lands suitable for warbler nesting.
- Encouraging governmental agencies to limit public use of warbler nesting areas during the nesting season.
- 4. Conducting an annual census of the warbler population, especially singing males.
- 5. Implementation of extensive cowbird control program on major nesting areas.

ENDANGERED SPECIES

ndations began in May 1972 under ildlife Service, the U.S. Forest Serural Resources, and the Michigan, Fifteen cowbird decoy traps were nesting areas in Crawford, Oscoda, we been operated each year from 25 placed in each trap as decoys. The d have a 1.2 m square entrance in are placed on a board beneath this ated with automobile exhaust which results of the trapping program for in Table 42. By 1981, 40,000 adult

Act of 1973 and the Michigan End, the Kirtland's Warbler Recovery of John Byelich, Chairman; G. W. les and R. Radtke, U.S. Fish and Ohio; N. I. Johnson, Michigan Dem has met twice each year since its Lit Kirtland's Warbler.

supervision of the U.S. Fish and f cowbird trapping on the nesting the third period of my field studies). in 230 nests. Eggs hatched in 190 is (69.6%). Nine hundred seventy-ved in these 230 nests of which 731 if fledged (63.3%). The number of 230 nests belonged to 198 pairs, pair per year was 3.11 (Table 43). burned regions is compared to the intations (Table 44). One hundred y burned regions. Eggs hatched in from 74 nests (69.2%). A total of gs hatched (77.5%) and 286 nest-oth nests and eggs in each region

ch size of 4.4 eggs. Even with the the average clutch size 4.2 eggs. unparasitized nests contained 94 a.5 eggs. Twenty-eight nests, both ge clutch size of 3.9 warbler eggs. 3 nests had an average clutch size

1966–1977.
Cowbirds,
f Brown-headed
Removal o
After
Success
Nesting
Warbler
Kirtland's
TABLE 42.

				Kirtland's Warbler	Warbler		
4					Nestlings	Er	
		Singing	No. of	Nestlings	Fledged	Number	pua.
	Cowbirds	Male	Pairs	Fledged	per Pair	Per Cer	of of
Years	Removed	Count	Studied	per Nest	During Year	Parasitized Nests	1 Nests
1966-1971	24 Eggs 18 Nestlings	201*	52	0.807	0.807	36 of 52 69.23	69.23
1972	2,200 Adults	200	56	2.72	3.35	2 of 32	6.25
1973	3,305 Adults	216	27	2.70	3.41	0 of 34	0.0
1974	4,075 Adults	167	54	2.87	3.35	6 of 63	9.52
1975	3,650 Adults	179	32	2.76	3.19	2 of 37	5.40
1976	4,299 Adults	200	30	2.70	2.97	2 of 33	90.9
1977	3,284 Adults	219	29	2.06	2.21	2 of 31	6.45

*1971 count

Numbers of adult cowbirds removed taken from Mattsson and DeCapita (1977: Table 4). Singing male counts taken from Mayfield 1972, 1973a, 1973b, Ryel 1976a, 1976b, 1978b

NEST OBSERVATIONS OF THE KIRTLAND'S WARBLER--A HALF CENTURY QUEST

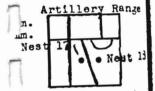
WALKINSHAW, L. 1988

.U·M·I Dissertation
Information Service

NESTENG SURCESS -VARTATION 66-70

outh, Sect. 17 ruck Trail & pad. lest 8.

m from the ening. It was



2-1-1 20-20-?

The only KW egg not

outh Sect.16

ound cover. It is 2.74 m tall. a hatched nestmale was caught 4.0 grams.

yout in 9 July). Soon the egg feet from the

> 1?-0-0 1C-1C-0C

Nesting Success of Kirtland's Warblers on the Artillery Range South, burned 19 August 1955, Sects. 15,16,17,727N,R2W,Crawford County, Michigan.

Nest Number	Obs	erved Conte		Eggs Hatch		You		
		KW	C	KW	C		_	
1900-1,	42.	0#	3E	0	0	0	0	3 Cowbird eggs rem.
2.	1.3.	0	2Y	0	2	0	2Y	fledged 2 Cowbirds
3.	44.	0	14	0	1	0	lY	4 1 H
1	15-	ō	14	ŏ	ī	ŏ	14	* 1 *
7,	45. 46.	ŏ	îy	ŏ	ī	ŏ	iŸ	# ī #
ξ,	17	ŏ	ìŸ	. 0	î	ŏ	lY	w î "
7,	48.	3	o T	2	ō	2	0	1001
	40.							Warblers
Total	- 1	4KM	9C	2KW	6¢	2KW		
- Nest	1,4	2. 1 K	W egg	found	outs	ide of	nes	t.
		_	_	_	_		_	
967-1,	49.	0	2E	0	2	0	0	2 C taken by Bluejay
2,	50.	2	0	2	0	2	0	2 KW fledged
3,	51.	4	0	3	0	3	0	3 KW "
4.	52.	<u>Li</u>	0	Ō	0	Ó	0	predation.
5	53.	3	0	Ö	ō	ō	0	deserted
6.	51. 52. 53.	ó	4E	ŏ	ŏ	ŏ	ŏ	deserted
rotal	74.	13KW	OC.	5KW	2C	5KW	<u> </u>	deserved
1958-1,	22	4K#	10	0	6	0 0	0	
900-1,	77.	41/11	10		- 0			predation
1969-1,	26	2	1	2	9	•	0	0 277 63 -44
1909-1,	50.	2		2		2		2 KW fledged
2,	57· 58.	4	1	0	0	0	0.	deserted
3,	58.	1	2	?	0	?	0	2 C eggs removed
4,	59. 60.	3	2	0	0	0	0	2 C eggs removed
5.0	60.	5	0	0?	0	0?	0	1 C egg removed 4 KW fledged
6.0	51.	L	0	4 -	Ō	4	0	J. KW fledzed
7.0	52.	3	2	ŏ	2	ŏ	(2)	2 C yg removed
A*?	53.	3	ō	1	ō	7	0	Not known
0,	54.	41354230	ĭ	ó	ĭ	Ó	ì	
rotal	54.							1 C fledged
CUAL		24KW	10C	6KN	3C	ÓKW	10	(probably 3 C fledged
1070 1	6-		•		•	• •	_	A - =
1970-1,6	٠ ڏر	3	2	3 2	0	3?	0	2 C removed
2,0	56.	3	1	2	0	2	0	1 C E removed
3,0	57. 58.	4	1	0 -	0	0	0	deserted-Cowbird
4.0	58.	5	0	4	0	4 3 1	0	4 KW fledged
5.0	59. 70.	Ŀ	1	J.	0	3	0	3 KW fledged; C E inf.
6.	70-	1	ĩ	ĭ	ŏ	า์	Õ	1 KW fledged; C E rem.
7'.	71.	4	ō	ō	ŏ	ô	ŏ	
ģ.,	7.	٥	0			ŏ	-	no eggs seen
٥,	72.	+	2	0	0	0	0 ·	deserted-Cowbird
, ,	73.	14	1	2	1	2	0	2 KW fledged; C Y rem.
10,	74.	3	0	1	0	1	0	1 KW fledged
11,	75.	3	0	0	o	0	0	predation
12,	76.	3745440143303431	0	0	ŏ	ō	ō	no eggs seen
13,	77.	3	2	3	2	30	ŏ	2 C y .removed
14,	78	7.	ō	3 3 0	2	3? 3? 3	0 -	2 0 J .1 01110 v 80
15.	70	4	0	3	0	2,4		2 150 61 - 4 4
15,		3	0	3	0	3	0	3 KW fledged
16,	37.	1	2	0	2	0	0	predator
17,8	51.	2	2	1	2	1	?	1 C, predator
Total	02.	1	1	0	_1	0	0	predator
OCAT		Takw	TOC	27KW	3C	17KN	OC	9 C (4E,5Y) removed
								, - (41,)1, 10,10,00
		,				9KW		ertain but doubtful 4 C might have fledge

ir.

nt Area. Sect. ord Co., Mich.

N

965 _{-74*N2} 9326

--74-N38

980

4003

ted in 1975

June 1975.

3

300

6

0 0

99

3 their 2nd

i eggs.

シ

Table 34. Kirolama's marbler Nesting Dist.to Area Eggs Eggs Young West LHW Nest Ht.of Dist.Hid- Dist.to Dense Laid Hatched Fleuged den Clearing growth No. No.Faced Close to Ground J.P. Tree Area No. Growth $-\underline{m} - \underline{c}\underline{m}$ m,cm 2.5 15 25 good 2 m rd. inside 1-166a N ARS 5555455550 4 ľú 25 122 15.2 25.2 25.2 2-167 * 7.3 m 11 SW LMA 4.57 3-168 2 m N bl open open ARS 4-169 NE good 5 m inside bl 5-170 1.83 ĺ m NE inside LMA 61 2.13 11 9.1 m 6-171 inside SE 0.91 7-172 WSW 1 m edge ARS 4.57 11 ** 8-173 SW bl 2.44 25 45 11 SW edge LMA 9-174 edge bl 17 53 10-175 W 2.44 inside LMA bl 11-176 20 11 inside 1.22 poor NE bl 11 1.22 30 12-177 E open open 45454554 bl 2.13 25 good 11 13-177a NE edge edge g 14-178 19 NW 30 edge edge 11 15-179 SE 3.96 45 edge edge ARS bl 3.0 0.61 3.35 1.21 91 28 16-130 0 N poor inside **b1** 3 m 17-181 NE good 150 m ARN 4 Ŀ bl 18 18-132 6 54 5 E 3 m ARS bl 17 edge 19-193 SW 61 edge ARN bl,g 10 OC OC 20-184 3.66 17 edge SE 3 edge ARS 3 bl 4536552 30 21-135 3.66 11 0 SE 1 òl 61,5 22.-185 .91 30 fair LMA6 SW 23-187 **b**1 7.01 121 ** LMA6 SE good 11 11 24-133 NNE 2.44 31 LMA5 g 1.52 ** ** 25-189 W 91 PC bl,g 26-190 11 ō Ó NE 2 ARS inside bl 1 m 27-191 28-192 SE 3.66 poor edge edge ARSW 30 bl 6.71 3.35 61 bcog edge edge 4 E ARSE bl 75 152 4553? 29-193 WW 1 m inside ARSE bl 10-194 11 3.96 2 m inside ARS bl 31-195 N 4.57 25 poor edge b1 edge 32-195 LMA ~-33-197 2? 34-198 ARN 10 10 10 --35-199 25 25 28 SE .91 good edge edge ML 0 0 b1,8 36-200 SW 1.82 ML 51 37-201 11 1.22 9 m SW edge AFN bl 33-202 NI 1.8 25 3 m inside 1 0 bl LMA 10 10 OC 39-203 19 3? 3 40-204 2.14 good bl SW 31 4 m inside LMA 41-205 2.44 28 39 SW good 1 m 352 3 g+ 42-205 LMA6 edge 1.52 61 edge bl SE 13-277 1.83 11 41 edge LMA6 61 edge 14-207n 1 m edge LMA 8 179 T33 119 (39) 105.11 1,521.2 The total included a nest I found Eggs

on PC but listed by Craig Orr, It my book Kirtland's Tables 37 & 45, pp.117 & 155 Included Craig Orr rec

aid ret

35

records.

31

73

Nests

County which owned m in thinning the Jack there was a Kirtland's at part of the project. Marquette, Mich. 19855. Anes nesting on the proplear Ishpeming. Land's Warblers. I figured in size or 96,068.73 sq. A Sparrow nest, photonow was real tame. He kept singing all the pines for food. So I mission to go down noto Marsh Creek area is about 15-16 mission was much different soil was much different soil was much different soil was much different soil was much different
--

		-KALIK	Nest No	#ANDLE	TO DATION	AS ALVII	TS - MIC	HIUAN.		Table	County
No	•	Band No.	Year, Mai	r Year		Fourth Year	Fifth Year	Sixth Year	Seventh Year	Eighth Year	Town, Rang Section
		39-34175 (2) F	6-23-40 38-7053 5-5-5				-i 21				Crawford 26N, LW, 5
2		70 - 94220 (7)	AR17-NN 5-28-6		NF	NF 	AR17 F.N.	ar16-n6 6-30-69 75 - 3 <u>6</u> 687		 2	Crawford 27N,2W,16
3.	7	0-94978 (6) F	AR17- 6-25-65	AR17 6-66		AR17-N 668	AR17 669	AR17-N2 5-31-70 61-24179 3,10-2-2	,		Crawford 27N,2W,17
4.	5	9-99062 (5) F	AR9- 06-30-65	NF	AR17-N6 7-04-67 74-0362 4C-0-0		AR17 669				Crawford 27N,2W,17
5.	11:	2-09l ₁ 28 (8)	AR9-NNF 5-30-66 F NB	NF	NF	NF	06-16-70	6-21-71 80-571	N31 AR16-N10 6-14-72 88 80-5718 5-11-0;14-	88 NB	Crawford 27N,2W,9, 16
6.	5	6-57l ₁ 12 (7)	AR17-N1 7-04-66 56-57413 1,30-0-0	7-03-67 NB	7-05-68 NNF	75-366	7 AR17-N3 9 6-01-70 93 121-93 -0 4,10-0	TAR17-NE 0 671 1335 NB	7 AR17-N1 6-16-72 NB 5-0-0		Crawford 27N,2W,17
7•	5		AR8-N2 7-05-66 56-57415 2C-2C-2C	Region Burned	nf	NF	NF	NF	AR15-N5 5-30-72 81-58990 2C-0-0; 1.2C-2C-	6-29-73 81-58948 5-5-5	Crawford
8.	5	6-57410 (1)	AR8-NNF 7-05-66 NB	****					******		Crawford 27N,2W,8

F= Female (his mate); N=Nest No.; NF= Not found; NNF= Nest not found; Success of nest and contents given 5-5-5 = 5 eggs laid, 5 hatched; 5 fledged. C= Cowbird LM= W of Lake Margrethe; AR= Artillery Range. F.N. Dr. Frank Novy banded or noted this bird.

p.2	- Table 59).	KIRTLANI	D'S WAR	BLER MA	ALES BANDE	D WHEN A	DULTS		Table 69	
NO.	Band No.	First Year	Second Year	Third Year	Fourth Year	rifth Year	Sixth Year	Seventh Year	Eighth Year	County T,R,Sect.	
9.	56-57416 (1) F	AR16-N7 7/05/66 56-57419 3-2-2								Crawford 27N,2W,16	M. 10
10.	74-03622 (3)	AR17-N1 6/30/67 74-03621 2C-2C-0C		AR17-N 6/28/1 75-366 5,10-0-	969 - 92					Crawford 27N,2W,17	
11.	74-03623 (1)	AR17-N3 7/01/67 74-03624 4/3/(3?)								Crawford 27N,2W,17	
12.	74-03629 (1)	AR17-N4 7/04/67 74-03630 4-0-0			 -					Crawford 27N,2W,17	300
13.	74-03634 (4) 74	AR17-N2 7/04/67 -03631 2-2-2	,a-,		61-2418	3,17 38 0 0;2,2c-1-2				Crawford 27N,2W,17	
14.	75 - 36689 (1)	AR17-N1 6/30/69 75-36686 3,1C-2-2								Crawford 27N,2W,17	
	75 - 36695 (2)	AR17-N9 6/29/69 F- NB	AR17-N18 7/09/70 61-2417	3					·	Crawford 27N,2W,17	
16.	75=35656 ⁻	0/29/09	0/18/70								
100 10 1 40	The stander is a second	14-14003	74-1486	winds a security.	a designation of	Sol her	W 1 . C.			Crawford 27N,2W,17	
		1.180=9=9	dande		Selfaborar	and the first of the second of	"在这个人				
NO.	Band No. 01-24177	Year ARIO-NO	dande		Non H	and the first of the second of	"在这个人			County T,R,Sect.	
17.	61-24177 (1)	Year AR16-N6 7/08/70 61-24171	Year	Third	NICON NO	Les BAND	A HERE	MUT Sixth		27N, 2W, 17	
19.	61-24177 (1) F 61-24176 (3)	Year ARIS-NG 7/08/70 61-24171 4,1C-1-1 ARIS-NI1 7/08/70 NB 3-0-0	AR16-N2 6/04/71 NB 3,1C-0-	713 AR 6/11 110- 0 5-5-	[7=n]1- 1/72 -09079	Les BAND	A HERE	MUT Sixth		County T,R,Sect. Crawford	
18. 19.	61-24176 (3) F 61-24176 (3) F 61-24180	Year AR16-N6 7/08/70 61-24171 4,10-1-1 AR16-N11 7/08/70 NB 3-0-0 AR17-N1 6-22-70 116-2462 3.20-3-6	AR16-N2 6/04/71 NB 3,1C-0- 3,1C-?-	713 ARI 6/11 110-0 5-5-7	[7=N]1- 1/72 -09079 -0	Les BAND	A HERE	MUT Sixth		County T,R,Sect. Crawford 27N,2W,16	
19. 19.	61-21176- (3) F 61-21180- (1) F 61-21180- (1) F 61-21183- (4)	Year AR16-N6 7/08/70 61-24171 4,1C-1-1 AR16-N11 7/08/70 NB 3-0-0 AR17-N1 6-22-70 116-2462 3,2C-3-(AR17-11 6-16-70 61-24174 4-3-3?	AR16-N2 6/04/71 NB 3,1C-0- 3,1C-?-	713 ARI 6/11 110- 0 5-5- 710 ARI 75-3	[7=N]1- 1/72-09079-0 	AR17-N6,286-15-73	Pirth Year	MUT Sixth		County T.R.Sect. Crawford 27N,2W,16 Crawford 27N,2W,16	
19. 19.	61-21176- (3) F 61-21180- (1) F 61-21180- (1) F 61-21183- (4)	Year AR16-N6 7/08/70 61-24171 4,1C-1-1 AR16-N11 7/08/70 NB 3-0-0 AR17-NI 6-22-70 116-2462 3,2C-3-(AR17-14 6-16-70 61-24174 4-3-3? AR16-N4 6-16-70 61-24189	AR16-N2 6/04/71 NB 3,1c-0- 3,1c-?- 8 3) AR17-N3 6-04-71 NB 2,1c-0-	713 ARI 6/11 110- 0 5-5- 710 ARI 75-3	[7=N]1- 1/72-09079-0 	AR17-N6,286-15-73	Pirth Year	MUT Sixth		County T.R.Sect. Crawford 27N,2W,16 Crawford 27N,2W,16 Crawford 27N,2W,17 Crawford	301
19. 19. 20. 21.	61-21/176- (1) F 61-21/176- (3) F 61-21/180- (1) F 61-21/183- (4) F 61-21/190- (1) F 61-21/190- (1) F	Year AR16-N6 7/08/70 61-24171 4,10-1-1 AR16-N11 7/08/70 NB 3-0-0 AR17-N1 6-22-70 116-2462 3,20-3-(AR17-11 6-16-70 61-24174 4-3-3? AR16-N4 6-16-70 61-24178 5-4-4 AR17-N16 6-23-70 61-24178 1.20-20-6	ARIO-N2 6/04/71 NB 3,1C-0- 3,1C-?- 8 3) ARI7-N3 6-04-71 NB 2,1C-0- 2,3C-0- NF	713 ARI 6/11 110.0 5-5-7 75-3 0 5-5-0 NF	[7=N]1 /72 -09079 -0 	AR17-N6,286-15-73	Pirth Year	MUT Sixth		County T,R,Sect. Crawford 27N,2W,16 Crawford 27N,2W,16 Crawford 27N,2W,17 Crawford 27N,2W,17 Crawford 27N,2W,17	301
79. 79. 70. 71. 72.	61-21176 (1) F 61-21176 (3) F 61-21180 (1) F 61-21183 (4) F 61-21190 (1) F 61-21190 (1) F 61-21191 (4) F	Year AR16-N6 7/08/70 61-24171 4,1C-1-1 AR16-N11 7/08/70 NB 3-0-0 AR17-N1 6-22-70 116-2462 3,2C-3-(AR17-11,6-16-70 61-24174 4-3-3? AR16-N4 6-16-70 61-24178 1,2C-2C-(AR17-N16 7-09-70 61-24178 1,2C-2C-(AR17-N18 7-09-70 61-24173 1,1C-1C-0	ARIG-N2 6/04/71 NB 3,1C-0- 3,1C-7- 8 3) ARI7-N3 6-04-71 NB 2,1C-0- 2,3C-0- NF 0 ARIG-N1 6-26-71 80-5720 2,1C.2.	713 ARI 6/11 110 0 5-5- 7 710 ARI 75-3 0 5-5 0 NF	[7=N]1- 1/72-09079-0 -0	ARI7-N6,28 6-15-73 75-3690 4-0-0 5-3-3 81-58923	Pirth Year	MUT Sixth		County T.R.Sect. Crawford 27N,2W,16 Crawford 27N,2W,16 Crawford 27N,2W,17 Crawford 27N,2W,17 Crawford 27N,2W,17 Crawford 27N,2W,16	301
19. 19. 20. 21. 22. 23.	61-21/176- (3) 61-21/180- (1) F 61-21/180- (1) F 61-21/183- (4) F 61-21/190- (1) F 61-21/190- (1) F 61-21/195- (3) F 80-57183- (2)	Year AR16-N6 7/08/70 61-24171 4,1C-1-1 AR16-N11 7/08/70 NB 3-0-0 AR17-N1 6-22-70 116-2462 3,2C-3-(AR17-11,6-16-70 61-24174 4-3-3? AR16-N4 6-16-70 61-24178 1,2C-2C-(AR17-N16 7-09-70 61-24178 1,2C-2C-(AR17-N18 7-09-70 61-24173 1,1C-1C-0	AR16-N2 6/04/71 NB 3,1C-0- 3,1C-?- 8 3) AR17-N3 6-04-71 NB 2,1C-0- 2,3C-0- NF 0 AR16-N1 6-26-71 80-5720; 2,1C,2, 4R17-N1 5-27-72	713 ARI 6/11 110.0 5-5-7	[7=N]1- 1/72-09079-0 -0	ARI7-N6,28 6-15-73 75-3690 4-0-0 5-3-3 81-58923	Pirth Year	MUT Sixth		County T.R.Sect. Crawford 27N,2W,16 Crawford 27N,2W,16 Crawford 27N,2W,17 Crawford 27N,2W,17 Crawford 27N,2W,17 Crawford 27N,2W,17 Crawford 27N,2W,17	301

No. Ban	d No.	First Year		Third Year	Fourth Year	Fifth Year	Sixth Year	Section Town, Range, etc.	
6. 80- (1	·57186	AR16-N11 6/24/71 61-24171 2-2-2						Crawford Co. 27N,2W,16	
27. 80-	-57191 !)	AR16-N6 A 6/24/71 5 80-57190 8	30/72					" '	_
	•57192 (2)		AR16-N9 6/18/72 81-58921 5-5-(4.)					"	
29. 80-	-57195 (1)	AR17-N1 6/28/1971 F- NB 5-4-0						Crawford Co. 27N, R2W, 17	
30. 81-	-58934 (1)	LMA5-N19 6/20/72 81-58935 5-5-5						Crawford Co. 28N, 1W, 5	
31. 81-	-58936 (2)	LMA5-N20, 6/20/72 61-24179 5-5-5 4-4-4	LMA5-N10, 5/30/73 61-24179 4-4-4 3-3-3	.33				Crawford Co. 28N,1W,5	
32. 81.	-58976 (3)	LMA5-N29 6/26/72 81-58975 4-3-3	LMA -5 NF Unknown	LMA5-N 6/01/1 Unknow 4-0-0:0	n			Crawford Co. 28N,1w,5	
	. 1 X + 2 W								
The same of the same of	and No.	First Year	Second Year	Third Year		h Fifth		h Co	unty , R-W
33. 81-	-58986	LMA5N25,3L	ļ					- Cra	ford

۰ ه	Band	No.	First Year	Second Year		Fourth Year	Fifth Year	Sixth Year	County T-N, R-W
3 •	81 - 589	F	LMA5N25, 34 6/26/1972 81-58980						Crawford T28N,R1W Sect.5
-		'	5 <u>-</u> 5 <u>-</u> 0 <u>;</u> 3 <u>-</u> 3 <u>-</u> (3	1?1			- 		
4.	81-589	987	ARS17-N16						Crawford
	(1)	F	6-27-1972 61-24178						T27N,R2W Sect.17
_			5-5-5						
۲.	81-589	288	PC-12-N27						Crawford
•	01-70	,00	6/24/1972						T25N,R3W,
	(1)	F	81-58989						Sect.12
_			<u>5-5-5</u>					1=7	
5.	81-590	000	LMA-5-N28	LMA-5-N19	LMA5-N12	LMA5- N3	LMA5-N	125 LMA NF	Crawford
			N35	6/22/73	N13	5/29/197	75 6-08-1		T28N, RIW
	(6)	F	6/12/1972 81 - 58999	820-89272	6/10/74	NB	(1) F N (2) 860-		Sect.5
				5-1-0	820-89228			2,1C-1C-0	
_					4-3-3;5-5		_ 2 ± ±,	2,2,7,2,3,7,7,7,7	
7 •	81-588	154	ARS-16-N24	ARS10-N20 6-29-1973	ARN9-N34	ADV O V	ml.		Crawford
	(4)			80-57193	6-27-1974				T27N,R2W, Sect.16
	(4,	F	80-57193	5-5-0		n F NB	,10		5000.10
_		_ 5.	-5-5;4-3- <u>3</u>	. 	1 <u>C-1</u> C-1 <u>C</u>	_ 5-5-5		- 	
8 .	820-86	202	ARS-16-N5	ARS-16-N18	3 ARS16-N2				Crawford
•	JE U -U,	,	6/19/1973	6/04/1974	N12				T27N.R2W
	(3)	F	61-24171	81-58974	05 &06,7				Sect.16
			5-5 - 5	5-5-5	81-58974 5-0-0:5-				

No.	Band No.			hird Tear	Fourth Year	Fifth Year	County etc.	
40.	820 - 89214 (1) F	LMA5-N11 N35 6/23/1973 81-58935 5-4-4:4-4-43	0				Crawford 28N,1W, Sect.5	
41.	820 - 89264 (1)F	LMA5-N31 7/02/1973 81-58968 141-1					**	
 42.	830-20501	ARN8-NNF 5/30/1974 ??					Crawford 27N,2W, Sect.8	
43.	830-20502	5/30/1974		ARN8-NNF 6/25/1976 ? ? _?				304
 M -	830 - 20503 (2)	6/03/1974	ARS16-N11 6/08/1975 NB 5-5-5				Sect.16	
45.	830-20504 (3) F	ARS16-N8 6/21/1974 75-36690 5-5-5_		ARS16-N26 6/26/1976 NB <u>4-3-0</u>				
46.	830 - 20510 (4)	ARS16-N3 6/21/1974 61-24178 5-2-2		ARN9-NNF 6/25/1976 ? ?	ARN8-NNF 5/13/1977 ? ?			
47 . Pat	(3)	LMA5-N6, կկ 6/22/197կ 633-2352կ	6/01/1975	LMA5-N4 6/03/1976 61-24179	***************************************		Crawford 28n,1w,5	
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116					6.71	A CONTRACT		
No.	Band No.	oo Pirst Year	Seco Year			AS ADULTS Fourth Year	County	
	830-20539		ARN8- N 4 6/02/19	Ye NF	1rd	ACCURATE TO THE PARTY OF THE PA	County T-R-Sect Crawford 27N,2W Sect. 8	_
48•	830-20539 (2) 1 830-20585 (1)	ARNS-N17 6/23/1971 820-89269	ARN8- N 4 6/02/19 9 ? ?	Ye NF	1rd	Fourth	T-R-Sect Crawford 27N,2W	_
48.	830-20539 (2) 1 830-20585 (1)	Year ARN8-N17 6/23/1971 820-89269 5-4-4 LMA5-24,1 6/22/1971 6/22/1971 1-5-5-5;4-4 LMA5-N7 6/16/1976	ARN8- N 1 6/02/19 ? ? 10 1-4-4 LMA5-N1 5/13/19	Ye NF 75	1rd	Fourth	Crawford 27N,2W Sect. 8	_
48.	830-20539 (2) 1 830-20585 (1) 860-40301 (2)	Year ARN8-N17 6/23/1971 820-89269 5-4-4 LMA5-24,1 6/22/1971 61-24179 5-5-5;4-4 LMA5-N7 6/16/1976 830-20530 5-5-5 LMA5-N13 6/17/1976	LMA5-N1 5/13/19 LMA5-N1 5/13/19 1-4 LMA5-N1 5/13/19 0 830-205 0-0-0;4 LMA5-N1 5/13/19 620-8926	NF 75 75 	1rd	Fourth	Crawford 27N,2W Sect. 8 	305
48.	830-20539 (2) 830-20585 (1) 860-40301 (2) 860-40302 (2)	ARN8-N17 6/23/1971 820-89269 5-4-4 LMA5-24,1 6/22/1971 61-24179 5-5-5:4-1 LMA5-N7 6/16/1976 830-20530 5-5-5 LMA5-N13 6/17/1976 820-89201 5-5-5 LMA5-N10 6/21/1976	LMA5-N1 5/13/197 LMA5-N1 5/13/197 10 14-14 LMA5-N1 5/13/197 820-8920 5-5-5 LMA5-NNF 5/13/197	Yen NF 75	1rd	Fourth	T-R-Sect Crawford 27N,2W Sect. 8 Crawford 23N,1W,5	305
48. 49.	830-20539 (2) 830-20585 (1) 860-40301 (2) 860-40302 (2) 860-40302 (2) 860-40302	MAS-N13 6/23/1971 820-89269 5-4-4 LMAS-24,1 6/22/1971 6/22/1971 6/16/1976 830-20530 5-5-5 LMAS-N13 6/17/1976 820-89201 5-5-5 LMAS-N10 6/21/1976 820-89229 19-4-4 LMAS-N20 6/21/1976	LMA5-N19 820-8920 - 5-5-5 LMA5-N19 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9 9	Yen	1rd	Fourth	T-R-Sect Crawford 27N,2W Sect. 8 Crawford 23N,1W,5	305

No.	Band No.	First	Second Year	Third Year	County T-R-Sect
 56.	860-40391	Year ARN9-NNF 7/18/1976 NB NNF			Crawford 27N,2W Sect.9
 57•	860-40393 (2)	LMA5-N29 7/19/1976 860-40392	LMA5-N5,27 5/15/1977 860-40326 5-0-0;4-0-0		Crawford 28N,1W Sect.5
 58•	 880-52701 (2)		LMA6-NNF 5/17/1977 ? ?		
 5 9 •	980-52601 (1)	Kyle Lk-N2 5/17/1977 830-20580 5-5-0			Crawford 27N,2W & Sect.20 &
6 0.	880-52607 (1)	ARN8-N9 5/13/1977 880-52608 5-4-4			Crawford 27N,2W Sect.8
61.	870-47013	Petawa, Ontar 7/1/1977 No female for No nest four	ound		ONTARIO, CANADA Petawawa No Military Base
62	Band no.?	Boon, T21N, R Wexford Co. 7-02-1972 with fledge	11W		Wexford Co. T21N,R11W, Sect.34 S of Boon

W-Pemale band no. AR, ARS, ARN- Artillery Range; Artillery Range South (burned 1955)
Artillery Range North, burned 1967.

No. Band No.	Piret (Second Year	Third	Fourth Year	County Town, Range
1. F-46468 (1) M	23 June 1932 Not Banded 1,2C-1,0C-?,0C				Oscoda 27 N, 1E, Sect.22
2. 38-70530 (3) M	LM5-N1 24/6/1938 not banded 4,1C-1-1		LM5-N1 6/23/1940 39-54175 5-5_		Crawford 26n,4W Sect.5
3. 56-57413 (1) M	ARS17-66N1 7/04/1966 56-57412 1,3C-0-0				Crawford 27N,2W Sect.17
4. 56-57415 (1) M	ARN8-66N2 7/05/1966 56-57414 20-20-30		 -		Grawford 27N,2W Sect.8
5. 56-57419 (1) M	ARS16-66N7 56-57416 7/05/1966 3-2-2				Crawford 27N,2W Sect.16
6. 74-03621 (1) M	ARS17-1967N1 6/30/1967 74-03622 0,2C-2C-0				Crawford 27N,2W Sect.17
7. 74-03624 (1)	ARS17-67N3 7/01/1967 74-03623 4-3-?				11
8. 74-03627	ARS17-67NĞ 7/03/1967				"

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_	Pable 70		First Year		cond	Third Year	Four Year		ifth Coar	Sixth Year	County Town, Ra- nge, Sec
. 7	4-03630 (1)	м	ARS17-67 7/04/196 74-03629 4-0-0	57							Crawford 27N,2W, Sect.17
). 7	(1)	 M	ARS17-6' 7/04/19 74-03631 2?-2-2	67				-			
 L. 7	74-14863 (3)	м	ARS17-16/19	68 6 7	ns17-69n3 /29/1969 5-36696	ARS17- 6/17/1 75-366 3-1-1	96				#
 2. 7	75-36686 (1)	м	ARS17-6 6/30/19 75-3668 3,1c-2-	9N1 - 969				 			
3. 1	 75-36687 (2)	м	ARS16-6 6/30/19 70-9422 4-4-1	59N6 A 969 6	RS17-70N9 /17/1970 0-94220 1C-2,1C-2			 ', 			Sect.16
4.	75 - 36690 (6)	М	ARS17-1 6/29/19 NB 4,1C-0-	N2 1	ARS17-70N1 /22/1970 NB 3-3-3	NF	ARS17- 6/14/1 61-241 5-5-	9 72 83	ARS17-7 73 6/29/19 61-241 4-0-0;5	83 5-5-	74 2504
 5.	 75-36691		ARS17-6	- — — — 69мЦ -	 			-			Sect.
6-	(1) 75≅38692°	М	6/29/19 NB 3.20-7- TRE17-1		and the same	odinan serimera					
	(1) 75=)5652	ACV TO STATE	- 3,20-7, - 3,817-1	50NS				W ADULT			
	(1) 755)8692	70	NB - 3,20-7 - 3,817-1 - 3,817-1	50NS	Third Year		urth	m Adulfa Fifth Year	Sixth Year		County T-R-Sect
No	75-3669 . Band N	76. 19. 19. 19. 19. 19. 19. 19. 19. 19. 19	NB 3,2C-7- AR817- C/89/1	Second Year	Third	For	urth	Fifth	Sixth	Seventh	
17.	75-3669 (1) - 75-3669 (1) - 61-2417 (4)	73 / M / 2 / 1 / M 61	NB 3.2C-7: ARS-69N7 6/29/1969 56-57412 ,2C-2G-0 ARS-N 6 7/07/70 1-24172	Second Year	Third Year	For Yes	urth ar S-N5 19/73 0-89202	Fifth	Sixth	Seventh	Crawford 27N,2W,
17.	75-3669 (1) - 75-3669 (1) - 61-2417 (4) - 61-2417	M 22 271 M 67 44	NB - 3.2C-7. - 7.29/1969 - 7.29/1969 - 7.29/1969 - 7.29/1969 - 7.07/70 - 24172 - 1C-1-1 - 1C-1-1 - 1C-1-1 - 7.09/70 - 7.5-36695	Second Year ARS-N1:6/24/7180-5718 2-2-2	Third Year	For Yes	urth ar S-N5 19/73	Fifth	Sixth	Seventh	T-R-Sect Crawford 27 N, 2W, Sect.17 Crawford 27 N, 2W
17.6 18.	(1) 75-3669 (1) 75-3669 (1) 61-2417 (4) 61-2417 (1) 61-2417 (1)	23 M 22 M 614 M 614 M	NB 3,2C-7: 7877-1 7879/19 ARS-69N7 6/29/1969 56-57412 2C-2C-0 ARS-N 6 7/07/70 1-24172 ,1C-1-1 ARS-N18 7/09/70 ARS-N18 7/09/70 61-24183	Second Year ARS-N1:6/24/7180-5718 2-2-2	Third Year	For Yes	urth ar S-N5 19/73 0-89202	Fifth	Sixth	Seventh	T-R-Sect Crawford 27 N, 2W, Sect.17 Crawford 27 N, 2W
17.6 	(1) 75-3669 75-3669 (1) 61-2417 (1) 61-2417 (1) 61-2417 (1)	23 (do - 1)	NB 3.2C-1: 2.29/1969 First Year ARS-69N7 6/29/1969 56-57412 2C-2C-0 ARS-N 6 7/07/70 1-24172 1C-1-1 ARS-N18 7/09/70 61-24183 2.3-3	Second Year ARS-N1:6/24/7180-5718 2-2-2	Third Year 6 ARS-N16 6/27/72 81-5898	AR: 6/: 82:	S-N5 19/73 0-89202 5-5-5	Fifth Year ARS-N3 5/31/74 830-2051	Sixth	Seventh	T-R-Sect Crawford 27N,2W, Sect.17 Crawford 27N,2W Sect.16
17. 18. 	(1) 75-3669 (1) 75-3669 (1) 61-2417 (1) 61-2417 (1) 61-2417 (1) 61-2417 (1)	23 (do-1) M 2 M 2 M 60 H 60 M 61 M 6	NB - 3.2C-7: - 3	Second Year ARS-N1:6/24/7180-5718 2-2-2	Third Year	AR: 6/: 82:	S-N5 19/73 0-89202 5-5-5 S-N17 19/73 NB -0-0 N33 17/73	Firth Year ARS-N3 5/31/74 830-2051 5-2-2 LMA-N24 N40 6/22/74 830-2058	Sixth Year	Seventh Year 6 IMA-NI4 5 6/03/76 19 830-20519	T-R-Sect Crawford 27N,2W Sect.16 Crawford 27N,2W Sect.16 Crawford 27N,2W Sect.17

No. Band	No.	First Year		Third Year	Fourth Year	County Town, Range Section
25. 61-241 (1)	.89 M	ARS17-70N4 6/15/1970 61-24190 5-4-4				Crawford 27N,2W, 17
26. 121 - 93 (1)		ARS17-70N3,13 6/16/1970 56-57412 3,2C-3,2C-(31)				"
27. 80 - 571 (1)		ARS17-71N4 6/22/1971 80-57184 2,2C-1C-0				Sect.16
28. 80-57] (2)		ARS16-71N5 6/23/1971 112-09428 2-2-2	ARS16-72N10 " 72N31 112-09428 6/14/72 5-4-0;4-3-3			
 29. 83-571 (2		ARS16-17N6 6/24/1971 80-57191 2-2-2	ARS16-17 N15 5/30/1972 80/57191 5-4-4	;		Sect.line 16-17
30. 80-57: (3		ARS16-N15 6/27/1971 80-57192 2,1c-2,1c-?		ARS16-N26 6/29/1973 81-58854 5-5-0		Sect.16
31. 80-57: (1		ARS16-71-N14 6/28/1971 61-24195 2,10-2,10-2				

No.	Band No.	*	First Year	Second Year	Third Year	Fourth Year	County Town, Range, Sect.
32.	81-58921	M	ARS16-72N9 6/18/1972 80-57193 5-5-(4)				Crawford 27N,2W,Sect.16
33.	81-58923	М	ARS17-72N1 6/18/1972 80-57183 5-3-3	ARS16-73N3 6/23/1973 61-24191 5-5-0			Sect.17
34.	81 - 58922 (1)	<u>M</u>	ARE15-72N7 6/18/1972 _NB 5-4-3				" Sect.15
15.	81 - 58935 (2)	M	LMA5-72-19 6/20/1972 81-58934 5-5-5	LMA5-73N11, 6/18/1973 820-89214 5-4-4;4-4-0			Crawford 28N,1W,Sect.5
6.	81-58943	M	ARS16-72N4 6/21/1972 61-24195 5-5-5				Crawford 27N,2W,Sect.16
7.	81-58974 (4)	м	ARS17-72N18 6/21/1972 NB 4-2-2		ARS16-74N18 6/06/1974 820-89202 5-5-5	ARS16-75N2 75N12 5/25/1975 820-89202 5-0-0;5-3-0	Crawford 27N,2W,Sects. 10,17
18.	81 - 58975 (1)	M	LMA5-72N29 6/26/1972 81-58976				Crawford 28N, 1W, Sect.5

10.	Band No.	Year	Second Year	Third Year	Fourth Year	Fifth Year	County Town, Range, Sect.
10.	(1)	PC12-72N27 6/21/1972 81-58988 5-5-5					Crawford 25N,3W Sect.12
11.	(3)	ARE15-72N8 6-28/1972 56-57414 1,2C-2C-1C		ARE15-N28 6/24/1974 NB _ 4-4-4			Crawford,27N,2W Sect.15
12.	(1)	LMA5-72N28, 6/25/1972 81-59000 3-3-3;4-4-4				 ,	Crawford,28n,1W Sect.5
±3•	820-89201 (5) M	LMA5-73N2 6/18/1973 116-24662 _5-4-4_			LMA5-76N13 6/17/1976 860-40302 5-5-5	LMA5-77N15 6/13/1977 860-40302 5-5-5	
44.	(1)	ARS16-73N14 6/19/1973 820-89203 					Crawford,27N,2W Sect.16
15.	(1)	LMA5-73N12 6/21/1973 80-57180 _5-5-5			•		Crawford,28N,1W Sect.5
46.	820-89239 (1)	PC12-73N25 6/28/1973 NB_5-5-5					Crawford,25N,3W Sect.12
17 •	820-89263 (1) M	ARN8-73N30 7/01/1973 81-58909		****	-		Crawford, 27N, 2W Sect. 8

18.	Band No.	First Year	Second Year	Third Year	Fourth Year	Fifth Year	County Town, Range, Sect.
-	820-89272 (1) M	LMA5-73N19 7/13/1973 81-59000 _ <u>5-1-0</u>			•		Crawford T28N, R1W, sect.5
9.	830-20518 (2) M	LMA6-74N23 N42 6/22/1974 820-89211 _6_5_5 ₁ 5_5_4	LMA5-75N14 6/17/1975 NB _4-4-0_			Part .	Crawford T28N, RlW, Sect.6
). _	830 - 20524 (1) M	LMA5-74N6 6/22/1974 830-20519 5-4-4_					Crawford T28N,RlW,Sect.5
·	830 - 20580 (4) M	ARS16-74N1 6/27/1974 830-20510 5-5-4			KL20-77N2 6/22/1977 880-52601		Crawford T27N,R2W, Sects.16,20
	860-40308 () M	LMA5-76N8, 32 6/17/1976 820-89206 4-4-3:4-4-4	! -				Crawford T28N,RlW,Sect.5
	() . M	LMA5-76N5 6/19/1976 820-89224 5-5-5					"
. 8	760 <u>-</u> Д0328 - (2) м	LMA5-76N12 - 6/20/1976	LMA5-77N17, 6/16/1977 820-89206	3e			

KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 3
HABITAT MANAGEMENT

Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan

MARC D. ABRAMS AND DONALD I. DICKMANN Department of Forestry, Michigan State University, East Lansing, MI, U.S.A. 48824 Received June 3, 1981

ABRAMS, M. D., and D. I. DICKMANN. 1982. Early revegetation of clear-cut and burned jack pine sites in northern Michigan. Can. J. Bot. 60: 946-954.

Revegetation of clear-cut and (or) burned jack pine (Pinus banksiana Lamb.) sites in northern lower Michigan characterized during the first 5 years following treatment. Burning promoted the establishment of a large variety of sp. typical of unburned areas. A total of 89 species was recorded on burned sites, of which 40 were exclusive, compared species on unburned sites, of which only 2 species were exclusive. Burned sites consistently showed greater species in compared with unburned sites of the same age. Low species diversity on the older unburned clear-cuts (years 3 to 6) and burned sites was directly influenced by the dominance of the sedge Carex pensylvanica. The total domination of Care. 86% relative cover) on many of these sites appears to be unique to northern lower Michigan. It is hypothesized that Care as an opportunistic species, monopolizes the space and soil resources liberated following disturbances and support excludes other species.

ABRAMS, M. D., et D. I. DICKMANN. 1982. Early revegetation of clear-cut and burned jack pine sites in northern Michigan. Can. J. Bot. 60: 946-954.

Des pinèdes à pin gris (Pinus banksiana Lamb.) ayant été soumises à une coupe à blanc et (ou) incendiées dans la région du Michigan inférieur, les auteurs caractérisent la reprise de la végétation pendant les 5 premières années après les traitens feu provoque l'établissement d'un grand nombre d'espèces qui ne sont pas typiques des endroits non incendiés. Autoespèces ont été notées sur les sites incendiés, y compris 40 espèces exclusives, tandis que sur les sites non incendiés, \$100 per les sites non incendiés non ont été relevées dont seulement 2 étaient exclusives. Les sites incendiés présentent toujours une richesse spécifique plus que les sites non incendiés de même âge. La faible diversité spécifique des sites coupés à blanc les plus âgés (depuis 3 à fait certains sites incendiés est directement attribuable à la dominance du Carex pensylvanica. La dominance de ce Carex (attribus) jusqu'à 86% de recouvrement relatif) dans plusieurs de ces sites semble être un phénomène unique à la région étudiée. 🛵 émettent l'hypothèse que ce Carex, agissant comme une espèce opportuniste, monopolise l'espace et les ressources édit libérées après les perturbations et qu'il élimine ou exclut les autres espèces.

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Introduction

The role of fire as an ecological factor and a management tool in the Lake States is well documented (Ahlgren 1974; Cayford 1970; Eyre and LeBarron 1944; Heinselman 1973; Vogl 1970). A large portion of this work focuses on the ecology and management of jack pine (Pinus banksiana Lamb.). Jack pine is a typical postfire pioneer species whose present distribution is directly related to wildfires following early pine logging (Benzie 1977). Throughout most of its range, jack pine produces serotinous cones and requires a mineral seedbed for optimum germination. Therefore, most attempts to manage jack pine have utilized prescribed burning.

Studies of prescribed burning have mainly focused on slash reduction, seedbed preparation, and responses of seedlings to various environmental factors (Beaufait 1962; Eyre and LaBarron 1944). Limited detailed work, however, has been conducted on plant succession on jack pine sites following logging and (or) burning in the Lake States (Ahlgren 1960; Krefting and Ahlgren 1974; Ohmann and Grigal 1979; Vogl 1970). Thus, to was undertaken to characterize early revegetal clear-cut and (or) burned jack pine sites in northern Michigan where this species is a predominant nent of the tree vegetation on sandy soils.

Description of study area

The work was conducted during the summers of 1980 in Roscommon, Crawford, Oscoda, and counties in northeast lower Michigan. The elevation counties generally lies between 275 and 365 m above with little surface relief. The topography is a direct result Wisconsin glaciation, with level areas consisting of and till plains or ground moraines (Veatch et al. 1923) the near-complete clearing by the lumber industry 1800's, these areas were largely occupied by dense and coniferous forests. Small areas of bog, man grassland were also present. Today these counties patchwork of small woodlots, second- and thir hardwood and coniferous forests, farmlands, brack lands, and swamp forests.

The Grayling sand soil series (a mixed, frig udipsamment) comprises large areas in these count characterized by its loose consistence, incoherent sandy or single-grained texture throughout, and per-

¹Michigan Agricultural Experiment Station journal article No. 9983.

r Michigan

nonretentiveness of moisture. Average moisture content during the growing season is very low to a depth of 1 m or ore, and fertility is correspondingly low. Reaction varies from medium to strongly acid to a depth of 1 m or more (Veatch et al. 1923).

The climate of these areas is characterized by cold winters. sort mild summers, a large number of cloudy days, low evaporation, and moderately high humidity (Veatch et al. 1923). Average yearly temperature generally falls within the range of 6 to 7°C, with mean monthly temperatures ranging from -8 to 19°C. Precipitation is fairly well distributed broughest the year, with a mean annual rainfall and snowfall of 77 an 80 cm, respectively (Anonymous 1971).

Jack pine forests dominate large areas of the above four counties. Because jack pine is an important pulpwood species and the nesting habitat for the endangered Kirtland's warbler, much attention has been paid to devising a workable silvicultural system for its perpetuation. For this reason large areas of jack pine forests are logged and burned each year. Wildfires are also a periodic occurrence in this region.

Methods

All bread and unburned sites used in this study were located the Grayling sand series and were chosen to encompass as little variation in topography and other environmental gradients as possible. However, no soil analyses were conducted on the study sites; therefore, the degree of soil uniformity among the sites is not known.

Only burns that occurred during the months of July, August, and September (summer burns) were included. One exception was site 10A (Table 2), which was prescribe-burned in October. Following treatment all areas were left unplanted. The range of site variation for burned areas is outlined under the trea at description (Table 2). Included in the burned areas fo dy were prescribed burns and wildfires in clear-cut mature jack pine, and prescribed burns and wildfires in 35-year-old standing jack pine. These variations represent concessions made by the authors because of a lack of available prescribe-burned clear-cut sites of mature jack pine.

On each site all vascular plants, including grasses, sedges, ferns, herbs, shrubs, and trees, were characterized by frequency and cover measurements. Frequency was determined using 1-m² circular plots randomized along transects. Transects were oriented to best include the entire area to be surveye. Over determinations were made by summing the distance ersected by each species along randomly placed 20-m transects. Generally, 30 frequency plots and three cover transects (60 m) were used to characterize each site. Deviation from this occurred because of high species richness (site 7B79-45 frequency plots and 90-m cover), low species richness (site 11-20 frequency plots and 40-m cover), and time constraints (site 1A-20 frequency plots and 40-m cover). On all sites a 10% or less increase in the number of species resulted from the final 10% increase in sample area (Cain 1938). Nomenclature for all species follows Voss (1972) for gymnosperms and Fernald (1950) for other taxa.

Results

The data presented are from certain sites sampled

once and other sites surveyed in both 1979 and 1980 (Tables 1 and 2). The age of these sites make up a sequence ranging from 0- (clear-cut the winter and spring previous to the summer sampling) to 5-year clearcut sites (Table 1) and 1- (burned the summer previous to sampling) to 6-year burned sites (Table 2). We are cautious in suggesting that these sites are typical of those ages. Although sites were rigorously selected, the type, severity, and seasonal timing of the disturbance on each site varied. Also, differences most certainly existed in the predisturbance floristic composition of each site. Therefore, in many aspects each site is unique, making direct comparisons difficult. Nonetheless, we do feel that certain consistent differences in burned versus unburned sites can be discerned.

A comparison of three different measures of diversity (total species richness (number of species), average frequency per plot, and Shannon index2) of sites averaged within years for a 6-year progression is shown in Fig. 1. Species were grouped into annuals and biennials, grasses and sedges, perennial herbs, and trees and shrubs. Relative cover, relative frequency, and richness data for each surveyed area by vegetational group are shown in Tables 1 and 2 for unburned and burned areas, respectively. The burned areas consistently showed a higher diversity than the unburned areas of the same age during years 1 to 5. This trend is most evident in the species richness data, where rare and dominant species contribute equally. Average frequency and Shannon index, which reflect number of species and equitability, were only slightly greater on the burned versus the unburned areas for years 1 and 2. With all three indices, the unburned areas showed a general decline in diversity over the time sequence. Burned sites initially decreased in richness but nonetheless retained a high level when compared with their unburned counterparts.

It is important to note that, although the average frequency per plot and the Shannon index initially were nearly equal on burned and unburned sites, these sites differed qualitatively in species composition and richness. In other words, a greater number of species, mostly rare, contributed to these indices on burned sites, whereas fewer, but more common, species contributed

on unburned clear-cuts.

As shown in Table 3, 89 different species were recorded on burned sites compared with 51 species on unburned sites. Forty species were exclusive to burned sites, whereas only two species were exclusive to unburned areas (Table 3). Three of the 11 annuals and biennials, 12 of the 21 grasses and sedges, 16 of the 34

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wer Michigan riety of species , compared with s ter species richne s 3 to 6) and certain tion of Carex (up d that Carex, acting and suppresses

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70). Thus, a study rly revegetation of es in northern lowe edominant compo soils.

area

ummers of 1979 and coda, and Ogemay The elevation of these 365 m above sea leve is a direct result of consisting of outwar ch et al. 1923). Before er industry in the last ed by dense hardwood of bog, marsh, and these counties are d- and third-grown lands, bracken grass

mixed, frigid, typ these counties and incoherent structure out, and perviousness

²Shannon index of diversity (H) = $-\Sigma P_i \log P_i$, where P_i is relative cover (Odum 1971).

TABLE 1. Relative cover (C), relative frequency (F), and species richness (R) for various vegetational groups on unburned clear-cut sites

Sito	Years	Area	Annua	Annuals and biennials	ennials	Grasse	Grasses and sedges	lges	Per	Perennial herbs	sq	Tree	Trees and shrubs	sqn	Total	Total
number	treatment	ha ha	S	F	R	S	F	~	S	F	R	S	F	R	R	per 60 m
1A	0	16	1	0.7	-	32.5	26.1	9	15.0	31.2	6	52.5	42.0	2	26	36.0
118	0	16	0.49		7	12.9	20.4	7	29.9	33.3	6	6.99	46.3	13	31	61.5
2	1	24	1		1	24.7	27.6	2	7.1	23.2	12	68.2	49.2	7	24	27.6
3A	2	16	}	1	ļ	49.6	43.8	6	21.6	21.6	6	29.7	34.6	6	27	50.7
3B79	2	91	1	1.9	_	36.5	24.8	2	13.6	31.2	01	49.6	40.7	6	25	37.1
3B80	3	16	١	I	ĺ	53.1	32.0	7	4.3	. 26.0	7	42.5	42.0	∞	22	46.9
4A79	3	32	0.1	1	_	83.4	52.7	7	5.1	16.4	9	11.4	30.9	9	20	37.7
4A80	4	32	1	١	1	0.99	50.0	9	0.3	9.01	5	32.9	39.7	∞	19	64.5
5A79	4	4	1	1		7.97	34.5	7	2.2	14.3	_	20.9	50.0	7	01	41.7
5A80	ક	4	1	١	1	67.3	37.1	5	2.9	19.3	4	29.8	43.5	2	4	7.44
9	5	91	I	I		77.3	45.6	3	0.2	2.9	3	22.5	51.5	10	16	30.1

SHANNON INDEX
SHECIES
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Fig. 1. (A) Species richness, (B) average richness per plot, and (C) Shannon index of diversity versus year treatment on burned and unburned sites. Vertical bars standard deviation. Only one observation at year 2 unband year 6 burned.

perennial herbs, and 19 of the 24 trees and sirecorded on all sites were present on unburned are contrast, burned sites contained all 11 annual biennials, all 21 grasses and sedges, 33 of perennial herbs, and 21 of the 24 trees and shrubs

Figure 2 shows only slightly higher cover valuation burned areas than comparable unburned areas. Outemporal sequence, burned areas showed a increase in cover through year 5, whereas no detrend was evident on unburned sites. However, site surveyed in 1979 and again in 1980 (Tables I showed an increase in total cover over that previous growing season.

The trend in relative cover and frequency of and biennials over the temporal sequence is sho Tables 1 and 2. On unburned sites, species in this were virtually absent, except for Melampyrum Lam. (cow wheat), which is present in the undof mature jack pine stands. On burned sites, spethis group, mainly Geranium bicknelli Britt. (gerand Corydalis sempervirens L. (rock-harlequin



TABLE 2. Relative cover (C), relative frequency (F), and species richness (R) for various vegetational groups on burned areas

Cita	T-0.04	Years	A	Annual	s and bi	ennials	Grasse	es and se	dges	Pere	nnial her	bs	Trees	and shr	ubs	Total	Total cover
Site number ^a	Treatment description ^b	since treatment	Area, ha	C	F	R	C	F	R	C	F	R	C	F	R	R	per 60 m
7A	PB-ST	1	11	14.2	13.3	4	30.5	34.4	10	2.5	13.3	12	52.8	39.0	10	36	35.8
7B79	PB-ST	1	26	25.6	12.0	5	27.0	34.6	13	8.1	18.0	13	38.7	34.6	14	45	28.7
7C	PB-CC	1	16	18.3	7.1	4	35.8	32.0	9	2.8	26.1	15	43.1	34.8	7	35	26.9
7D79	PB-CC	1	24	0.1	2.8	3	73.5	44.6	9	8.5	24.3	12	17.0	27.1	10	34	30.6
7B80	PB-ST	2	26	_	1.1	2	60.8	44.0	10	12.9	14.7	10	26.3	40.1	8	30	43.7
7D80	PB-CC	2	24	_			71.6	56.3	9	12.4	21.1	8	15.4	22.5	8	25	48.5
8A79	WF-ST	2	32	0.1	1.8	4	44.0	39.2	14	2.8	17.6	16	53.0	40.5	13	47	47.4
8A80	WF-ST	3	32	0.1	2.2	2	39.4	33.2	12	6.6	23.1	15	54.2	41.5	11	40	52.8
9A79	PB-ST	3	31	0.6		2	63.7	41.0	12	1.2	14.9	12	34.4	44.2	12	38	54.9
9B79	WF-ST	3	30	_	-		60.2	49.6	7	1.1	3.5	5	38.5	47.0	6	18	42.9
9A80	PB-ST	4	31	_	0.5	1	62.7	40.7	11	1.2	18.0	13	36.0	40.7	11	36	56.7
9B80	WF-ST	4	30	_	_	_	71.8	50.0	7	0.7	9.9	8	27.1	40.1	6	21	54.7
10A79	PB-CC	4	26	_	1.6	1	71.8	35.7	13	15.2	39.3	13	13.0	23.3	9	36	58.2
10B79	PB-CC	4	23	0.2	3.9	1	53.5	40.0	14	22.9	23.3	10	23.4	32.3	14	39	45.4
10A80	PB-CC	5	26	0.1	1.7	2	57.3	38.2	11	18.5	32.9	16	24.1	27.2	7	36	75.7
10B80	PB-CC	5	23	0.8	5.4	3	57.3	37.3	10	8.0	23.5	8	33.5	33.9	14	35	61.6
11	WF-CC	6	6				91.4	59.0	6	0.5	10.3	1	7.8	30.8	6	13	31.2

[&]quot;See Table 1

or Melampyrum lim or Melampyrum lim resent in the unders burned sites, specificknelli Britt. (geram

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- 5, whereas no delth sites. However, earlies in 1980 (Tables I are cover over that of

unburned areas. Over areas showed a ste

the 24 trees and ship ant on unburned areas ned all 11 annuals a

sedges, 33 of the

^bPB, prescribed burn; WF, wildfire; ST, standing timber (35-year-old jack pine); CC, clear-cut mature jack pine (50-65 years old).

TABLE 3. Plant species encountered on burned and unburned sites in northern lower Michigan

Species exclusive to burned areas (40 species total) Annuals and biennials (eight species)

Brassica nigra L.

Cirsium sp.

Corydalis sempervirens L.

Erigeron canadensis L.

Geranium bicknellii Britt.

Krigia virginica L.

Lithospermum arvense L.

Silene antirrhina L.

Grasses and sedges (nine species)

Agropyron trachycaulum Link

Andropogon scoparius Michx.

Carex rugosperma Mack.

Festuca sp.

Muhlenbergia mexicana L.

Panicum capillare L.

Panicum xanthophysum Gray.

Poa pratensis L.

Sorghastrum nutans L.

Perennial herbs (18 species)

Anemone riparia Fern.

Aster junciformis Rydb.

Aster sagittifolius Wedemeyer

Convolvulus spithamaeus L. Equiseteum hvemale L.

Hieracium canadense Michx.

Hieracium gronovii L.

Lechea minor L.

Physalis virginiana Mill

Polygala polygama Walt.

Polygonum cilinode Michx.

Potentilla arguta Pursh.

Potentilla simplex Michx.

Potentilla tridentata Ait.

Rumex acetosella L.

Senecio tomentosus Michx.

Scrophulariaceae (unidentified)

Viola adunca Sm.

Trees and shrubs (five species)

Acer rubrum L.

Ceanothus ovatus Desf.

Quercus alba L.

Rubus hispidus L.

Symphoricarpos albus L.

Species exclusive to unburned areas (two species total)

Spiranthes gracilis Bigel. (perennial herb)

Corylus americana Walt. (shrub)

Species common to both burned and unburned areas

(49 species total)

Annuals and biennials (three species)

Arabis glabra L.

Lactuca canadensis L.

Melampyrum lineare Lam.

Grasses and sedges (12 species)

Agrostis hyemalis Walt.

Andropogon gerardii Vitman Bromus kalmii Gray Carex pensylvanica Lam. Danthonia spicata (L.) Beauv. Dichanthelium depauperatum Muhl. Deschampsia flexuosa L. Koeleria macrantha Pers. Oryzopsis asperifolia Michx.

Oryzopsis pungens Tort.

Panicum columbianum Scribn.

Schizachne purpurascens Tort.

Perennial herbs (15 species)

Anemone quinquefolia L.

Antennaria neglecta Greene

Aster laevis L.

Campanula rotundifolia L.

Epigaea repens L.

Fragaria virginiana Duchesne

Gaultheria procumbens L.

Helianthus occidentalis Ridd.

Hieracium aurantiacum L.

Hieracium venosum L.

Liatris novae-angliae Lunell

Maianthemum canadense Desf.

Pteridium aquilinum Desf.

Solidago spp.

Viola pedatifida G. Don.

Trees and shrubs (18 species)

Amelanchier sp.

Apocynum androsaemifolium L.

Arctostaphylos uva-ursi L.

Comptonia peregrina L.

Crataegus sp.

Diervilla lonicera Mill.

Pinus banksiana Lamb.

Populus tremuloides Michx.

Prunus serotina Ehrh.

Prunus virginiana L.

Quercus spp. (red oak group)

Rosa blanda Ait.

Rubus pensilvanicus Poir.

Salix glaucophylloides Fern.

Salix pellita Arderss.

Vaccinium angustifolium Ait.

Vaccinium myrtilloides Michx.

Vaccinium vacillans Torr.

dominated in the 1st year after burning and 15% relative cover on all sites, with a maximum (26%) on site 7B79. A possible heat stimul germination of these species is indicated by reduction and subsequent low levels in years following fire.

Perennial grasses and sedges were dominant burned and unburned sites (Tables 1 and 2), but sites showed a greater richness of these species

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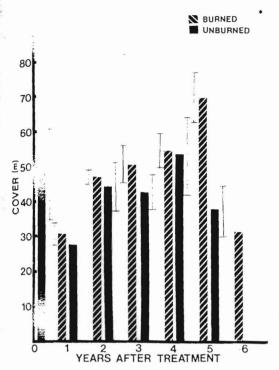


Fig. 2. Total vegetational cover (metres) versus years after treatment on burned and unburned sites. Vertical bars are \pm standard deviation. Only one observation at year 2 unburned and year 6 burned.

year in the sequence. During years 2 and 3 the highest number—pecies was recorded on unburned sites, with lower least during years 4 and 5. The number of species appears remarkably consistent on the burned sites for years 1 through 5, but a drastic decrease, approaching that of the unburned sites, was observed at year 6 (site 11). Site 9B (years 3 and 4) also showed an atypically low number of grasses. Frequently occurring grasses and sedges found exclusively on burned sites included Andropogon scoparius Michx. (little bluestem), Muhlenbergia mexicana L., and Carex rugosperma Mack. (sedge).

Numb of species, relative cover, and relative frequency of perennial herbs are tallied in Tables 1 and 2 for unburned and burned sites, respectively. The number of herbs on both the burned and unburned sites was similar for year 1, but thereafter a steady decline occurred on the unburned sequence, whereas the burned sequence retained a relatively high number of herbs through year 5. Again, atypically low levels of herbs were recorded at year 6 (site 11) and on site 9B. Bracken form (Pterium aquilinum L.) and wintergreen (Gaulderia proumbens L.) were the dominant contributors to relative cover in this species group. All other cerennial herbs contributed little to the relative cover, but added greatly to the species richness on all sites, specially those that had been burned. Some frequently

occurring perennial herbs exclusive to burned sites included *Hieracium canadense* Michx. (Canadian hawkweed), *Rumex acetosella* L. (sheep sorrel), and *Senecio tomentosus* Michx. (groundsel).

The number of species of trees and shrubs was higher on burned than on unburned areas of the same age, but little change in either sequence occurred during years 1 to 5 (Tables 1 and 2). Of the four major species groups, trees and shrubs showed the least increase in species richness after fire. Relative cover of these species showed a decrease with time in both sequences. However, sites 4A, 5A, 10A, and 10B showed substantial increases in the cover of this species group over the 1979 and 1980 growing seasons (Tables 1 and 2). Initially, unburned sites had a much higher cover of trees and shrubs, but by year 4 and 5 nearly equal cover occurred in both sequences. The species dominating this group on both burned and unburned sites include Vaccinium spp. (blueberry), Populus tremuloides Michx. (aspen), Quercus spp. (oak), Prunus serotina Ehrh. (black cherry), and Rubus pensilvanicus Poir. (dewberry).

Carex and Vaccinium comprised the majority of cover on nearly all sites (Fig. 3). The cover of Carex pensylvanica Lam., a strong competitor on jack pine sites, steadily increased on unburned clear-cut sites to a

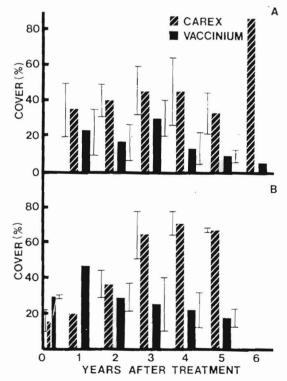


Fig. 3. (A) Percent cover of *Carex* and *Vaccinium* versus years after treatment on burned sites and (B) percent cover of *Carex* and *Vaccinium* versus years after treatment on unburned sites. Vertical bars are \pm standard deviation. Only one observation at year 2 unburned and year 6 burned.

th a maximum lead heat stimulation icated by the drawels in years 2 to

re dominant on boll and 2), but burn hese species for each

maximum of 70% at year 4. On burned sites, Carex generally stabilized at a much lower level than comparable unburned sites; however, at year 6 after burning, site 11 had the highest cover value for Carex of any site surveyed in this study (86%). Vaccinium spp. showed a trend opposite that of Carex over time, with decreases in dominance that seemed to mirror the corresponding increases in Carex dominance. To facilitate data gathering in the field, the frequency and cover of blueberry was quantified simply as Vaccinium spp. The dominant species encountered on the study sites were V. angustifolium Ait. (late low blueberry), V. myrtilloides Michx. (velvetleaf blueberry), and V. vacillans Torr. (early low blueberry).

Discussion

The increase in species diversity and dominance of certain plant groups occurring after fire seen in this study is a phenomenon well documented in a variety of ecosystems (Ahlgren and Ahlgren 1960; Christensen and Muller 1975; Dyrness 1973; Little and Moore 1949; Purdie and Slatyer 1976; Shafi and Yarranton 1973). This increased diversity after fire is temporary, however, usually lasting only a few years. A shift is typically seen in plant composition and dominance away from invading species, which establish themselves by seed initially after fire, to those species present before the burn, which reestablish themselves largely by vegetative means.

The postfire successional trends previously reported from the Lake States, however, do not always follow this pattern. For example, Ohmann and Grigal (1979) studied the early revegetation of the Little Sioux wildfire in northeastern Minnesota but did not find an abundance of disturbance species. Except for the presence of a few "fire followers," such as geranium and rock-harlequin, species composition before and after fire was nearly identical. Vogl (1970), working in the northern Wisconsin pine barrens, found that the frequency of occurrence of barren species did not show a significant response to burning. Changes in understory balsam fir and paper birch vegetation following timber harvest and burning in northern Minnesota was reported by Outcalt and White (1981). They showed decreased diversity of nearly all species groups on logged and burned sites compared with unburned logged sites; however, high densities of geranium and rock-harlequin after fire were found. Ahlgren (1960) showed a substantial increase in vegetation the first 2 years after fire in northeastern Minnesota. Plants that reproduced by seed were temporary and began to decline by the 3rd and 4th year. Only those species that were of vegetative origin maintained an important position during a 5-year period after fire. Ahlgren (1959) grouped vegetational data from 11 series of plots in the northern coniferous forests of Minnesota and found 60 species exclusive to burned areas species exclusive to unburned areas, and 35 species exclusive to unburned areas, and 35 species moreases in species richness are caused by fire. Krei and Ahlgren (1974), however, reported change species composition from this same study area, specially by site, and showed that burning resulted inconsignificant change or a decrease in species rich compared with unburned controls.

The above studies report data from prescribed and wildfires that took place during the spring (Ahi 1960, 1974; Ohmann and Grigal 1979; Vogl 1970 summer (Ahlgren 1960, 1974; Outcalt and White 19 but none reported a large site-specific increase in spe diversity after fire as was seen in our study. We found did Ahlgren, that burning clearly promotes the lishment of a large variety of species not typical unburned areas. A total of 89 different species recorded on burned sites compared with 51 on unbur sites. Burned sites in our study consistently sho greater species richness compared with analogous burned sites (Fig. 1A). Increases in the number species of annuals and biennials, grasses, and peren herbs following fire were found. The establishmen new species following fire can result from viables. stored in the forest floor (Ahlgren 1979; Livingston) Allessio 1968; Tredici 1977) or from seed transpor by wind and animal vectors.

The longevity of many of the fire followers is showed years after fire many are gone. In the latery following fire, species that perpetuate themse mainly by vegetative means and that were probable members of the preexisting vegetation dominated and 5-year-old burned sites (sites 10A and 10B) present study retained a high level of diversity suppose a mixture of fire-stimulated grasses and herbs, where presence appears to be waning, and trees and show (probably present before burning), whose dominant increasing (Table 2).

There are many interacting factors that affective getational cover on these study sites. Time following disturbance and species number and equitability certainly important. Initially following disturbance as clear-cutting or burning, the gaps created recolonized and cover increases with time. On study however, Carex pensylvanica formed a monocover and prevented the establishment of a strait canopy. This explains the anomalous large decreases were seen between years 5 and 6 on the ibusequence in Fig. 2.

The decrease in diversity on the unburned sequand the low diversity of certain burned sites is line the dominance of Carex pensylvanica. The lodiversity on unburned sites is closely matched increased cover of Carex. Further evidence exists

e least dive clative cove cars 4 and 6 carex produ though this m. From sceptible to ith certain t eep into th burning the lower level dominants co meventing i Michx. and rasses), Pt Populus tren The decre sequence ap reduced abil unlight. A mas the vigo chade of slas open all is. mature, unc burned sites in the shade full sunlight exposed area who found ntermediate

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the unburned sequence ourned sites is linked ylvanica. The loss losely matched by the er evidence exists in

the least diverse burned sites (9B and 11), which have relative cover values for Carex of 67 and 86% during years 4 and 6, respectively. Burning appears to stimulate Carex production in the 1st year after treatment, although this response depends on the intensity of the burn. From personal observation Carex appears more susceptible to injury from very "hot" burns compared with certain trees and shrubs whose rootstocks penetrate deep into the mineral soil. From years 3 to 5 after burning the dominance of Carex stabilized at a much lower level than on equivalent unburned sites. Other dominants competing with Carex on older burns and prevening its spread include Oryzopsis asperifolia Michx. and Schizachne purpurascens Torr. (tussock grasses), Pteridium aquilinum (bracken fern), and Populus tremuloides (aspen).

The decrease in blueberry in the later years of each sequence appears to be, at least in part, related to a reduced ability of these species to compete in full sunlight. A consistent pattern observed on these sites was the vigorous growth of blueberry in and around the shade of slash piles, while Carex dominated the larger open and the shade of slash piles, while Carex dominated the larger open and the shade of slash piles, while Carex dominated the larger open and the shade of slash piles, while Carex dominated the larger open and the shade of slash piles, while Carex dominated the larger open and the shade of an uncut stands, clear-cut sites, and burned sites that Carex is outcompeted by blueberry in the shade of an uncut stand, but the reverse is true in full sunlight. The inability of blueberry to compete in exposed areas is consistent with Hoefs and Shay (1980), who found that V. angustifolium grew faster under intermediate shade than in full sun in southeastern Manitoba.

An increase in sedges following fire has previously been demented (Ahlgren 1960; Outcalt and White 1981; Van 1970). However, the overwhelming dominance of Carex observed in our study seems to be unique to jack pine sites in northern lower Michigan. There are indications that a Carex meadow, once established, is capable of excluding tree and shrub seedling reproduction for many years (Niering and Goodwin 1974; Noble 1980). In fact, on all sites surveyed during 1979 and 1980, jack pine reproduction was conspicuously absent; none of the areas in this study showed adequate jack pine stocking. We feel that the competitiveness of Carex greatly contributed to the failure of jack pine regeneration.

There are several possible mechanisms that explain the dominance of Carex pensylvanica. One possibility may be the ability of Carex to exploit nutrients and space made available following a perturbation such as clearcutting and (or) burning. Recent studies involving disturbances have shown that certain exploitative species, the to their life-history characteristics, can monopol presources liberated by disturbances and suppress or exclude other species. Marks (1974) showed pin therry (Prunus pensylvanica) to be such an exploitative

species on New Hampshire clear-cut sites. Bakelaar and Odum (1978) concluded that a few opportunistic species already established on abandoned fields in Georgia were able to expand their niches after fertilization by preempting certain subordinates, thus reducing overall diversity. Ahlgren (1960) also showed that nutrients released following fire have a fertilizing effect that stimulates the growth of certain species. Though results of a study initiated in May 1980 to test this hypothesis are not yet available, it is conceivable that the release of *Carex* may be via a similar mechanism.

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ECOLOGICAL EFFECTS OF FOREST FIRES

I. F. AHLGREN AND C. E. AHLGREN

Quetico-Superior Wilderness Research Center, Ely, Minnesota

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esis rates in low light intensity. ture, the maximum photosynthetic it intensity. Therefore, this species, for optimum growth at different

generally believed to be favored bed conditions are improved (54, 212, 213) reported that the ecoconditions for most conifers is oval of the forest floor, thus favoris over that of deciduous species. lies in the initial root system. In long, with about the same length ver, the fleshy cotyledons permit oot system before the first leaves iree inches tall. The roots of hardourned, deep litter to mineral soil ater demand, while those of pines oil before drying out only if the loved, as by burning. Similar exaser (105) for results of laborad that humus did not contain a 1, and that if jack pine seeds were red thoroughly, good germination it pure stands of hardwoods were Ontario. On swamps, spruce and nd spruce and mixed hardwoods dispersed after fire, a significant o fire (154). Buell and Borman that in the absence of fire bassfollowing paper birch and white

was of great value in exposing ed mineral soil dries more slowly, nd temperature than the humus seedling growth. Although the ritional value, he believed this to .11) pointed out that forest trees most frequent fire followers. Tryon (326) and Isaac (163) reported that seed bed conditions could be made poor by addition of charcoal which increases soil temperature sufficiently that it may kill seedlings. However, Retan (277) noted that under nursery conditions, the addition of charcoal to heavy clay soil produced a marked improvement in coniferous seedling growth. Ooyama (262) stated that extracts of unburned litter inhibited seed germination and seedling growth of some species, especially the pines. Gemmer et al (118) asserted that ash stimulated germination but inhibited radicle penetration of longleaf pine seedlings.

Burning as a method of slash disposal in order to eliminate the hazard of wildfires is frequently proposed (187, 192, 211, 222, 226, 235, 246, 254, 342, 343, 344, 345, 352, 353 also 33, 120, 132, 358), although it is considered costly and dangerous by others (61, 192).

JACK PINE. Of the northern species, jack pine is most often recognized as a frequent post-fire species (175, 199, 232 and others). The ecological adaptation to fire of the serotinous cones has been pointed out (60, 4, 100, 101, 197, 198). Seed remains viable within the cone for many years, and the cones are opened by heat. Consequently, when a jack pine forest burns, or when the slash in a cut-over area is burned, seed is readily available. However, Watson (337) believed that proper restocking could occur after fire only if there were at least 75 seed trees left per acre. On many sites, however, jack pine reproduction is prolific and many fewer seed trees are necessary. Eyre (101) also pointed out that a large number of seed trees is necessary for restocking jack pine stands after burning, and that the seed is often killed by fire. Eyre emphasized the possibility that seedlings which come up immediately after late summer and autumn fires will not be strong enough to survive the winter. Johnson (170) believed that all methods of slash disposal, including fire, were detrimental to jack pine reproduction. The Lake States Experiment Station reported (189, 190) that spring fires frequently do not damage merchantable trees but are responsible for lack of reproduction in older stands. Mitchell (244) reported damage to older trees and the elimination of smaller ones.

Requirements for germination and young seedling growth are often met ideally by post-fire conditions. The exposure of mineral soil as a seedbed is advantageous (4, 62, 91, 113) because it is necessary for the young roots to reach a more steady supply of moisture than exists in forest litter and humus. Partial shade is required for good germination (60, 112, 113), and this is usually furnished by the characteristic

lush herbaceous growth the first year following fire⁽⁴⁾. Direct sunlight is advantageous for later seedling growth. This condition is usually present in the opening created by fire, once the seedlings rise above the herb-shrub layer. Bensend (27) found that jack pine seedlings require 200 to 250 ppm nitrogen for optimum seedling growth. Since fire is frequently reported to release nitrogen into the soil, this condition may also be met by fire.

There are frequent reports (102, 190) that spring fires were particularly destructive of seedlings and smaller jack pine trees but caused little damage to merchantable timber. Summer fires, since they are usually hotter, crown and burn deeper, did considerable damage to larger trees. Damage to trees of all size classes at any season was great enough, however, that burning to control brush, etc., in the productive stands could not be recommended. Rudolph et al (282) suggested that the distribution, in Minnesota, of jack pine having the fire-favored serotinous cones may have been influenced by the state's fire history.

WHITE PINE. Many worker have recognized that the existing white pine stands very frequently occur on burned-over land (39, 60, 64, 159, 196, 221, 245), although Cary (53) pointed out that fire is not necessary for the establishment of white pine on all sites. Kell (175) reported that white pine occurs as a pioneer on clay-loam sites after fire, while jack and red pine invade sandier, drier soils. Perry (267) found that white pine seed germinated best on burned soils, although subsequent growth was better on unburned soil. However, Lunt (219) reported that burning increased height growth by 8.1%, and volume growth by 18.8%, probably because of the higher pH, nitrogen, potassium and calcium concentrations in the topsoil. Cary (53) and Chapman (59) pointed out that white pine frequently comes in after blowdowns as well as after fires, so that the effect of fire may be largely one of opening an area to light. Maissurow (231) also held this view, since he maintained that white pine would reestablish after logging without burning if the areas were logged properly with due respect for good seed years.

RED PINE. Published references to the effect of fire on red pine are few, and it would appear that knowledge of fire and this species is very incomplete. Lunt (219) found fire stimulated height and volume growth of both red and white pine. Kell (175) observed that in Itasca Park, Minnesota, red pine was a post-fire pioneer on coarse soils, along with jack pine. Perry (267) reported that red pine seedlings grew better on

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Cowbirds				
male	fem	juv total	total	
1621	619	21		
2006				
2195	***************************************	163		
2026	1463			
2193	1994			
1845	1405	34		
1754		18		
1954		16		
1538	1429		2967	
1770	1085	1	2856	
1568	893	38	2499	
2128	2196		4324	
2183	1936		4119	
2644	2082	14	4740	
2328	1781	75	4184	
2291	1549	60	3900	•
2932	2589	19	5540	
2907	2881	2	5790	
3818	3771	6	7595	
2576	2088	6	4670	
44277	36052	871	81200	total
2214	1803	44	4060	ave
554	712	56	1232	sd
25	40	128	30	sd as % ave
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From M. DeCap	itafax 18 No	v 1991		
Questions:				
How should we	deal with differ	ent trapping eff	ort over years	
	acres does this i			
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Commentsas	k Kepler, Sykes	, & Bocetti abo	ut recent rates	of parasitism
No effort made	to collect data a	bout rates of pa	rasitism after	1981

Summary of Cowbird Trapping Results in Northern Michigan Kirtland's Warbler Nesting Areas, 1972 - 1991

		Brown-head		Catch		
Year	Male	Female	Juvenile	Total	Traps	Per Trap
1972	1621	619	21	2261	15	150.7
1973	2008	1214	125	3345	19	176.1
1974	2195	1717	163	4075	22	185.2
1975	2028	1463	161	3650	28	130.4
1976	2193	1994	112	4299	38	113.1
1977	1845	1405	34	3284	38	86.4
1978	1754	1639	18	3411	40	88.1
1979	1954	1721	16	3691	35	105.5
1980	1538	1429	0	2967	37	80.2
1981	1770	1085	1	2856	36	79.3
1982	1568	893	38	2499	35	71.4
1983	2128	2196	0	4324	35	123.5
1984	2183	1936	0	4119	31	132.9
1985	2644	2082	14	4740	30	158.0
1986	2328	1781	75	4184	31	135.0
1987	2291	1549	60	3900	38	102.6
1988	2932	2589	19	5540	41	135,1
1989	2907	2881	2	5790	42	137.9
1990	3818	3771	6	7595	38	199.9
1991	2576	2088	6	4670	43	106.3
(20)	44277	36052	871	81200	34 '	120.8

^{*} mean traps per year (672/20)

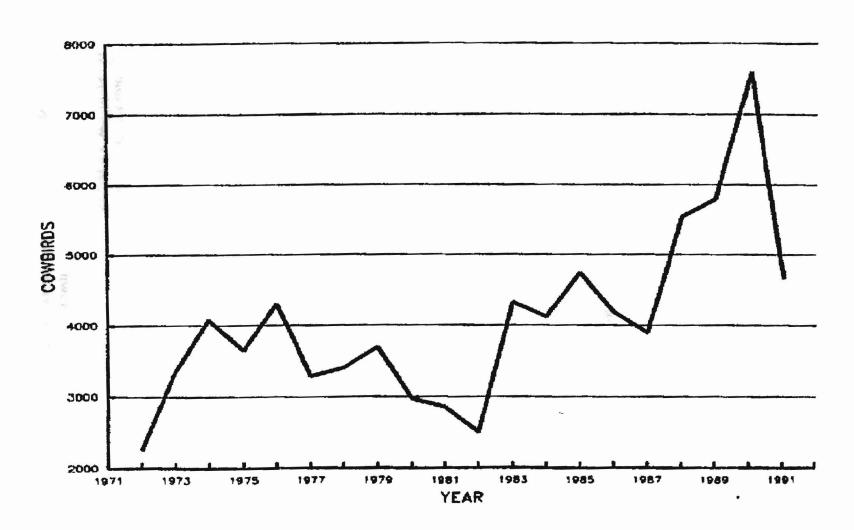
Unpublished Data

U.S. Fish and Wildlife Service, Wildlife Assistance Office, East Lansing, Michigan

November 18, 1991

[&]quot; mean birda per trap per year (81200/672 "trap years")

BROWN-HEADED COWBIRDS REMOVED ANNUALLY, 1972 - 1991, FROM NORTHERN MICHIGAN KIRTLAND'S WARBLER NESTING AREAS



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Summer Records and Management Implications of Kirtland's Warbler in Michigan's Upper Peninsula

John R. Probst

INTRODUCTION

The Kirtland's Warbler (Dendroica kirtlandii) occupies a limited nesting range in the jack-pine (Pinus banksiana) plains of northern lower Michigan, and winters in the Bahamas. Although it is presumed to have been more widespread in the distant past (Mayfield 1960), the current breeding range is an area about 130 by 160 km. Migrants and stray summer males have been collected and observed across a much broader range from Missouri to the southwest, Minnesota to the northwest, and Virginia and Massachusetts to the east of the known nesting range (Tilghman 1979, Walkinshaw 1983). This paper describes a successful search for the Kirtland's Warbler in Michigan's Upper Peninsula. I examine the role of long distance dispersal vs local dispersal in the population dynamics and geographic distribution of this endangered species. These conclusions lead to recommendations for choosing habitat for Kirtland's Warbler management.

METHODS

Extensive areas of seemingly appropriate jack-pine habitat in Michigan's Upper Peninsula were located using old USDA Forest Service vegetation maps, compartment records from the Hiawatha National Forest, and suggestions from persons familar with the region. Typical Kirtland's Warbler habitat is densely stocked jack-pine stands of wildfire origin that range from 1.2 to 4.8 m in height (Walkinshaw 1983). Dense jack or red pine (Pinus resinosa) plantations can also be used by Kirtland's Warblers but logged, unburned jack-pine stands regenerated by non-serotinous seeding usually lack sufficient tree density for breeding warblers. All suitable stands are on poor, porous, sandy soils; the plant communities are characterized by low, open ground vegetation. A preliminary survey of 12 potential areas (Fig. 1) was made along major roads and trails from 1978 to 1981. Four areas were selected as having the best potential as Kirtland's Warbler habitat.

Nine areas, including the four most suitable ones, were visited from 1979 to 1984 to check for Kirtland's Warblers. We surveyed segments of the Lake Superior shoreline for singing males in 1979, and searched areas near the town of Raco in 1980, 1983 and 1984. Jack-pine habitat near Rapid River in Delta County was visited in 1980 and 1982, and

Marquette County was searched in 1982, 1983 and 1984. Larry Walkinshaw and I independently searched Baraga County for Kirtland's Warblers in 1983. Stands were checked for male Kirtland's Warblers by playing tape-recorded calls and listening for singing males. No set methods were used for determining the location or duration of stops or listening stations, as practiced by Tilghman (1979). Because the area surveyed was large, censusing was conducted from 7 am to 3 pm CDT (0700-1500), the period when Kirtland's Warblers sing actively (Mayfield 1960, Hayes and Probst, unpubl. ms). If a singing male was heard, the tape recorder was shut off and attempts were made to sight the bird, estimate its age (adult or subadult plumage), and locate a female in the vicinity.



Figure 1: Major areas of pine forest types in Michigan's Upper Peninsula:

- 1. Watersmeet (Gogebic Co.)
- 2. Covington (Baraga Co.)
- 3. NW Marquette Co.

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- 4. Gwinn (Marquette Co.)
- 5. Ensign (Delta Co.)
- 6. Chicago L. (Delta Co.)

- 7. Shingleton (Schoolcraft Co.)
- 8. Munising (Alger Co.)
- 9. Grand Marais (Alger Co.)
- 10. Deer Park (Luce Co.)
- 11. Whitefish Pt. (Chippewa Co.)
- 12. Raco (Chippewa Co.)

RESULTS AND DISCUSSION

Most stands I examined that were within the proper height range for Kirtland's Warblers were too sparsely stocked with jack-pine and/or red pine to be good habitat, except for one wildfire area in Marquette County. This stand was near Gwinn, Michigan, one-half mile (.8 km) south of Sawyer Air Force Base. The area was burned in 1968 and contains about 200 ha of suitable habitat. It is located on county, State and privately owned land.

I censused the west half of this stand on 31 May 1982 and did not hear any Kirtland's Warblers. On 9 July 1982, I returned to check the east half of the burn, even though it was too late in the breeding season for consistent singing. By 11:45 AM CDT (1145), I had concluded it was too warm, too late in the day, and too late in the season to continue, so I explored the area to evaluate its habitat quality. I continued to play the tape sporadically and heard a Kirtland's Warbler sing twice around 12:05 PM (1205), 8 to 10 min after I had shut off the tape recorder. I approached the bird and heard it sing a third time, but was unable to sight it or get another response to the tape. Three more isolated, single songs were heard about 100 m west of the first location within a 2 ha area. All six songs were delivered within a 6 ha area. No birds of either sex were sighted. I checked the burn area to the east, and then returned to the site of previous singing but heard nothing and left about 2:30 PM (1430). Unfortunately, I was unable to return again that year.

On 5 June 1983, I found a singing male Kirtland's Warbler 100-200 m south of the 1982 location and was able to observe it closely for over 90 min. This bird was also seen in subsequent weeks by Michigan Department of Natural Resources personnel from Gwinn and by Larry Walkinshaw. It was also observed by John Byelich and Nels Johnson of the Kirtland's Warbler Recovery Team. No other Kirtland's Warblers were discovered in the burn area. No Kirtland's Warblers were found in 1984, although the area was searched in both early and late June.

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Implications for Population Dynamics

Because of the limited breeding range and restrictive habitat requirements of the Kirtland's Warbler, the entire breeding population can be estimated in a single season. Such censuses were taken in 1951, 1961, and 1971 (Mayfield 1953, 1962, 1972) and every year thereafter (Ryel 1983). By 1971 there was a 60% drop in population to 201 males from 502 in 1961. As a result, the Kirtland's Warbler was declared an endangered species. The principal reason for this decline was probably nest parasitism by the Brown-headed Cowbird (Molothrus ater) (Ryel 1981a). The rate of parasitism was 69% by 1971 (Walkinshaw and Faust 1974).

During the past decade, the Kirtland's Warbler Recovery Team has implemented programs to increase nesting success, including a successful cowbird control program (Kelly and DeCapita 1982). However, the increased production of fledglings has been offset by losses, and the annual census has shown little or no increase for the past 12 years. Ryel (1981a) discussed some of the possible causes of Kirtland's Warbler mortality, especially losses on the wintering grounds, and Trautman (1979) stressed losses during migration. Reproductive potential may be depressed because of reduced pairing success and post-nesting mortality of fledglings (Probst, unpubl. ms).

The records reported here of Kirtland's Warbler in Michigan's Upper Peninsula are additional evidence for the dispersal of numbers of birds away from the traditional nesting grounds. There are specimen and sight records of this species in places well away from the known nesting grounds and the presumed migration route. Seven other sightings of Kirtland's Warblers were recorded outside lower Michigan during the breeding season from 1977 to 1981: four in Wisconsin, two in Ontario, and one in Quebec (Ryel 1981b). At least one of these nine extra-liminal birds had returned from a previous year. Harrington (1939) described a loose cluster of Kirtland's Warbler males in Ontario in 1916 that could have been a colony, but no nests were found. Eight specimens have been collected in places outside the presumed migration route in Ontario, Illinois, Missouri, Minnesota, and Virginia (Mayfield 1960, 1975). Tilghman (1979) also reported nine verified sight records of migrants in Wisconsin during the past 125 years. There are also sight records of male Kirtland's Warblers from central Minnesota in 1944 (Hiemenz 1980) and from northern Minnesota in 1958 and 1964 (Gullion 1964). Two unconfirmed sightings were also recorded in northern Minnesota (September 1982 and May 1983). The fact that nine of the accepted sight records occurred in the seven years between 1977 to 1983 suggests that long distance dispersal of Kirtland's Warblers may not be a rare event.

Species that occupy temporary habitat for 8 to 15 years should have powerful dispersal ability. This idea is supported by the Kirtland's Warbler's dispersal to habitat in widely scattered localities in northern lower Michigan as well as in adjoining states and Canada, as summarized in the preceding paragraph. Searchers may have encountered only a few of the many birds dispersing to remote locations (Mayfield 1983). The male reported above from Michigan's Upper Peninsula in 1982 gave a very weak response to recorded songs. This suggests some males may not respond to such stimuli and could be overlooked. Females would probably not be discovered unless paired with a singing male. Searches of likely habitat would not encounter any birds located in atypical habitat such as more mature jack-pine or other conjfer types. All suitable habitat

would have to be checked two to three times in the breeding season of every year to verify the presence or absence of male Kirtland's Warblers, because adult birds of some species (including Kirtland's Warbler) may shift locations between years (Walkinshaw 1983), or even within years (Nolan 1978, Greenwood and Harvey 1982). Kirtland's Warblers can abandon early territories, and/or appear in new locations as late as 23 June (Probst, unpubl. data), so extensive, systematic searches are necessary to estimate the magnitude of long-distance dispersal.

Thus, I believe many Kirtland's Warblers could be dispersing to areas outside of the traditional nesting grounds each year. These vagrants would not contribute to the annual census in most years, and would only rarely pair with a female. Extra-liminal birds could have formed colonies in the past, but such populations would not persist if new areas of suitable habitat did not develop nearby.

The future is questionable for the Kirtland's Warbler in Michigan's Upper Peninsula. Currently, the most promising areas for subsequent search are the Gwinn, Baraga County, Raco, and Rapid River areas (Fig. 1). Other habitat patches I have identified are too small, overmature, or mesic to be suitable. Some new plantations in the Hiawatha National Forest near the towns of Raco and Rapid River will be the proper age for Kirtland's Warblers by the late 1980s, but the tree density is marginal. The management potential for Kirtland's Warbler habitat in Michigan's Upper Peninsula is low because a management area would have to be extensive enough to support a population of birds that is sufficient to maintain a colony during the 8 to 12 years a stand is suitably aged for Kirtland's Warblers. At a density of 3 males per 40 ha (data in Mayfield 1962), 120 to 160 ha of habitat would be required to support about 10 males. If jack-pine were managed on a 50 year commercial rotation, five such stands totalling 600 to 800 ha would be needed for each management area. The minimum habitat required as described above assumes occasional recolonization from the main nesting grounds and regular colonization of young stands from adjacent occupied stands. (If management areas were to be self-sustaining, more land would be required than the 600 to 800 ha estimate.)

Dispersal and Colonization

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There is concern about those adult warblers that do not return fo the lower Michigan breeding grounds in the spring (Mayfield 1983). In addition, only 9-12% of banded nestlings have been recaptured in subsequent years (Walkinshaw 1983). Thus, Mayfield (1960) has suggested that yearlings may colonize new breeding areas, and Walkinshaw found some evidence that young birds establish new colonies. Species that occupy temporary early successional habitat are generally capable of extensive

dispersal, but it is unlikely that yearling Kirtland's Warblers could regularly find widely scattered habitat and breed successfully there. Field Sparrows (Spizella pusilla) (Adams and Brewer 1981) and Prairie Warblers (Dendroica discolor) (Nolan 1978) also show a very low return rate for banded nestlings, but a given habitat patch for those two species can be sustained by attracting colonists from a much larger range and population. Many Kirtland's Warblers could disperse to areas outside of the traditional breeding range in lower Michigan without any compensatory immigration into the known nesting grounds.

The probability of individuals of a species colonizing isolated habitat patches is related to the patch size and distance from sources of colonists (e.g., Fritz 1979). Migrant bird species may have fewer barriers to dispersal than exist for sedentary resident species, so Mayfield (1983) has suggested that many spring migrants may miss a restricted nesting range due to navigational errors. However, if most breeding habitat is selected during the post-breeding natal dispersal of juveniles (Brewer and Harrison 1975, Weise and Meyer 1979), then it seems probable that smaller or more distant habitat patches would remain unoccupied. I suggest that the fragmentation of suitable habitat within the range may be as serious a barrier to successful natal dispersal of juveniles as the size of the nesting range is to successful navigation by migrants.

Even in the main Kirtland's breeding area, colonizing males may not pair successfully in new colonies, old colonies, marginal habitat, and peripheral habitat (Probst and Hayes, unpubl. ms). Reduced pairing success may also explain the slow buildup of colonies on the periphery of the breeding range, such as Fletcher Burn at the western edge. At the eastern edge of the range, no nests or breeding pairs have been recorded in Rollways Burn, an area of 300 to 500 acres of suitable habitat.

Habitat Management Recommendations

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If it is true that the density of dispersers decreases with distance from the core breeding range, and that pairing success also declines with distance (in spite of the warbler's ability to find remote habitat on occasion), I conclude that: the best management strategy at this time is to direct any additional habitat management to areas within or adjacent to the present breeding range. Within the present breeding range, stand rotation ages should be adjusted to provide a few years overlap between occupied stands to increase the probability of Kirtland's Warbler colonization.

Currently habitat management is slowly expanding habitat at the periphery of the present breeding range. This approach is desirable and should be continued if the range is expanded without degrading the central areas. However, habitat in Michigan's Upper Peninsula, as well as in other states and Canadian provinces, is decidedly disjunct and not

peripheral. Thus, full-scale management plans for Kirtland's Warbier in disjunct habitat should be delayed until breeding pairs are found, unless there are other wildlife or silvicultural benefits from such management. For the present, it should suffice to improve the tree stocking in potentially suitable plantations in the Great Lakes region. If these stands attract breeding pairs, a more aggressive management program could be implemented.

SUMMARY

I searched nine areas in Michigan's Upper Peninsula for Kirtland's Warbler during 1979-1983. In both 1982 and 1983 a male was found in a 14 and 15-year old burn near Gwinn (Marquette Co.). These sightings represent the first records from the Upper Peninsula. Most other locations surveyed for Kirtland's Warblers or their habitat were too small, overmature or mesic to be suitable habitat for Kirtland's Warblers, but four areas are suggested for further searches.

Recent extra-limital records suggest that many young birds could disperse to areas outside the traditional nesting ground in northern lower Michigan, and this dispersal could be one reason why the population has not increased appreciably over the past decade. Because this species occupies habitat that is only temporarily suitable, such dispersal may be adaptive. If most dispersal occurs during the post-natal period of juveniles, few birds will reach small or distant habitat patches. The fragmented distribution of habitat within a limited breeding range may explain the frequency of unoccupied habitat. Dispersal may be an additional reason for the low pairing success of Kirtland's Warblers in habitat of marginal quality.

I recommend that habitat management be directed to areas within or adjacent to the present breeding range, with a gradual expansion at the periphery of the present range. The probability of stand colonization could be increased by adjusting the stand rotations to provide a few years overlap between occupied stands.

ACKNOWLEDGMENTS

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Several individuals provided suggested locations of potential suitable habit for Kirtland's Warblers in Michigan's Upper Peninsula. I especially wish to thank John Byelich and Bill Taylor for providing data on forest types from the Hiawatha National Forest. Jerry Ostrom provided an out-of-print map from an early Forest Service Survey. Richard Brewer, Dick Buech, Bill Irvine, Larry Ryel, James Sweeney, Nancy Tilghman, and Jerome Weinrich made helpful suggestions on the manuscript. Don Rakstad assisted with the 1983 and 1984 field work and with the manuscript preparation.

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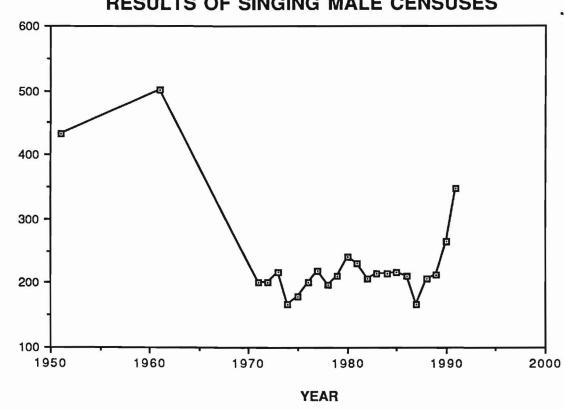
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KIRTLAND'S WARBLER

BRIEFING BOOK

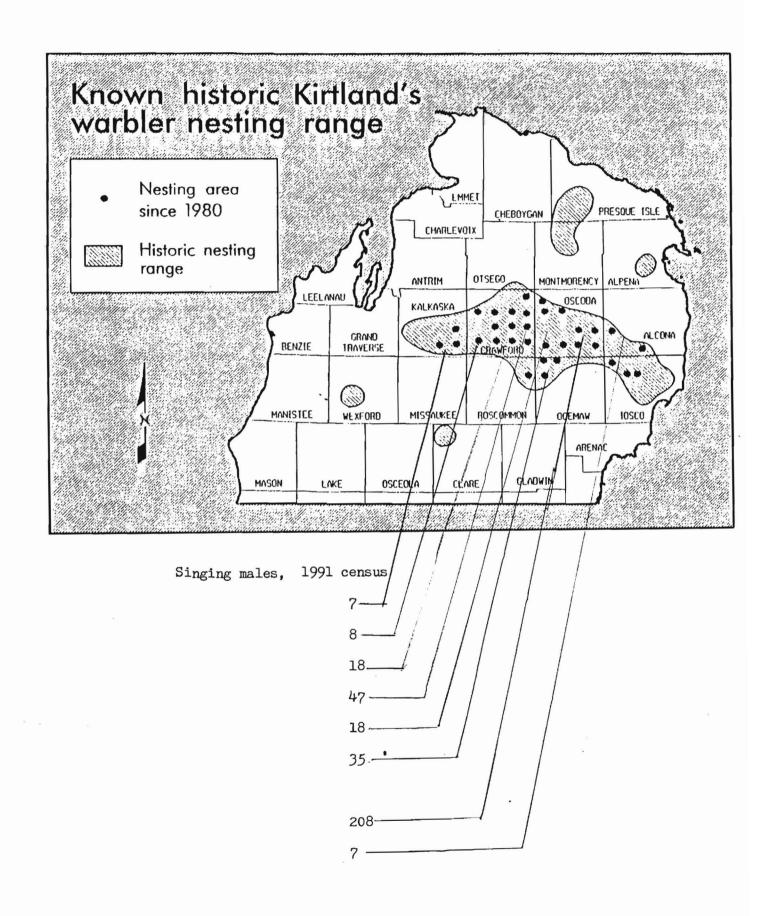
SECTION 4
PRELIMINARY PVA DATA
&
VORTEX ANALYSIS ON WARBLERS

KIRTLAND'S WARBLER DATA: RESULTS OF SINGING MALE CENSUSES



NUMBER OF SINGING MALES

	Column 1	Column 2
1	1951.000	432.000
2	1961.000	502.000
3	1971.000	201.000
4	1972.000	200.000
5	1973.000	216.000
6	1974.000	167.000
7	1975.000	179.000
8	1976.000	200.000
9	1977.000	218.000
10	1978.000	196.000
11	1979.000	210.000
12	1980.000	242.000
13	1981.000	232.000
14	1982.000	207.000
15	1983.000	215.000
16	1984.000	215.000
17	1985.000	216.000
18	1986.000	210.000
19	1987.000	167.000
20	1988.000	207.000
21	1989.000	212.000
22	1990.000	265.000
23	1991.000	347,000



1991 Michigan Kirtland's Warbler Census

County	Area	Singing Males	
Alcona	Pine River Byron Lake	6	
Alcona County To	tal		7
Crawford .	Eldorado Markle Road Fletcher Plantations Stephan Bridge Walsh Road Bald Hill	3 1 8 5 1 47	
Crawford County	Total		65
			÷
Kalkaska	Fletcher Plantations Sharon Plantation	5 2	
Kalkaska County	Total		7
Ogemaw	Hippie Burn and Adjacent Ogemaw KWMA (all plantation)	8 27	
Ogemaw County To	tal		35
		•	
Oscoda .	Muskrat Lake Plantation Red Oak Plantation Big Creek McKinley Plantation Mack Lake Burn	1 1 12 4 _208	
Oscoda County To	tal		226

Roscommon

St. Helen Plantation Forest Fire Experiment Station

4 (2 in plantations)

Roscommon County Total

Michigan Total

347

Oscoda County	65%
Crawford County	19%
Ogemaw County	10%
Alcona County	2%
Kalkaska County	2%
Roscommon County	2%
	100%

Mack Lake Burn = 60+%

In Burn Areas 264 = 76%In Plantations (+other) 83 = 24%

Federal 235 = 68%

POPULATION VIABILITY ANALYSIS DATA FORM - BIRDS

Species: Kirtland's Warbler, Dendroica kirtlandii

Species distribution: Breeding range throughout history about 160 km east-west

by 136 km north-south. Nesting sites are transitory.

Northern Lower Michigan.

Study taxon (subspecies):

No subspecies.

Study population location:

Mainly in Crawford and Oscoda Counties.

Metapopulation - are there other separate populations? Are maps available?: Map attached

(Separation by distance, geographic barriers?)

Nesting groups ("colonies") scattered within breeding range according to current habitat available.

Specialized requirements (Trophic, ecological):

Nests only in dense homogeneous growth of jack pines between 6 and 20 years after forest fire.

Age of first reproduction for each sex (proportion breeding):
Males and females breed as yearlings, but proportion unknown.

a) Earliest:

b)Mean:

Clutch size (N, mean, SD, range): First Clutch 3 eggs 4 eggs 5 eggs 6 eggs 2nd Clutch 3 eggs 4 eggs 5 eggs N=171, Mean=4.78 20 38 127 N = 368 20 Number fertile: Mean=4.00

85%, judged only from number of eggs present that hatched

Number hatched:

85% of eggs present at hatching time

Number fledged:

33% of eggs laid, calculated by Mayfield method

Laying Season:

Mean date of first egg, May 25; mean date of last egg, July 7.

Laying frequency (interclutch interval):

Eggs laid at daily intervals; second nestings about 7 days after fledging of 1st second nestings about 2 days after loss of second nestings about 2 days after loss of second nestings about 2 first nest.

Yes (as in previous question).

Duration of incubation:

14 days

Hatchling sex ratio:

Unknown. Suspected to be even.

Egg weights:

Mean 1.79, N=50 weighed within 2 days of laying.

Hatchling weights (male and female):

About 1.3 g., no know difference between sexes.

Age(s) at fledging:

Mean 9.4 days

Adult sex ratio:

About 1:1, but all observations show slightly more males (biases toward males).

Adult body weight of males and females:

Males: mean 13.6; females: Mean 14.2 (probably an artifact of pre-egg-laying gain).

Reproductive life-span (Male & Female, Range):
Oldest male on record, 9 years; oldest female, 8 years.

Life time reproduction (Mean, Male & Female):

Life expentancy of adults about 2 years.

Social structure in terms of breeding (random, pair-bonded, polygyny,

polyandry, etc; breeding male and female turnover each year?):

Usually pair-bonded, polygyny 0-15% of males varying by year.

Proportion of adult males and females breeding each year:

?? About 50% nest each year. (This question puzzling)
Non-nesting females not found; non-nesting males zero in some studies and
up to 15% in one study in one site.

Dispersal distance (mean, sexes):

65% of adult males return to within 1 km. About 50% of adult females return to same locality.

Migrations (months, destinations):

Fall migration, August 20 to October 5.

Spring migration arrival on nesting grounds, mean May 12. Earliest on coast of Territoriality (home range, season): Georgia, April 12.

Defended territory 0.6 ha to 10 ha. But distribution in habitat seldom more than 1 pair per 20 ha.

Age of dispersal: than 1 pair per 20 ha.

Family stays near but not exclusively in its territory in post-breeding season.

Maximum longevity:

As noted above, 9 years for banded male.

Population census - most recent. Date of last census. Reliability estimate.:

1991- 347 singing males, estimated accuracy within 10 %.

Projected population (5, 10, 50 years) .:

Estimates very unreliable because future population depends on forest fires.

Past population census (5, 10, 20 years - dates, reliability estimates):

1951 - 432 males 1971 - 201 males 1990 - 265 males
1961 - 502 males 1971-1989 - 167-242 males 1991 - 347 males
Population sex and age structure (young, juvenile, & adults) - time of year.:

Fecundity rates (by sex and age class):

Production 2.2 fledglings per pair of adults per year.

Mortality rates and distribution (by sex and age) (neonatal, juvenile, adult):

Survival rates of adults from June to June about 65% of previous year's population.

Calculated survival rates for fledglings about 36% (not actually observed).

Population density estimate. Area of population. Attach marked map.:

See attached map.

Sources of mortality-% (natural, poaching, harvest, accidental, seasonal?).:
All mortality is natural.

Habitat capacity estimate (Has capacity changed in past 20, 50 years?): Increased since 1986 by virtue of Mack Lake fire.

Present habitat protection status.:

Projected habitat protection status (5, 10, 50 years) .:

Environmental variance affecting reproduction and mortality (rainfall, prey, predators, disease, snow cover ?).:

Possible benefit to the warbler from wet winter in the Bahamas.

Is pedigree information available?:

Attach Life Table if available.

Date form completed:

September 22, 1991

Correspondent/Investigator:

Name: Harold F. Mayfield

Address: 1162 Nannette Drive

Toledo, Ohio 43614

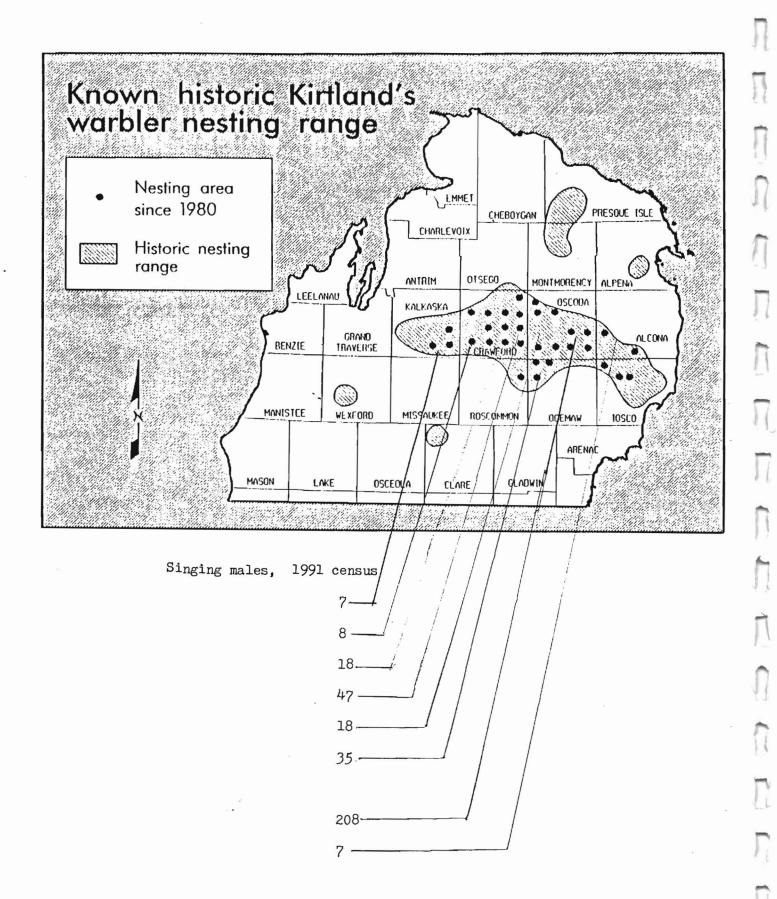
Telephone: (419) 385-5365

Fax:

References:

Comments:

If you have questions about my answers, call or write me.



for Weinrich & Boushelle POPULATION VIABILITY ANALYSIS DATA FORM - BIRDS Kirtlands' Warbler ser Mayfield a Walkenskew (Books)
Probat Species distribution: Study taxon (subspecies): Study population location: Metapopulation - are there other separate populations? Are maps available?: probably not " populations (Separation by distance, geographic barriers?) Specialized requirements (Trophic, ecological): above ref Age of first reproduction for each sex (proportion breeding): above uf a) Earliest: b) Mean: Clutch size (N, mean, SD, range): Number fertile:

Acres

Number hatched:

Number fledged:

Laying Season:

Laying frequency (interclutch interval):

sami

Are multiple clutches possible?

ys - sagre

		- 3
	Duration of incubation: previous ref - Mayfield Walkershaws books	n
	Hatchling sex ratio:	
	same	П
	Egg weights:	
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		11
	Hatchling weights (male and female):	
	some	П
	Age(s) at fledging:	
	sime	_
	Adult sex ratio:	3
	sem	
	Adult body weight of males and females: same + Lykes + Kipler (45FW5 - athers, 6a)	N
	same + signi / athers, oa	
	Reproductive life-span (Male & Female, Range): Walhankaw	
	Life time reproduction (Mean, Male & Female):	
	Life time reproduction (Mean, Male & Female): some + Mayfield	-
	Social structure in terms of breeding (random, pair-bonded, polygyny,	
	-1	
	polyandry, etc; breeding male and female turnover each year?): some T Bosette	
	Proportion of adult males and females breeding each year:	
	About 50% nest each year.	I
	some of Doce out	
	Dispersal distance (mean, sexes): Probst, Mayfield, Walkinskaw Migrations (months destinations):	
	Migrations (months, destinations): Nayfield, Walhinskow	1
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Ũ	Age of dispersal: Mayfield, Probot, Walkinshow, Boatte Mayfield, Probot, Walkinshow, Boatte Claim Smith thisis, Kepler + Sypes	1
	Age of dispersal:	
/ X	Age of dispersal: Claim Summer as hatched	T
'iti		Z.
1	Maximum longevity: Mayfield - Walkinslaw 1971-91 90%+	te.
y C	ropulation census - most recent. Date of fast census. Reflability estimate	1
	see attacked (1990) - lost census June 1991 347 Mi, Iwi-	-
	Projected population (5 10 50 years): (sunging of what m	1
	Probat will provide - preparation perparation perparation forward	
	Trabet well proved - now - well	1
	peper in sees	-

allested sec previous Past population census (5, 10, 20 years - dates, reliability estimates):

1951 41961 possibly less than 90%; 61 higher (2) Population sex and age structure (young, juvenile, & adults) - time of year .: Walkinshow, Mayfuld, Prolest Fecundity rates (by sex and age class): Walkinshow, Maybuild Mortality rates and distribution (by sex and age) (neonatal, juvenile, adult): Population density estimate. Area of population. Attach marked map.: will bring what s some + Probat Sources of mortality-% (natural, poaching, harvest, accidental, seasonal?).: Valuminous for 51,61,71-91 Habitat capacity estimate (Has capacity changed in past 20, 50 years?): definitely - directly correlates of census to date Present habitat protection status.: See Probata my projections from Symposium + in Projected habitat protection status (5, 10, 50 years).:

Same

guess!

public possibly same duction
but husbandly
security

Environmental variance affecting reproduction and mortality (rainfall, prey, predators, disease, snow cover?).: Rych Burgayne paper se reinfall in Bakers,
also pers comm w/a Dr. Fluck really) in Freefort - 1976

Is pedigree information available?: None documented for the best low temp

a little via Walkerskau by Walkeridaw Attach Life Table if available. weeth probability 10 the years for person som + Mayfield to Min likely a factor an annual production possibly alor processing processing Date form completed: 12/3/91

Correspondent/Investigator:

Name: Jerry Weinrich + for Gory Boushelle

Address: Haughteh Leke Wildlife Research St

Houghton Lake Hts, Mi 48630

Telephone: 422 - 5/9/ (Home - 5/7-345-06/5)

Fax: (net yet!)

References:

Mayfields and Walkinskow's books (+ papers)

vekers are consent researchers who

will probably be filling out a returning

this form - (Sypes & Keples are USFWS

employees, Bocitle USFWS funded

Probat - USFS)

Comments: Sharon - Jan - Ron -

This may look like a cap-out on filling out this form (it probably is!), but clif be lasty to have the 1991 census report done by thustons. I do think though that others will be providing most of this confo, if not from their own data then from walkinshows a Mayfield's backs. All have Census Unfo + Habitat Profestions (state) for the January session. May questions on what I did put on this form, or anything I'd can (should) being or provide please will me. How much of the census records to you need or want me to being?



United States Department of the Interior



FISH AND WILDLIFE SERVICE PATUXENT WILDLIFE RESEARCH CENTER

Southeast Research Station School of Forest Resources The University of Georgia Athens, Georgia 30602

November 15, 1991

Jan Eldridge Staff Biologist U.S. Fish and Wildlife Service Federal Bldg., Fort Snelling Twin Cities, Minnesota 55111

Dear Ms. Eldridge:

Attached please find the Kirtland's Warbler PVA questionnaire and two reprints. I have marked three important references from the literature cited of the main paper. Other important papers (e.g. by John Probst) will undoubtedly be mentioned by John.

Rather than answer most questions, we have sent <u>all</u> our original banding and sight record data to Sharon Moen, at her request, and she will in turn use it to come up with the needed figures. I have indicated on the questionnaire where these data will be used.

I hope this helps.

Sincerely,

Cameron B. Kepler

Attachments

RECEIVED

NOV 1 8 1991,

DIVISION OF ENDANGERED SPECIES

POPULATION VIABILITY ANALYSIS DATA FORM - BIRDS

Species: Kirtland's Warbler Species distribution: Study taxon (subspecies): Study population location: Metapopulation - are there other separate populations? Are maps available?: (Separation by distance, geographic barriers?) Specialized requirements (Trophic, ecological): Age of first reproduction for each sex (proportion breeding): a) Earliest: b) Mean: Clutch size (N, mean, SD, range): -Number fertile: Number hatched: in the literature in Walkinshaw 1983 Number fledged: and Mayfield 1960 Laying Season: Laying frequency (interclutch interval): Are multiple clutches possible? Yes

Duration of incubation: Hatchling sex ratio: in the literature in Walkinshaw, Egg weights: and Mayfield Hatchling weights (male and female): Age(s) at fledging: Adult sex ratio: Can be derived, in part, from our banding data set. Adult body weight of males and females: Will derive from our banding data set. Reproductive life-span (Male & Female, Range): Recapture rates from banding data and sight records.. Life time reproduction (Mean, Male & Female): Social structure in terms of breeding (random, pair-bonded, polygyny, polyandry, etc; breeding male and female turnover each year?): Proportion of adult males and females breeding each year: About 50% nest each year. Dispersal distance (mean, sexes): Will derive from our data set. Migrations (months, destinations): Territoriality (home range, season): Age of dispersal: 1 year (see our data set). Also need to know frequency of dispersal (see Table 1). Maximum longevity: Population census - most recent. Date of last census. Reliability estimate.:

Projected population (5, 10, 50 years) .:

Past population census (5, 10, 20 years - dates, reliability estimates):

Population sex and age structure (young, juvenile, & adults) - time of year.: Will derive from our data set.

Fecundity rates (by sex and age class):

Mortality rates and distribution (by sex and age) (neonatal, juvenile, adult): Will derive from our data set (see Table 2).

Population density estimate. Area of population. Attach marked map.:

Sources of mortality-% (natural, poaching, harvest, accidental, seasonal?).:

Habitat capacity estimate (Has capacity changed in past 20, 50 years?):

Present habitat protection status .:

Projected habitat protection status (5, 10, 50 years) .:

Environmental variance affecting reproduction and mortality (rainfall, prey, predators, disease, snow cover ?).:

Is pedigree information available?:

Attach Life Table if available. Attached Table 3 (preliminary)

KIRTLAND'S WARBLER MOVEMENTS BETWEEN COLONIES

DATES	BANDED AS REMAINED	ADULTS MOVED	BANDED AS REMAINED	IMMATURE MOVED
1986 to 1987	10	0 (0%)	2	1 (33%)
1987 to 1988	16	1 (6%)	11	5 (31%)
1988 to 1989	35	0 (0%)	13	3 (19%)
1989 to 1990	50	1 (2%)	25	12 (32%)
ALL YEARS	111	2 (2%)	51	21 (29.2%)

KIRTLAND'S WARBLER RETURNS IN MICHIGAN BY AGE

		IMMATURE		ADULT				
PERIOD	YEAR RECORDED	NO. RETURNED NEXT YEAR	RETURN RATE	YEAR RECORDED	NO. RETURNED NEXT YEAR	RETURN RATE		
1986-1987	12	2	16.7%	17	12	70.6%		
1987-1988	52	17	32.7%	43	22	51.2%		
1988-1989	54	15	27.8%	69	45	65.2%		
1989-1990	104	27	26.0%	88	63	71.6%		
TOTAL	222	61	27.5%	217	142	65.4%		

RETURN RATES FOR KIRTLAND'S WARBLERS IN MICHIGAN
(Approximate annual mortality rates)

BIRDS RETURNING IN:

YEAR BANDED	1984	1985 ^a	1986	1987	1988	1989	1990
1984	-	(5)	5	4	2	2	1 *
1985	-	(1)	1	1	1	0 .	0
1986	, -	-	-	9	6	3	2
1987	~	-		-	30	22	17
1988	-	-	-		-	33	24
1989	-	-	-	-	-	-	46
TOTAL AND % RETURNS	•,	(5)	. 6	14 (48.3%)	39 (41.1%)	60 (48.8%)	90 (46.9%)
TOTAL NEW BANDINGS	20	1 ^b	23	81	84	132	149
TOTAL BANDED POPULATION	20	6+	29	95	123	192	239

and observations were made in 1985; These BIRDS were sighted in subsequent years.

bthe Governor, Banded on Eleuthera (Bahamas) on 2/26/85, IS FIRST TALLIED AS A RETURN IN SUMMER 1986.

LATE RECORD OF KIRTLAND'S WARBLER ON THE BREEDING GROUNDS

PAUL W. SYKES, JR. AND DOUGLAS J. MUNSON

An extensive mist netting operation (N = 200 nets) was part of an ongoing Kirtland's Warbler research project in Michigan during the post-breeding period (mid-July to early October), 1988. Mist nets were in place at 2 study areas 13 September 9 October (5,220 net-hours) in Crawford (N=104 nets) and Oscoda (N=70 nets) Counties. We alternated operation of nets at the 2 areas. On 1 October 1988, we captured an adult female (age and sex determined by combination of plumage, molt condition, and wing chord; Sykes and C. B. Kepler, ms. in prep.) Kirtland's Warbler in the southeastern part of the 1980 Mack Lake Burn, Huron National Forest (T25N R3E S22, Oscoda Co.). This locality (latitude 44°32'45" N, longitude 84°03'30" W) is 12.9 km SE of Mio. The bird was in excellent condition, weighed 15.4 g, had a wing chord (unflattened) of 66.0 mm, and was fat class 4 (furculum full of fat but not bulging; see Helms and Drury, Bird Banding 31:1-40, 1960). We uniquely banded the warbler with USFWS band No. 2020-63149 on the right tarus above a blue band, and with 2 yellow bands on the left tarsus. We took color photographs of the bird held in the hand, and it was released at 1321 h at the exact site at which it was captured. Total handling time was about 20 min. The bird flew off strongly upon release and gave several chip notes, typical behavior for this species upon being released.

This 1 October date is the latest for a Kirtland's Warbler on the breeding grounds. Mayfield (The Kirtland's Warbler, Cranbrook Institute of Science, 1960) states: "... the majority leave [the nesting region] in the first week of September; and ... they become rare after the middle of September, although an occasional straggler may remain until late in the month." The previous late dates were 29 September 1975 (Schempf, P. F., JPW 54:40, 1976) and 29 September 1987 (Sykes et al., ms. in press, Wilson Bull.).

We thank Cameron B. Kepler and Chandler S. Robbins for helpful reviews of this note.

—Sykes: U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Southeast Research Group, School of Forest Resources, The University of Georgia, Athens, GA 30602; Munson: U.S. Forest Service, Huron National Forest, Mio Ranger District, 401 Court Street, Mio, M1 48647.



United States Department of the Interior



FISH AND WILDLIFE SERVICE Federal Building, Fort Snelling Twin Cities, Minnesota 55111

FWS\AFWE-SE

September 9, 1991

RECEIVED

NOV 1 2 1991

DIVISION OF ENDANGERED SPECIES

Dr. Lawrence H. Walkinshaw 915 North Onondaga Road Holt, Michigan 48842

Dear Dr. Walkinshaw:

The Kirtland's Warbler Population Viability Analysis (PVA) meeting will be held January 7-9, 1992. The gathering will be held at the Minnesota Valley National Wildlife Refuge Visitor Center. The meeting is scheduled to begin at 8:00 a.m. on January 7 and conclude around 4:30 p.m. on January 9. There will be a great deal of material to cover during these three days, so please be prepared for evening work sessions.

You are being invited to participate in this first PVA workshop for U.S. Fish and Wildlife Service Region 3 because of your past and/or current involvement with the Kirtland's warbler. For this workshop to succeed, all participants must be willing to freely exchange their data and be prepared to discuss their interpretations. Hard numbers (or best approximations) and estimates of their variability must be readily available to crank into the models, so come equipped to provide numbers.

In order to supply the participants with workshop materials in advance, and to conduct the most beneficial session, we will need certain species information prior to the meeting. To accomplish this, I ask that you complete the enclosed "Population Viability Analysis Data Form - Birds," and return it to this office no later than November 1, 1991. Do not feel that you have to try to fill in every blank on each page. Rather, concentrate on those sections for which you feel you are one of only a few experts, have data that few others have, or have a unique interpretation of data. The section dealing with habitat ("habitat capacity estimate") is too simplistic an approach for the Kirtland's warbler situation. What we should have are estimates of available habitat quantity and quality in future years. I would like Jerry Weinrich and John Probst to work up estimates for this section.

Long to be late here are some of my data. Vary Walkinshow

A block of rooms will be reserved at the Holiday Inn International, 3 Appletree Square (I-494 and 34^{th} Ave. S.), Bloomington, MN 55420 (612-854-9000), for January 6-9. It is within easy walking distance of the refuge headquarters (about 400 yards). We will be sending information closer to the time of the meeting on accommodation details.

The U.S. Fish and Wildlife Service, Division of Endangered Species, is willing to reimburse the travel expenses of any individual who would otherwise be unable to attend. Let us know as soon as possible of your needs so we can have a Travel Authorization prepared in time. We will need a fairly precise estimate of your travel costs, so have good estimates of plane fare, vehicle mileage, etc., handy when you contact us.

If you have any questions about the data needed or about travel expense reimbursement, call Jan Eldridge or Ron Refsnider in this office (612-725-3276).

Sincerely,

Ronald F. Refsnider

Acting Chief, Division of

7/

Kenalte Referredin

Endangered Species

Enclosure

POPULATION VIABILITY ANALYSIS DATA FORM - BIRDS

Species:

Kirtland's Warbler

Species distribution:

Study taxon (subspecies):

11 one

Study population location:

(rawford, Oscoda, Ogenew, Roscommon Courtier

Metapopulation - are there other separate populations? Are maps available?: (Separation by distance, geographic barriers?)

Jack pine 4-18 Specialized requirements (Trophic, ecological):

Age of first reproduction for each sex (proportion breeding):

a)Earliest:

I year (probable) b) Mean:

Clutch size (N, mean, SD, range): 4.78 (first clutch-1972-1978) (171 nests)

1,093 eggs; 38x 4 eggs; 127x 5 eggs; 4x 6 eggs)

Number fertile:

1,093 eggs

4:00 (2nd clutch-1972-1978 (36 nests))

8x 3 eggs; 20x 4 eggs; 8x 5 eggs)

Number hatched:

787 hatched

657 fledged

Conly 85 eggs failed to hotch

182 nosts

Laying Season: 24 May - 3 July

Laying frequency (interclutch interval): 7.1 days (4-11 days) between fledging of young and 1st agg second next)

11 cases 1972-1978 Known. Are multiple clutches possible? (2)

25 July 197 (1976)

Mestling bonded go Art. Rays Sc. 110-09079-22 July 1967-1972-1974 434m 43 Km 116-24628- 30 July 1968-116-24635 - 25 June 1970 1972-1977 9 Same aren Muskial lake Macklete 23 June 1974 - 29 June 1975 850-72516 Pere Cheney 1973 Some aren 1,6 km 25 June 1972 , 8 km from both 81-58948 1977 Art. Range S. Place 26 June 1972 - 1973-1978 183 m 81-58978 Some alse Lovells Ham Aren _ 28 Lun 1974 968 m 28 June 1973 -820-89228 Lovells Lourles 13 July 1976 28 June 1973 (74,75?) Lovells Lovells 1975-73 July 1974) 1 July 1973 820-89252 820-892 88 27 Vuly 1873 1974-1975 229 in Levolls Lovells 29 June 1974 830-20517 1975 743 m Lovells Closors 1976,1977 22 June 1974 1975?-1976-1977 Losells . Lovells 27 Jun 1974 1975 1976 Lovells 1977 zuesti 1976. Losells both lost Localle 11978 Art Rege N.

13-15 days (mcan 14,2 days) Duration of incubation: ing sex ratio: 7.

Figs: 517e (253eggs (8.3 ± 0.7 mm (15.5-19.9) mm, × 14.2 ± 0.6 mm (10.8-16.6) mm. Hatchling sex ratio: Egg weights: 1,8 grans Hatchling weights (male and female): /,2-1,8 9/ams 8-11 days 96 records mean 9,35days (7x8days;54x9days;29x10days;6x11days nearly 50-50 Age(s) at fledging: Adult sex ratio: 2 12,4-15,8 grams (mean, 13,7 grams) Adult body weight of males and females: \$ 12.2 - 16.0 grams (Meen, 13.8 grams) Reproductive life-span (Male & Female, Range): 3 2-9 42005 7 1-7 years Life time reproduction (Mean, Male & Female): one female Tyears Social structure in terms of breeding (random) pair-bonded, polygyny, polyandry, etc; breeding male and female turnover each year?); Proportion of adult males and females breeding each year: most Dispersal, distance (mean, sexes): from \(\frac{25m}{229m} \left(\frac{9}{200} \frac{87288}{400} \right) + 0 \)

Migrations (months, destinations): \(\frac{329m}{229m} - 676km \)

Migrations (months, destinations): \(\frac{13375}{13375} \)

Territoriality (home range, season):

Age of dispersal: on 15tyr (13) later -

Maximum longevity: 8 9 years & 7 years

Population census - most recent. Date of last census. Reliability estimate.:

Projected population (5, 10, 50 years).:

3

Past population census (5, 10, 20 years - dates, reliability estimates):

Population sex and age structure (young, juvenile, & adults) - time of year.:

Fecundity rates (by sex and age class):

Mortality rates and distribution (by sex and age) (neonatal, juvenile, adult):

Population density estimate. Area of population. Attach marked map.:

Sources of mortality-% (natural, poaching, harvest, accidental, seasonal?).:

Habitat capacity estimate (Has capacity changed in past 20, 50 years?):

Present habitat protection status.:

Projected habitat protection status (5, 10, 50 years).:

Environmental variance affecting reproduction and mortality (rainfall, prey, predators, disease, snow cover ?).:

Is pedigree information available?:

Attach Life Table if available.

Kirtlafid's Warbler nestlings which were found in future years Not allowed to capture birds in 1975 FEMALES .

Band No.	Date fledged		Date Refound Nesting	Where D	istance
110-09079	22 July 1967	Mack Lake	1972-1974	Art.Rang.So.	43 km
116–24628	30 July 1968	"	1970	п	43 km
116–24635	25 June 1970	"		Mack Lake Muskrat Lake	m 25 km
850-72516	23 June 1974	Pere Cheney	1975	Art. Mang. No.	17.6 km
81–58948	25 June 1972	Art.Range So		rt.Range So. rt.Range No.	1.6 km 0.8 km
81 – 58978	26 June 1972	Lovells Man	1973,1974	Lovells Man.	183 m
820-89228	28 June 1973	Lovells Man.	1974	Lovells Man.	968 m
820-89229	28 June 1973	Lovells Man.	13 July 76	Lovells man.	85 m
820-8925 3 2	1 July 1973	Lovells Man.	1974 ? 1975	Lovells Man.	ca 800 m
820-89288	27 July 1973	Lovells Man.	1974,1975	Lovells Man.	229 m
830–20517	24 June 1974	Lovells Man.	1975 , 1976 , 1977	Lovells Man.	743 m closer
830–20530	22 June 1974	Lovells Man.	1975 ? 1976 , 1977	Lovells Man.	ca 400 m
830–20555	27 June 1974	Lovells Man.	1975 ? 1976	Lovells Man.	ca 900 m
869-40326	1976	Lovells Man.	1977 1978	Lovells Man. Art.Range No.	917 m 15.3 km

Kirtland's Warbler male nestlings which were found in future years Not allowed to capture birds in 1975

MALES

BAND NO.	DATE FLEDGE	D WHERE	DATE REFOUN	ND WHERE D	ISTANCE MOVED
75–36698	1 July 1969	Art.Range S Crawford Co.	July 1971 1972 1973	Mack Lake Oscoda Co.	43 km
116–24662	July 1972	Mack Lake	28 May 1973 1974 1975 1972 Illed27 S	1 "	47 km
81–58909	21 June 1972	Art.Rng. So.	1973 1974 1975 1976 1977	1 " 5 " 11	1.6 km
81–58913	23 June 1972	Lovells Man.A	rea 1973 25 June 1981	DOVCITO IMITATION	183 m 15 km
81–58930	25 June 1972	" fo	ound 1973 no 1974 1975 1976 1977	nest found	same then
81-58944	25 June 1972	Art.Rang.So.	Jume 1973 1975	Muskrat Lake	21 km same
81–58947	25 June 1972	Art.Range So.	June 1973_ 1976 Nests not		1.6 km
81-58962	28 June 1972	Art.Range So Crawford Co.	1973 nest r 1974 1975 1976 1977 1978	Art.Range No. not found nest " " " "	1.38 km same same same SAME 0.8 km N
81–58977	26 June 1972	Lovells Man. An	rea 1973	Lovells.Man.Area (no nest) " Kyle Lake	395 m same 16 km
81–58979		Lovells Man. An edged at least	rea 1973 1974 1975 1976 19 77	Muskrat Lake " " "	20.5 km
820-89206		Lovells Man. A	rea †1974 1975	Muskrat Lake same 1978 l ovells Man.Area	20.5 km a 0.8 km from where bor

MALE KIRTLAND'S WARBLERS BANDED AS NESTLINGS WHICH RETURNED TO NEST

BAND NO.	DATE FLEDG	ED WHERE	DATE REFOUND NESTING	WHERE	DISTANCE
820-89211		Lovells Man. Area (with F820-89252) (with F830-20532)	26 June 1974 (5 23 July 1975(4 y 23 July 1975 (4	g) "	1183 m N same terr
820-89230	1 July 1973	Lovells Man. Area	5 July 1974 L 25 June 1975	ovells Man.	395 m same terr
					same mate
830–20589	5 July 1974	Art.Rang.So.	1975 (not 24 June 1976 A 1977		ca 1.6 km same
		(1978 nest not f	found) 1978	"	same
	24 June 1976 30-20589)	Art.Range No.	1978,1979,1980,	yg) Art.Range No same terr. ts not always fo	
81–58970	29 June 1972	Art.Range So. caught Crawford Co.,Mich.	21 June 1978 (no nest found)	Black Riv.Falls Wisconsin	
830–20521	24 June 1974	Lovells Man.Area, Crawford Co.,Mich.	27 May 1978	Quebec 101 km E of Pembroke,Ontario 72 km N of Ottar	

Kirtland's Warbler Most records are from banded birds L.H.Walkinshaw

allrecords from Crawford, Oscoda, Ogemaw counties . One record from roscommon; one from Wexford counties, Michigan.

Both male and female produce eggs or young the first year. (banded birds)

My oldest male was 9 years old; the oldest female 7 years.

Clutch sizes First clutch: 4.78 eggs (1972-1978) (171 nests)

(2 x 3 eggs; 38 x 4 eggs; 127 x 5 eggs; 4 x 6 eggs).

Second clutch: 4.00 eggs (1972-1978) (36 nests)

(8 x 3 eggs; 20 x 4 eggs; 8 x 5 eggs).

During this period 1,093 eggs were observed of which 787 hatched and 657 fledged.

72 % 60.11 %

Only 85 eggs failed to hatch.

Laying frequency 7.1 days between fledging of young from one nest and laying

of first egg in second nest.

(banded birds) No birds attempted a third nest.

Period between fledging and first egg varied between

4 and 11 days.

Laying Season: First eggs depended on when warm weather started:

(2nd clutches ca 24 May first clutches

banded birds) mean for second clutches first laid egg was 3 July

1972-1978- I actually found 11 cases of birds producing young from one nest then nesting a second time. (banded birds)

Incubation periods: 13-15 days (mean 14.2 days)

Size of eggs: (253 eggs) Length, $18.3 \pm 0.7 (15.5-19.9)$ mm

Width $14.2 \pm 0.6 (10.8-16.0)$ mm (10.8 very small).

Weight 1.8 grams

Hatching weights of nestlings: 1.2 to 1.8 grams.

Ages at fledging: 8-11 days. 96 records - mean 9.35 days

(7 x 8 days; 54 x 9 days; 29 x 10 days; 6 x 11 days).

Adult body weights: Male - mean 13.7 grams (12.4-15.8) grams.

Female mean 13.8 grams (12.2-16.0) grams (female birds weighed during breeding season

are usually heavier)

Males were found breeding their first year up until 9 years old if they survived.

Females were found breeding their first year up until 7 years old.

Kirtland's Warblers

Most males selected their future territory their first spring. I found they moved most often to an area of younger jack pines. On at least 2 occasions a male moved after the first year to a new location. It was apparent it might have been because they lost eggs or young to some predator.

With females it was never certain. One female lost 2 nestings at Lovells moved to the Artillery range North the next year.

Females moved shorter distances than males. 85 m to 43 km (14)

Males moved from 183 m to long distances such as Black River Falls, Wisconsin and Quebec. But those that moved far out of state were not found with mates.

Maximum longevity: One male lived to be 9 years old.

One female lived to be 7 years old.

Pedigrees of several birds published in my $2\ books$

Lawrence H. Walkinshaw

<u>KIRTLAND'S WARBLER SURVIVORSHIP TABLE</u> <u>BASED ON C. KEPLER'S DATA</u>

Survival	adult fe	males		adult m	ales		unkno	wn		total		
Year	surv.	start	end	surv.	start	end	surv.	start	end	surv.	star	end
span											t	
84 to 85	0.00	3	0	0.67	3	· 2				0.33	6	2
85 to 86	1.00	1	1	1.00	3	3	1.00	3	3	1.00	7	7
86 to 87	0.71	7	5	0.75	8	6	1.00	3	3	0.78	18	14
87 to 88	0.47	15	7~.	0.46	26	12	1.00	3	3	0.50	44	22
88 to 89	0.60	25	15	0.66	38	25	1.00	3	3	0.65	66	43
89 to 90	0.65	26	17	0.82	61	50	0.75	4	. 3	0.77	91	70
90 to 91	0.26	46	12	0.58	89	52	0.75	4	3_	0.48	139	67
average	0.53			0.71			0.92			0.64		
st dev	0.32			0.17			0.13			0.23		
87 to 90 only												
average	0.57			0.65			0.92			0.64		
st dev	0.10			0.18			0.14			0.13		

Survival	juv fem	ales		juv male	es		unknov	vn ju∨		total		
Year span	surv.	start	end	surv.	start	end	surv.	start	end	surv.	star t	end
84 to 85	1.00	1	1				0.23	13	3	0.29	14	4
85 to 86							er .				0	0
86 to 87	0.40	5	2	0.25	4	1	0.00	4	0	0.23	13	3
87 to 88	0.42	24	10	0.42	24	10	0.00	5	0	0.38	53	20
88 to 89	0.14	22	3	0.38	29	11	0.33	3	1	0.28	54	15
89 to 90	0.27	33	9	0.38	61	23	0.20	10	2	0.33	104	34
90 to 91	0.13	30	4	0.24	58	14	0.16	19	3	0.20	107	21
average	0.39			0.33			0.15			0.28		
st dev	0.32			0.08			0.13			0.06		
87 to 90 c												
average	0.28			0.39			0.18			0.33		
st dev	0.14		8.48 23.	0.02			0.17			0.05		

Hi Ulie! This is the promised table concerning year by year Kirtland's Warbler survival. Males, females, and unknowns (unsexed) are separated as are adults and juveniles. "Start" is the numerator and "end" is the denominator in the equation used to derive "Surv." (survival during "Year Span").

I calculated the averages and standard deviations for all years but feel the interval between 1987 to 1990 is most representative of the population given sample sizes and the possibility of identifying birds

KIRTLAND'S WARBLER SURVIVORSHIP TABLE BASED ON C. KEPLER'S DATA

in 1992 that were missed this past season. Keep in mind that females are more difficult to find and an estimated 85% of the current population is unbanded (Kepler pers. comm).

I did not try to match up mythical band combinations with their most likely actual sequence, nor did I error check the data set, yet. The numbers may after <u>slightly</u>if and when I accomplish these two tasks.

Hope you and the rest of the crew have fun at the Christmas Celebration. Best of luck and speed when compiling the briefing document.

Cheers,

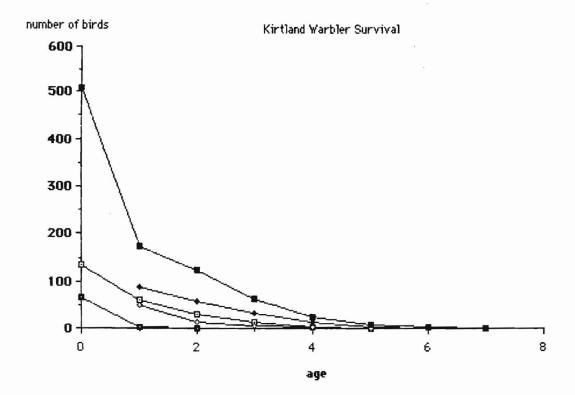
Sharon

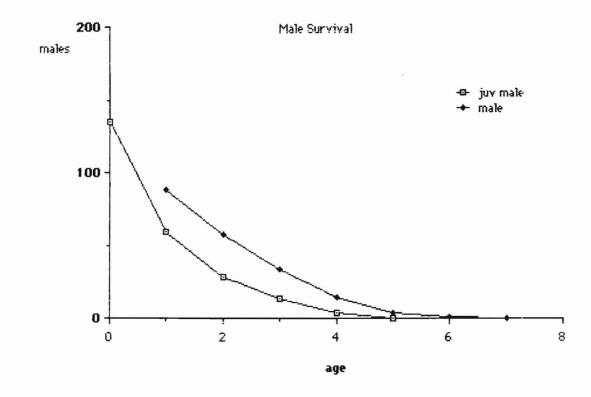
12/9/91

3	0.45	13	0.59	34
4	0.31	4	0.41	14
5		0	0.29	4
6			0.25	1

FEMALES

Age		juv		adults
0		65		49
1	0.06	4	0.27	13
2			0.46	6
3			0.67	4
4			0.25	1



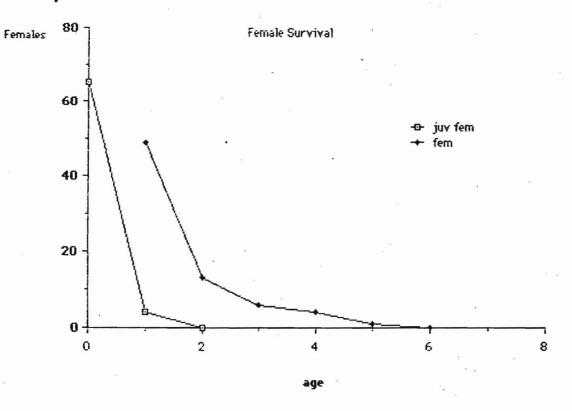


ÅLL

Age	lx									
0	1		508							
1	0.34	0.34		174						
2	0.25	0.72			125					
3	0.13	0.51				64				
4	0.05	0.39					25			
5	0.02	0.32						8		
6	0.01	0.38							3	
7	0	0.33								1

MALES

Age		juv		adults
Ū		135		
1	0.44	60		88
2	0.48	29	0.66	58



lay-hatch-fledge

From	Walkin:	shaw 88	}]							
year	eggs	hatch	8	fledge	% of laid	nest	hatch	%	fledge	% of lai	d		
1974	179	130	73	119	66	43	35	81	31	72			
1975	162	119	73	102	63	37	31	84	26	70			
1976	134	104	78	39	29	33	27	82	23	70			
1977	132	87	66	64	48	31	23	74	19	61	broken down into	1 and 2 clutc	h
1979	61	45	74	40	66	12	11	92	10	83			
1980	12	9	75	9	75								
total	680	494			55	156	127	81	109	70			
sd			4		17			6		8			
3d as 9	8		5		30	Ĭ		8		11			

73 150 115 92

39 29

23

neet loss.dat

Predators						
		1004 40 0 000				
year		lost to pred			source	
na	57	38	67		Mayfield '60	
uear	≠ eggs	lost to pred	nercent			
72	135	24	18		Walkinshaw '8	<u></u> द
73	150				Walkinshaw '8	
74			&		Walkinshaw '8	
75		4			Walkinshaw '8	
76		*************************	A		Walkinshaw '8	
77	· A	A	*******************	A	Walkinshaw '8	
total	971			ave	Walkinshaw '8	**************************
sd .				sd		<u></u>
			å	sd as % ave	ò	
	•			00 00 10 010		
Predators:	<u> </u>	•		•	***************************************	
1) Blue Jay			•	······································		
2) 13-line		uirrel	<u></u>			•
Crow		<u> </u>	<u></u>	<u> </u>		
Red Squirre	1		<u></u>	•		<u></u>
	:					
		•	: :			•
Desertion		<u></u>	•		•	
		•	<u> </u>			<u></u>
nests	deserted	percent	•	source	comments	
57			<u></u>	Mayfield '60	******************************	\$
			• :		maybe related	to cowbirds
	·•	•	<u></u>			<u> </u>
year	#eggs	deserted	percent		<u> </u>	
72	135				Walkinshaw '8	 3
73			A		Walkinshaw '8	***************************************
74			3		Walkinshaw '8	
75			4	·····	Walkinshaw '8	
76		*************************	4	• :	Walkinshaw '8	***************************************
77			\$	<u> </u>	Walkinshaw '8	
total	971		3	ave	Walkinshaw '8	
3d	:		&	3d		
			***************************************	sd as % ave		:
			:	:		
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nest loss.dat

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uear	55 6 5	≠ eggs	losses	noroost		·	••••••
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	67	13				Walkinshaw '8	
	68	4		A		Walkinshaw '8	
••••••	69	24	A			Walkinshaw '8	
	70	48	31	65		Walkinshaw '8	**********************
	71	29	17			Walkinshaw '8	
	72	135	48	36		Walkinshaw '8	
	73	150	58	39		Walkinshaw '8	3
	74		77	30		Walkinshaw '8	
	75	162	60	37		Walkinshaw '8	3
	76	134	45	34		Walkinshaw '8	3
	77	132	68	52		Walkinshaw '8	3
total		1093	436	53	ave	Walkinshaw '8	3
3d				20	sd		
				39	sd as % ave		
		475	40	~~~			
	72	135	48 50	36		Walkinshaw '8	*************************
	73	150	58			Walkinshaw '8	************************
	74		77		*************	Walkinshaw '8	
•••••	75	162	60	37		Walkinshaw '8	
	76	***************************************		34		Walkinshaw '8	
	77	132	68	52	Å	Walkinshaw '8	************************
total		971	356	********	ave	Walkinshaw '8	3
sd					sd		
		***************************************	***************************************	20	sd as % ave	•••••	
year		# eggs	losses	fledged	% fledged		
	72	135	48	87	64		
•••••••	73	150	58	92	61		••••••
••••••	74	258		181			
••••••	75	162	60	102	A		•
***************************************	76	134	45	89	66	,	••••••
•••••	77	132	43 68	64	48		
total	<i>i i</i>	971	356	*		A. I.A	
cotai 3d		7/1	330	015	A	ave	
3U	•••••				35 56	************************************	***************************************
				<u> </u>	56	sd as % ave	

vortex test file

Question •	kw1.dat	Justification	
Input file name	kw1.dat	data file as written below	
Output file name	kw1.out		
data files produced for potting	Ч		
N from each run (y) or means across runs (n)	ÿ	*checkmay not work	
full table printed	n	if y only first 5 runs	
≠ repeats	50		
# years	20	1971-91; release from cowbirds	
extinction reports	1	yearly	
* pops	1	all in one pop	
EY(r) correlated w/ EY(s)	y	simplisity	
types of catastrophies	0	simplisity	
nbreeding depression	n	simplisity	
nonogamy or polygyny	Р	polygynous	
mean agef begin breeding	1 -	(Maufield, Walkinshaw)	
mean agem begin breeding	1	(Mayfield, Walkinshaw)	
Max age	9	9 years (Mayfield)	
Sex ratio at birth	0.5	1:1 (Mayfield)	
Max # young/litter	6	max # eggs per clutch	7
% f produce O young	31	Walkinshaw pg 120	
K f produce 1 young	0	Walkinshaw pg 85	7
% f produce 2 young	0	Walkinshaw pg 85	
% f produce 3 young	3	Walkinshaw pg 85	
% f produce 4 young	20	Walkinshaw pg 85	
% f produce 5 young	45	Walkinshaw pg 85	
%fproduce 6 young	1	Walkinshaw pg 85	
6D in % f of producing litters due to EY	0	simplisity	
% mort of f between age 0 & 1	78 (42	Walkinshaw pg 167	-
5D in % mort of f between age 0 & 1	+14, D	simplisity	
% mort of adult f	<i>51</i> 59	Walkinshaw pg 167	
6D in % mort of adult f	<i>19</i> 0	simplisity	
% mort of m between age 0 & 1	63 26	Walkinshaw pg 167	
SD in % mort of m between age 0 & 1	<i>7</i> 0	simplisity	
% mort of adult m	37 38	Walkinshaw pg 167	
5D in % mort of adult m	17 0	simplisity	
Are all adult males in breeding pool	и 80 у	simplisity	
Stable age dist in starting pop	ÿ	simplisity	
≠ in starting pop	201	201 singing-1971, not enough mem if 402	
K	1000	goal, not enough mem if 2000	
SD in K due to EY	0	simplisity	"
trend in K	n	simplisity	
Harvest	n	simplisity	
Suppliment	n .	simplisity	
Do you want to run another model	¥		
notes:	HIGH!!		-

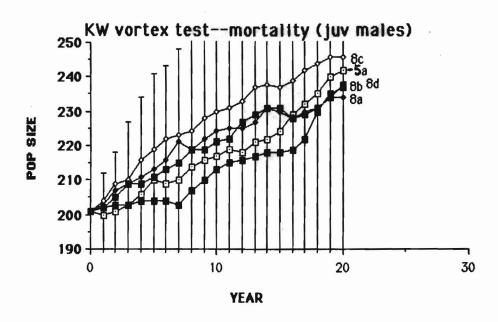
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FILE JUSTIFICATION

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		37	based on Walkinshaw	<u>:</u> :
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<u> </u>		<u> </u>		
3		22	based on Walkinshaw (pg 102?)	
20		18	based on Walkinshaw	
45		43	based on Walkinshaw	· · · · · · · · · · · · · · · · · · ·
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50	Walkinshaw pg 119 (+egg to fledge mort)	85	guess	
0		0		· •
38	Walkinshaw from Morse (89)	38	based on Walkinshaw/morse	: : :
0		0		: : :
50	Walkinshaw pg 119 (+egg to fledge mort)	85	guess	
0		0		
38	Walkinshaw from Morse (89)	38	based on Walkinshaw/morse	
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2	2		2
18	18		18
43	43		43
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83 guess	75	guess	70
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35 Walkinshaw guess	35	<u> </u>	35
0	0		0
83 guess	75	guess	70
0	0		0
35 Walkinshaw guess	35		35
0	0	··•···································	0
y	Ų		<u> </u>
Ÿ	y		
201	201		<u>y</u> 201
1000	1000		1000
0	0	:	0
n	n	<u></u>	n
n	n		n
n	n	··•	n
		:	

Input files kw8a-8d.dat: Simplest path, juvenile survival--males

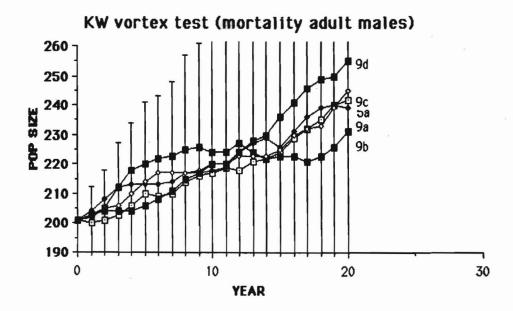


8a: male juvenile mortality = 85% 8b: male juvenile mortality = 80% 5a: male juvenile mortality = 75% 8c: male juvenile mortality = 70% 8d: male juvenile mortality = 65%

Conclusion: Practically no effect. Should figure out how dramatically mortality must vary before seeing effect.

Note different reale

Input files kw9a-9d.dat: Simplest path, adult survival--males



9a: male adult mortality = 45%

9b: male adult mortality = 40%

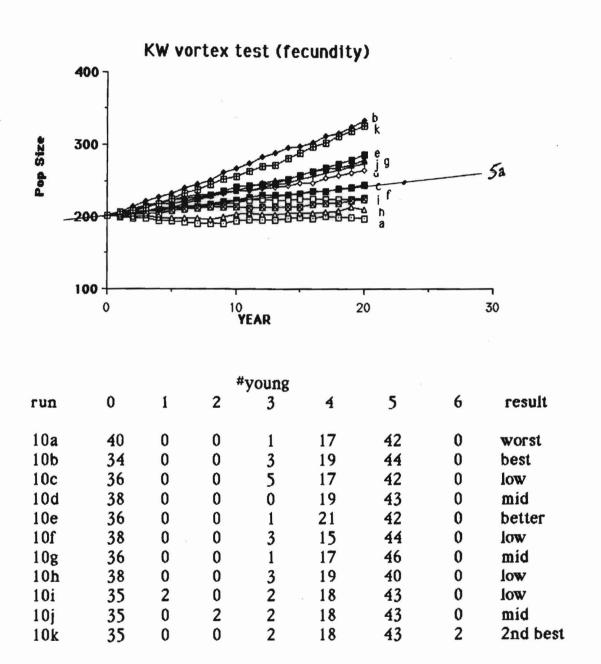
5a: male adult mortality = 35%

9c: male adult mortality = 30%

9d: male adult mortality = 25%

Conclusion: A bit more sensitive than juv. male mort, but not by much. Strange curvy lines?

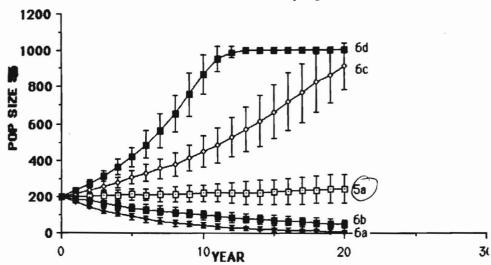
Input files kw9a-9d.dat: Simplest path, nesting success



Conclusion: Population is stable if scenario 10a. Otherwise, +-50 variation after 20 years. How best to handle this section?

Input files kw6a-6d.dat: Simplest path, juvenile survival--females





6a: female juvenile mortality = 85%

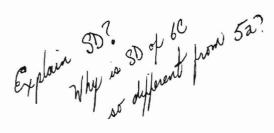
6b: female juvenile mortality = 80%

5a: female juvenile mortality = 75%

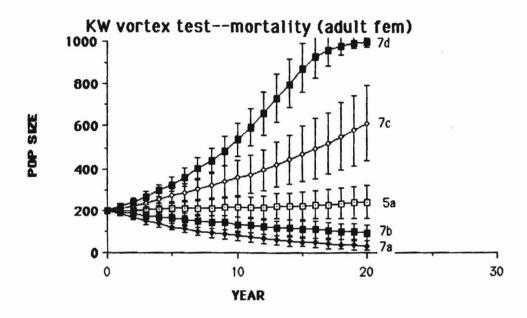
6c: female juvenile mortality = 70%

6d: female juvenile mortality = 65%

Conclusion: Pop sensitive to fem juv mort. Not as much so if lambda < 1.



Input files kw7a-7d.dat: Simplest path, adult survival--females



7a: female adult mortality = 45%

7b: female adult mortality = 40%

5a: female adult mortality = 35%

7c: female adult mortality - 30%

7d: female adult mortality = 25%

Conclusion: Less sensitive that fem juv. mort. Still not as dramatic when lambda<1. Why?

POPULATION VIABILITY AND THE KIRTLAND'S WARBLER

Richard J. Baker

Nongame Wildlife Program Minnesota Department of Natural Resources 500 Lafayette Road, Box 7 St. Paul, MN 55155-4001

Introduction

The field of population viability is young and still heavy on theory (as new disciplines tend to be). It draws from a wide variety of subjects, including ecology, genetics, and population biology, and in this short paper I can only scratch the surface. However, I will try to cover three things. First, I'll review the concept of population viability and what is behind it. Next, I want to discuss how this concept is being applied in the form of population viability analysis. Finally, I'll try to look at what population viability might say about the management of the Kirtland's warbler.

First, a note on history. The concept of population viability more or less grew out of its inclusion in the Planning Regulations of the National Forest Management Act of 1976 (36 CFR 219). This document stated that "Fish and wildlife habitat shall be managed to maintain viable populations of existing native and desired non-native vertebrate species in the planning area." Since that time, much effort has been devoted to clarifying this mandate and exploring its implications. Mark Shaffer (1981), now with the U.S. Fish and Wildlife Service, conducted some of the first work on population viability on the grizzly bear population in the yellowstone ecosystem. More recently, the concept of population viability has been applied to the management of the red-cockaded woodpecker and the spotted owl. A book on the subject (Soule 1987) came out last year. Just the same, population viability is in its infancy.

The Concept of Population Viability

Let's start with a definition that I've synthesized from several recent sources. Population Viability can be thought of as the probability that, given a certain set of conditions, a population will be secure for a period of time from factors that threaten its persistence. In other words, viability is a measure of the risk of extinction, and the goal of managing for a viable population is to prevent the decline and eventual extinction of that population. A typical description of the viability of a population might say that "Populations X, given current conditions and thus-and-such management, has a 95% probability of persistence for 100 years."

There are many forces in nature that affect the risk of a populations extinction, and contributors to the field have come up with subtly different ways of organizing them. Shaffer (1987) has combined these factors into four groups: genetic uncertainty, demographic uncertainty, environmental uncertainty, and natural catastrophe.

Genetic Uncertainty affects the amount of genetic variation found a population's gene pool (Table 1). This genetic variation is important for several reasons. For one, the offspring of a population with greater genetic variation may be better able to survive and reproduce than the offspring of a population that has reduced genetic variation. Additionally, the ability of a population to adapt to changes in its environment depends in large part on the amount of genetic variation it has in its gene pool. These abilities to produce offspring (known as "fitness") and to adapt to change are important to a population's viability. Two phenomena are the principal causes of loss of genetic variation. These are inbreeding, where the mating of close relatives results in the loss of genetic variation; and genetic drift, where random changes in the gene pool through time result in the loss of variation. A viable population must have a large enough effective population size to avoid the effects of inbreeding and drift.

Table 1.

Genetic Uncertainty

Examples: * inbreeding

* genetic drift

Affects

viability by: * reducing genetic variation

Resulting in: * lower reproduction

* reduced survival of young

* reduced ability to adapt to environmental change

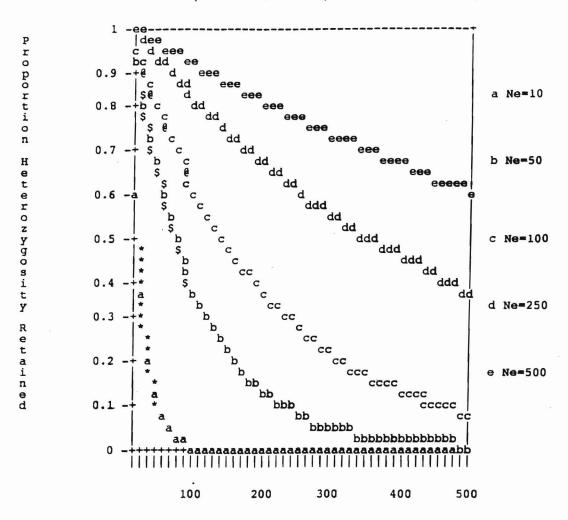
Notice that I said effective population size rather than census population size. We normally talk in terms of census population size, which is the actual number of individuals one would count. A census, however, doesn't reflect how the population responds to inbreeding and drift. By calculating an effective population size (N_a) , we can adjust for these factors. Basically, it takes into account the fact that not all individuals in a population contribute the same number of genes to the next generation's gene pool. In addition to inbreeding and drift, reasons for this include uneven sex ratio, unequal survival of young, and changes in population size. Imagine a simplistic example where some individuals in a population don't mate, others produce offspring that die, and those that do produce surviving offspring don't produce the same number. As a result, several individuals are not contributing to the next generation's gene pool, and some are contributing much more than the others. These factors will often translate a census population size into an effective population size half as large.

Population genetics gives us models for estimating the rate at which genetic variation is lost in a population (Figure 1). An effective population size of 500, according to theory, would lose only 1% of its genetic variation after ten years, 10% after one hundred years, and 40% after five hundred years. By comparison, an effective population size of 100 would lose 5% after ten years, and 40% after one hundred years. The loss of 40% of a populations genetic variation might seriously jeopardize its ability to adapt to change beyond 100 years. However, genetic uncertainty is most critical either in the short term for very small populations or in the very long term for large populations.

Figure 1.

LOSS OF GENETIC VARIATION

(AS HETEROZYGOSITY) DUE TO DRIFT



Number of Generations

Demographic Uncertainty is the second set of factors that can threaten viability (Table 2). For any individual in a population, there is always a chance that in any year, it will die or have no surviving offspring. In a large population, this doesn't present a problem, but in a small population, the cumulative effect of this possibility can have devastating consequences. As an extreme example, there is always a chance that in a population of 20 individuals, there will be no reproduction in a certain year, or all offspring will be of one sex. Clearly, in a population that reproduced only once, this would result in extinction. However, this example demonstrates that demographic uncertainty is actually only important to the viability of very small, closed populations, since the chance of such random events decreases quickly as a population grows.

Table 2.

Demographic Uncertainty

Examples: * low number of offspring

* skewed sex ratio in offspring

Affects

viability by: * reducing reproductive potential

of next generation

Resulting in: * vulnerability to genetic

uncertainty

* vulnerability to further demographic uncertainty

Environmental Uncertainty is a group of influences on viability that affects the birth and death rates of entire population (Table 3). It includes such things as climatic change, reduced habitat quantity or quality, and increased predation, competition, and parasitism. Unlike demographic uncertainty, these factors influence viability independently of population size.

Natural Catastrophe, like environmental uncertainty, affects the birth and death rates of an entire population regardless of size (Table 4). Natural catastrophes include climatic change, disease, fire, flood, drought, and windstorm. There is a general consensus that environmental uncertainty and natural catastrophe are the most critical to viability of all but very small populations, since only a very large population size or a very widely distributed population can protect against such unpredictable events.

Environmental Uncertainty

Examples:

- * reduced habitat quality
- * reduced habitat quantity
- * increased predation, competition, parasitism

Affects

viability by:

- * reducing resource availability
- * reducing birth rate
 * reducing survivorship

Resulting in:

- * reduced population size
- * vulnerability to demographic

uncertainty

Table 4.

Natural Catastrophe

Examples:

- * drought
- * flood * fire
- * climatic change

Affects

viability by:

* reducing habitat quality

and/or quantity

* reducing population size

Resulting in:

* vulnerability to environmental

uncertainty

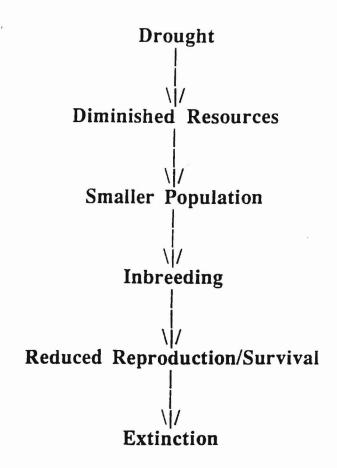
* vulnerability to demographic

uncertainty

All of these factors are interconnected so that they not only contribute to each other, but some may lead to others (Figure 2). For example, a natural catastrophe such as a drought may stimulate an event of environmental uncertainty, such as a decrease in habitat quality or resource availability. This in turn could knock a resident population down to a small size, at which point it may become susceptible to the effects of genetic or demographic uncertainty. A recent article (Gilpin

and Soule, 1986) refers to this as an extinction vortex, where the influence of different factors culminates in extinction.

Figure 2.



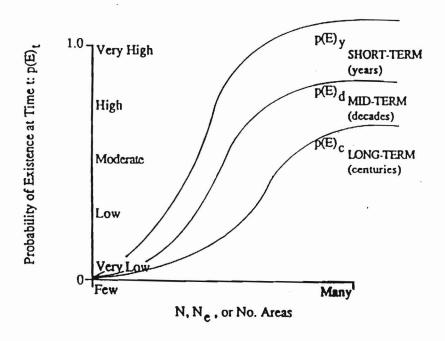
Population Viability Analysis

Recall my example of a typical description of the viability of a population, which read "Population X, given current conditions and thus-and-such management, has a 95% probability of persistence for 100 years." I'd like to point out that there are four variables in this statement. These are 1) the population size, 2) the set of conditions, 3) the length of time, and 4) the probability of persistence. It can almost be thought of as an equation with four unknowns where the effects of population size and the conditions in which that population exists equal the probability of persistence for a certain length of time. This could be represented as:

(Population Size) (Conditions) = (Persistence) (Time)

and can be depicted as in Figure 3.

Figure 3. A risk model for population viability. As a general rule, the probability of existence at a future time, p(E), increases in proportion to population numbers (N), effective population number (N), and the number of distinct geographic areas occupies by a species. The appropriate scales and the shapes of the curves for different time preferences depend on biological assessments based on a population's life history, demographic, genetics, and the nature of its environment. (From Salwasser et. al. 1986)



The task of solving this equation has come to be known as a Population Viability Analysis or PVA. PVA is the applied end of what is an otherwise rather theoretical concept. As far as I know, this type of analysis has been conducted for only a few species. As I mentioned, Mark Shaffer has done this for the grizzly bear at Yellowstone National Park. More recently, this approach has been applied to the red-cockaded woodpecker and the spotted owl. Again, the purpose of a PVA is to assess the risk of a populations extinction given a certain set of conditions. To give you a sense of what is involved in this, I think it would be useful to look briefly at the PVA for the spotted owl, which was conducted by the Forest Service's Pacific Northwest Region and released last year (USDA, Forest Service 1988).

The spotted owl is a species that appears to depend on old-growth forest in the Pacific Northwest for its existence. This forest has great timber value, and the problem has been how to provide for timber production while maintaining a viable population of the owl. In the final environmental impact statement, seven alternatives were being considered for future management of this habitat. The PVA involved evaluating the effect of each alternative on the viability of each of several distinct sub-populations of the owl.

The first step in the spotted owl PVA was to assemble all available information on the biological and ecological characteristics of the species. As with most species, in some areas such as distribution and habitat use, a great deal was known, while in other areas, like demography, there was relatively little information. Along with biological and ecological information, it was necessary to assemble information on the status of the owl's habitat, its current and future quality and quantity, and any current and anticipated activities affecting the population and/or its habitat.

Once all this information had been assembled and reviewed, it was possible to conduct the actual analysis. For the spotted owl, there was interest in assessing viability in each sub-population. In addition, the Forest Service wanted to obtain an estimate of viability over five different time periods. These were 0, 15, 50, 100, and 500 years into the future. The assessment involved evaluating, one by one, the effect of genetic uncertainty, demographic uncertainty, environmental uncertainty, and natural catastrophe on each combination of population, condition, and time.

Genetic uncertainty was investigated by estimating the effective population size of each sub-population. The formula used accounted for unequal sex ratio, dispersal distribution, reproductive success, overlapping generations, fluctuating population size, and inbreeding. The resulting value was used to determine in which cases loss of genetic variability would be unacceptable. Demographic uncertainty was evaluated by constructing a Leslie matrix to model change in the size of each sub-population. Computer simulations were then run to see if a sub-population would fall below an acceptable density. Finally, the effects of environmental uncertainty and natural catastrophe were "assessed subjectively", to quote the EIS. For each of the four factors, different conditions were determined to result in very high, high, moderate, low, or very low viability, the definitions of which are shown in Table 5. The results allowed them to produce a table depicting the viability of each option (Table 6 is an example). This is what they are using to help them choose between their management alternatives, along with other considerations.

Population Viability and the Kirtland's Warbler

Thus far, I have tried to give you a glimpse of what population viability is and how it is applied in management decisionmaking. I'd like to finish by exploring with you the implications of this concept for the Kirtland's warbler. Obviously, the spotted owl PVA involved a great deal of work on the part of a large staff of experts. Just the same, it has received a lot of criticism for its shortcomings (e.g. Lande 1988). I want to make it clear that I have not attempted to conduct a Population Viability Analysis for the Kirtland's warbler. However, I think we can learn something from speculating about the population viability of this species.

Table 5. Following are Definitions of the Probability Levels Used in the Viability Rule Set (Table B-14) (From USDA-FS, 1988)

VERY HIGH:

Continued existence of a well-distributed population on the planning area at the future date is virtually assured. This is likely even if major catastrophic events occur within the population, research finds that the species is less flexible in its habitat relationships, or if demographic or genetic factors are more significant than assumed in the analysis.

HIGH:

There is a high likelihood of continued existence of a well-distributed population in the planning area. There is limited latitude for catastrophic events affecting the population or for biological findings that the population is more susceptible to demographic or genetic factors than was assumed in the analysis.

MODERATE:

There is a moderate likelihood of continued existence of a well-distributed population in the planning area at the future date. There is no latitude for catastrophic events affecting the population or for biological findings that the population is more susceptible to demographic, genetic, or habitat distribution factors than was assumed in the analysis.

LOW:

There is a low likelihood of continued existence of a well-distributed population in the planning area at the future date. Catastrophic, demographic, genetic, or habitat distribution factors are likely to cause elimination of the species from parts or all of its geographic range during the period assessed.

VERY LOW:

There is a very low likelihood of continued existence of a well-distributed population in the planning area. Catastrophic, demographic, or genetic factors are highly likely to cause elimination of the species from parts or all of its geographic range during the period assessed.

Table 6. (From USDA-FS, 1988)

Summary of Relative Security From Threats to Population Viability by Year and Alternative 1

Olympic Peninsula

(This assumes isolation because of distance from the Washington Cascades)

	Pla pe	Planning period			Projections beyond planning period	
Year	: 0	15²	503	100°	1505	
Alternative						
A	Н	М	L	VL	VL	
C ₃	Н	М				
D	Н	M				
F ⁴	H	M	М	М	L	
G	Н	M				
M	Н	Н				
L	Н	Н	Н	M	М	

¹ See "Relative Security From Factors That Could Threaten Population Viability" in the text for an explanation of this table and definitions of security ratings.

² Period of Forest Plans.

¹ No Action Alternative.

¹ Preferred Alternative:

⁵ Projected ratings of security from factors that could threaten viability beyond year 15 are based on the assumption that both the alternative and planning directions on other ownerships are continued in subsequent planning periods. This is purely hypothetical. The ratings are shown only for Alternatives A, F, and L to portray the estimated range of possible future conditions. Ratings in years beyond the current planning period (first 15 years) would depend on decisions made for those future planning periods. For example, a decision to protect additional spotted owl habitat after year 15 would shift the ratings in future years toward those portrayed for Alternative L.

If we were to conduct a PVA, we would begin by formulating the equation we want to solve. Unlike the spotted owl case, we don't have a set of management alternatives we need to decide between. Instead, we have a recovery plan, which provides us with some givens. Recognize that I am simplifying things quite a bit here. Regarding probability of persistence, I think it is fair to say that the goal of the recovery plan is to insure the persistence of the species into the future. To interpret this literally, "insure" means 100% probability of persistence. Since we all know that nothing is certain in this world, we might want to think in terms of a very high probability of persistence. Time could also be considered infinite in the context of the recovery plan. That is, the goal of the plan is to insure viability for as long as possible. For our purposes, however, we might want to take the lead of the spotted owl PVA, and ask about population viability in the short term, say 5-15 years (a realistic planning interval), and in the long term of, say 500-1,000 years (a period that could reflect fitness and adaptability). Regarding condition, there's a fair bit known about the current situation. The recovery plan provides a lot of information about anticipated condition, in terms of habitat management and the like. We could also use the recovery plan's population goal of 1,000 pairs in the equation. Conversely, we could base our analysis on the current population size of about 210 pairs. Thus, there are possible values available for all the variables. Alternatively, a PVA could be used to test the effects of other values for any of the variables. For example, we could construct the formula to ask how much a larger population goal would improve viability, or how additional habitat would affect it, or what the viability looks like for year 1000.

I have not done any of these. But I would like to look briefly at the possible effects of each class of factors on the viability of the Kirtland's warbler in the short term. As I've explained, genetic uncertainty is directly tied to effective population size. In the genetic context, given the species' breeding distribution (Figure 4), the entire species would seem to be a single population. This is true because the results of large juvenile dispersal distances can be assumed to result in a population that mixes at a rate that produces essentially one large gene pool. Consequently, we would want to calculate the effective population size of the entire population.

Several characteristics of this species will produce an effective population size less than the census population size, most importantly, polygamy and unmated males. It seems that there is not sufficient information on sex ratios, reproductive success, or other factors to calculate an accurate effective population size as was done for the spotted owl, but it would not be unrealistic to assume that the effective population size in somewhere around half the census population size. This seems to be true for many bird species (Barrowclough 1980). If this were true, then it would give us an effective population size of 210. According to theory, this population size would retain 98% of its genetic variation after ten years, 79% after one hundred years, 56% after two hundred fifty years, and 30% after five hundred years. Thus, if maintained at this population level for 250 years, the loss of less than half its genetic variation would not be catastrophic. Once the population reached the goal of 1,000 pairs, it would retain 78% of its

genetic variation after 500 years, and 61% after 1000 years, both easily acceptable rates of loss.

Figure 4.



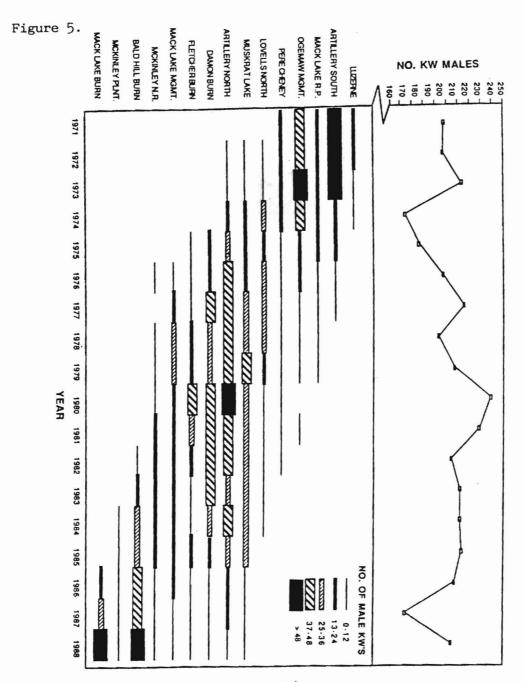
U.S. Forest Service Essential Habitat

State Forest Essential Habitat

Military Area Habitat

KIRTLAND'S WARBLER HABITAT IN MICHIGAN

Regarding demographic uncertainty, we could similarly consider the entire species to be one population. If we assume that what we call colonies are established through juvenile dispersal, then any demographic events that result in the extinction of one colony would have little effect on the rest of the population. Although individual colonies may blink in and out of the picture over time (Figure 5), as long as there are sources of dispersers, suitable vacant habitat should be reoccupied as it becomes available. With regard to both genetic and demographic uncertainty, it is also possible that the species has existed at relatively low population levels for so long that it is somewhat adapted to cope with these factors.



Environmental uncertainty and natural catastrophe are less easy to dismiss. Since habitat quality and quantity varies among management areas, each colony must be considered a separate sub-population, each subject to the effects of these factors. So the question must be, how does environmental uncertainty and natural catastrophe affect the viability of each colony. The recovery team was clearly aware of environmental uncertainty in focusing their efforts on the habitat acquisition and improvement, cowbird control, and other activities. a result, environmental uncertainty is being kept under control by the recovery plan. But, it is critical to the viability of this species that the recovery plan be faithfully carried out into the future. There is plenty of evidence that reduced habitat quality or cowbird predation at a number of colonies could easily knock the population down to a level at which it would become vulnerable to a serious species-wide population decline. Predation, increased habitat fragmentation, an overabundance of marginal habitat, or a synchronous decline in habitat quality are other examples of sources of environmental uncertainty that could have a serious impact on the species. It will remain important to continue to monitor all sources of environmental uncertainty and respond to them with management as necessary.

However, my biggest concern about the population viability of the Kirtland's warbler regards natural catastrophe. While environmental uncertainty can be more or less anticipated and combated through management, natural catastrophe occurs when and where you least expect The only way to counteract the effects of natural catastrophe on population viability is to make sure that the population is so widely distributed that the entire population is never going to be hit by the same catastrophe. Given the current distribution of the Kirtland's warbler, a natural catastrophe could have a devastating effect on the species. At present, there are two main colonies, at McKinley Plantation and Mack Lake Burn (Figure 5). If a fire were to burn through one of these during breeding season, viability of the species could be seriously threatened. Again, the solution to reducing the risk of natural catastrophe is to increase the distribution of the species. This could be done by taking advantage of surplus reproduction and relocating juveniles to unoccupied suitable habitat, especially if they would otherwise be dispersing into marginal habitat. Additional habitat could be acquired and restored to fill in some of the gaps that currently exist between management areas, thereby improving dispersal among sites. Since, in the context of natural catastrophes, disjunct sites would be most effective in providing refuge, this would best be done beyond the current range of the species. Finally, to counter the threat of natural catastrophe like drought and hurricane on the wintering ground, it appears critical that work be continued on the development and implementation of captive breeding techniques. I know that most of these suggestions would be very expensive, and none would insure success, but I believe that it is critical to the viability of this species that steps in this direction be continued.

I'd like to leave you with a note of idealism. Notice that I have not referred to $\underline{\text{Minimum}}$ Viable Populations, which is a term you may have heard. As you can now see, a general rule is that the larger and more widely distributed the population, the greater is its viability. We

used to talk about minimum viable populations, probably in part because the acronym MVP is so catchy. However, the word minimum has been dropped more recently, and not for simple semantic reasons. As Soule (1987) has pointed out, in the same way that physicians prescribe the optimal conditions for health, not the minimal ones, the resource manager should plan for a robust and bountiful population, not a minimum. The point is that population viability analysis does not provide a magic number above which a population is safe from extinction. I would encourage you to manage for robust and bountiful population of the Kirtland's warbler.

Acknowledgment

I would like to thank John Probst for his most helpful discussions, suggestions, and review of this paper, and for the use of Figure 5.

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KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 5
KIRTLAND'S WARBLER BIBLIOGRAPHY

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KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 6
SMALL POPULATION BIOLOGY

Small Population Biology & Population and Habitat Viability Assessment

Robert Lacy, Tom Foose, Jon Ballou and Jan Eldridge

January 1992

Many wildlife populations that were once large and continuous have been reduced to small, fragmented isolates in remaining natural areas. The final extinction of these populations usually is a matter of chance, resulting from one or a few years of bad luck--even if the causes of the original decline were quite preventable, such as over-hunting and habitat destruction. Few endangered species have recovered adequately and some have gone extinct in spite of protection. This reveals the acute risks faced by small populations and the need for a more intensive, systematic approach to recovery. The purpose of Population and Habitat Viability Analyses (PHVA's) is to help managers understand the risks facing small populations, to identify the relative importance of the factors that put a small population at risk, and to evaluate the effectiveness of various management strategies.

When populations get very small, evolutionary and ecological processes change. All of the things we know about general population management no longer apply. The classic approach to understanding a large population is a life table analysis. The problem with using life tables for small populations is that even if the population is growing (in good shape according to the life table analysis), it will fluctuate wildly, so it could still go extinct at any time. The stochasticity in small populations is categorized according to four causes: demographic fluctuation, environmental variation, catastrophic events, and genetic drift.

- 1. Demographic Fluctuation luck of the draw. Flux in all populations occurs even if the environment is constant, and all animals have the same chance. This means that the probability of being male and female, alive or dead, is a coin toss. In a large population this kind of variation all evens out in the end and doesn't really matter, but in small populations it could be important. It is possible, by bad luck, to have every animal happen to die one year. A classic example of this kind of bad luck is the dusky seaside sparrow where all six of the last birds were male.
- 2. Environmental Variation flux in demographic probabilities. This is the externally imposed variation in the probability of birth and death. In one year, mortality may be 10%, the next year because of drought, 90%. The same environmentally induced variance may occur in reproductive rates, mortality rates, or carrying capacity.

- 3. Catastrophic Events the extreme of environmental variation. We consider it separately for a couple of reasons. If you look at the typical distribution of environmental flux, catastrophes are outliers. You wouldn't predict hurricanes by studying average wind patterns. It is usually so far out, it doesn't fit the normal day to day, year to year variation. The impact on the population may be very sever. The population could be adapted to year to year "normal" variation but not to catastrophe. Often catastrophes will wipe out the species. A species may hang on and then get hit by a catastrophe. We think of them as aberrant events but over a long time period, they are predictable, hurricanes hit at one out of every 30 years, forest fires hit with some probability. Catastrophes include storms, fires, disease, and The Unexpected.
- 4. Genetic Drift & Inbreeding. Small populations fluctuate genetically just as they do in numbers. It is a sampling problem. In a large population each generation is a good sample of the one that existed before. In a small population each generation is a poor example of the others. Genes that are in flux could hit 0 and so alleles are lost, over time there is a significant loss of genetic diversity. So, the longer the population is small, the greater the loss. Inbreeding also increases as populations become smaller. Loss of genetic diversity has been associated with an increase in vulnerability and susceptibility to environmental problems, reproductive difficulties, and disease -- it affects each species differently. Genetic drift can decrease and worsen the demographic situation. In general, in mammals 1% loss of genetic diversity means 1% loss in reproductive fitness. Loss of genetic diversity will also limit the ability of populations to adapt as environments change.

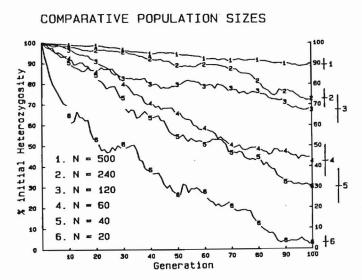


Figure 1. The average losses of genetic variation (measured by heterozygosity or additive genetic variation) due to genetic drift in 25 computer-simulated populations of 20, 50, 100, 250, and 500 randomly breeding individuals. Figure from Lacy 1987a.

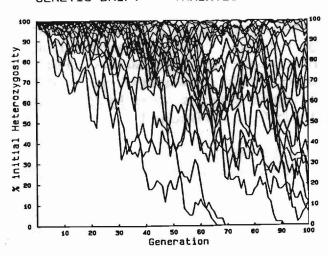


Figure 2. The losses of heterozygosity at a genetic locus in 25 populations of 120 randomly breeding individuals, simulated by computer. Figure from Lacy 1987a.

All of these characteristics feed back on each other in a nasty way...in what is called an extinction vortex. External force (hunting, habitat loss), cause the original decline but when a population becomes very small, you set into motion a series of problems that can spiral down into an extinction vortex. The fluctuation of population size makes inbreeding worse than if size were constant, the demographic fluctuations can negatively impact the population and cause further stochasticity, etc. The spiral is fast unless management is very aggressive. Part of the management problem is to keep populations out of the vortex. The size below which a population is likely to get sucked into the extinction vortex has been called the Minimum Viable Population size (or MVP).

Recently, techniques have been developed to permit the systematic examination of many of the processes that put small populations at risk. By a combination of modeling techniques, the probability of a population persisting a specified time into the future can be estimated. The population models used in PHVA's allow you to do "what-if" scenarios by looking at the data, and management schemes, to try to mitigate the probability of loss.

There are several approaches to modeling the variability of population extinction. One approach is to develop a mathematical formula, based on various population parameters; two examples of this approach are Goodman (1987), and Dennis et. al, (in prep.). There are advantages to a mathematical formula--- it looks precise because you get a number at the end. The disadvantage is that the number may not mean much. Usually the models have a very limited number of factors (exponential growth rate, variance, maximum population size). They suffer from being too simple; they do not include important factors; for example, Dennis et. al. assumes no carrying capacity, exponential growth, no genetic events, and no catastrophes. All models make assumptions, it is important to think about those assumptions.

The approach used in a stochastic models such as VORTEX is to try to understand the extinction vortex. It doesn't depend on a complicated mathematical formula; instead, the program makes the computer think it is the population. Computers are very good at flipping coins, determining the probability is "x" of something happening. The model combines information on life history, distribution, genetics, estimates of disease and catastrophic events (natural and man induced) in a computer simulation that allows rapid evaluation of critical factors for small population recovery. VORTEX was developed by Robert Lacy of the Chicago Zoological Park, based on original programs written by James Grier of North Dakota State University (Grier 1980a, 1980b, Grier and Barclay 1988).

The driving questions behind the model are: How small is critical, how big is enough? These are important questions and the strategy for using the model requires that managers set some goals. For example:

Goal 1. The probability of survival desired for the population (e.g., managers may want 95% probability of survival, or they may settle for a 50% chance)

Goal 2. The percentage of the genetic diversity to be preserved (managers can predetermine what level of diversity they are willing to tolerate, for example, 90%, means that they will only tolerate a loss in heterozygosity of 10%).

Goal 3. The period of time over which demographic security and genetic diversity are to be sustained (e.g., 50 years, 200 years).

An example of a management strategy for an endangered species could start with the question; What is the minimum population size necessary to ensure a 95% probability of survival for 200 years with 95% of the average genetic heterozygosity retained?

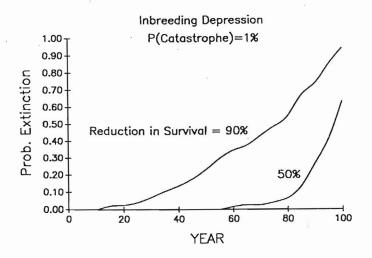


Figure 3. Hypothetical example of population extinction results from the VORTEX PVA model. The model includes negative effects of inbreeding and a catastrophe probability of 1%. The probability of extinction is shown over time for two different levels of catastrophe severity: a 90% reduction in survival vs 50% reduction in survival.

The advantage of simulation models like Vortex is that they can get bigger and bigger by adding things on. The model asks the user to input a lot of population parameters. The model is dependent on knowledge, you need to know sex ratios, birth and death rates, etc.; without this information, you can't do anything. You must recognize where data are weak so you can test the sensitivity of the model. This indicates where you need more data.

The primary use of the model in developing conservation strategies is in conducting "what if" analyses. For example, what if survival were decreased in the wild population as a result of a disease outbreak? How would that effect the extinction of the population and retention of genetic diversity. These "what if " analyses can also be used to evaluate management recommendations. For example, how would probability of population extinction change if the carrying capacity of the reserve holding the animals were increased by 10%.

The key to success of the PHVA approach is that it is accessible. The PHVA workshops conducted by CBSG bring management and expertise together to form a consensus on the priorities for species recovery. It is done in a way that makes information and assumptions explicit. The technique does not rely on "intuition" and it is valuable because everyone has access to the information that is used for management recommendations.

DEFINITIONS

<u>Population and Habitat Viability Analysis</u>. A systematic evaluation of the relative importance of factors that place populations at risk. It is an attempt to identify the most important factors for the survival of the population. In some cases, this may be easy - habitat destruction is often a critical factor for most endangered species. But at other times, the effects of single factors, and the interaction between factors, are more difficult to predict. To try to gain a more quantitative understanding of the effects of these factors, computer models have been developed that apply a combination of analytical and simulation techniques to model the populations over time and estimate the likelihood of a population going extinct.

POPULATION VIABILITY ANALYSIS (PVA) Process of Evaluating the Interacting Factors Affecting Risks of Extinction Life History Environmental Variation Catastrophes Demographic Variation Inbreeding Depression

Figure 4. Population Viability Analyses (PVA) model the effects of different lifehistory, environmental and threat factors on the extinction and retention of genetic diversity in single populations.

Demographic Fluctuation - luck of the draw. Flux in all populations occurs even if the environment is constant, and all animals have the same chance. This means that the probability of being male and female, alive or dead, is a coin toss. In a large population this kind of variation all evens out in the end and doesn't really matter, but in small populations it could be important. It is possible, by bad luck, to have every animal happen to die one year. A classic example of this kind of bad luck is the dusky seaside sparrow where all six of the last birds were male.

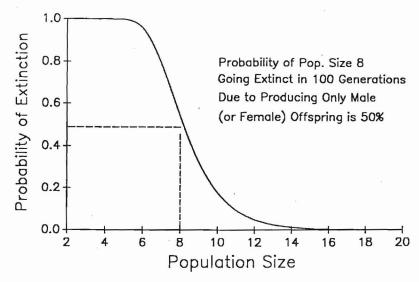


Figure 5. Example of demographic variation: Probability of extinction by 100 generations due solely to producing only one sex of offspring during a generation.

<u>Environmental Variation - flux in demographic probabilities</u>. This is the externally imposed variation in the probability of birth and death. In one year, mortality may be 10%, the next year because of drought, 90%. The same environmentally induced variance may occur in reproductive rates, mortality rates, or carrying capacity.

Catastrophic Events - the extreme of environmental variation. We consider it separately for a couple of reasons. If you look at the typical distribution of environmental flux, catastrophes are outliers. You wouldn't predict hurricanes by studying average wind patterns. It is usually so far out, it doesn't fit the normal day to day, year to year variation. The impact on the population may be very sever. The population could be adapted to year to year "normal" variation but not to catastrophe. Often catastrophes will wipe out the species. A species may hang on and then get hit by a catastrophe. We think of them as aberrant events but over a long time period, they are predictable, hurricanes hit at one out of every 30 years, forest fires hit with some probability. Catastrophes include storms, fires, disease, and The Unexpected.

Genetic Diversity. Expected heterozygosity (proportion of individuals in the population that carry functionally different alleles at a locus) in progeny produced by random matings.

Genetic Drift. Small populations fluctuate genetically just as they do in numbers. It is a sampling problem. In a large population each generation is a good sample of the one that existed before. In a small population each generation is a poor example of the others. Genes that are in flux could hit 0 and so alleles are lost, over time there is a significant loss of genetic diversity. So, the longer the population is small, the greater the loss. Loss of genetic diversity has been associated with an increase in vulnerability and susceptibility to environmental problems, reproductive problems, and disease -- it affects each species differently. Genetic drift can decrease and worsen the demographic situation. In general, in mammals 1% loss of genetic diversity means 1% loss in reproductive fitness. (Refer to figures 1-2).

Inbreeding and Inbreeding Depression- mating between relatives. When numbers of breeding animals become very low, inbreeding becomes inevitable and common. Inbred animals often have a higher rate of birth defects, slower growth, higher mortality, and lower fecundity (inbreeding depression). Inbreeding depression results from two effects: 1) the increase in homozygosity allows deleterious recessive alleles in the genome to be expressed (whereas they are not in non-inbred, more heterozygous individuals); and 2) in cases where heterozygotes are more fit than homozygotes simply because they have two alleles, the reduced heterozygosity caused by inbreeding reduces the fitness of the inbred individuals. In both cases, the loss of genetic variation due to inbreeding has detrimental effects on population survival.

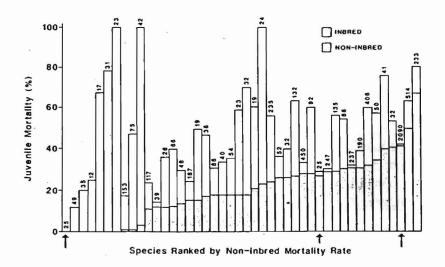


Figure 6. Effects of inbreeding on juvenile mortality in 45 captive rnammal populations (From Ralls and Ballou, 1987).3

Extinction Vortex. The genetic and demographic process that come into play when a population becomes small and isolated feed back on each other to create what has been aptly but depressingly described as an extinction vortex. The genetic problems of inbreeding depression and lack of adaptability can cause a small population to become even smaller -- which in turn worsens the uncertainty of finding a mate and reproducing -- leading to further decline in numbers and thus more inbreeding and loss of genetic diversity. The population spirals down toward extinction at an ever accelerated pace.

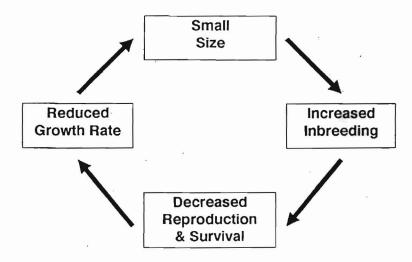


Figure 7. "Extinction Vortex" caused by negative feedback effects of inbreeding in small populations.

Minimum Viable Population Size. Populations large enough to permit long-term persistence despite the genetic, demographic, and environmental problems. Below this size, a population is likely to get sucked into the extinction vortex. There is no single magic number that constitutes an MVP for all species, or for any one species all the time. MVP depends on both the genetic and demographic objectives of a program and the biological characteristics of the population. An analysis can suggest ranges of population sizes that will provide calculated protection against stochastic problems.

The following are important biological factors for Minimum Viable Population Size:

Effective Population Size (N_c). The effective population size is a measure of the way animals reproduce and transmit genes to the next generation. It is important when you need to calculate the rate of genetic loss from generation to generation. Populations where all males and females reproduce are "effectively" larger and lose genetic diversity at a slower rate than a population where only some reproduce even though the census size of both populations is the same. An unequal sex ratio of breeding animals, greater than random variance in lifetime reproduction, and fluctuating population sizes all cause more rapid loss of variation than would occur in a randomly breeding population, and thus depress the effective population size. There is extensive literature on how to estimate a population's effective size; however, the number of animals contributing to the breeding pool each generation can be used as a very rough estimate of the effective size. The effective size of the population is usually much less than the actual number of animals; estimates suggest that Ne is often only 10 to 30% of the total population. Seemingly large populations will lose significant levels of genetic diversity if their effective sizes are small. As a consequence, if the genetic models prescribe an Ne of 500 to achieve some set of genetic objectives, the MVP might have to be 2000.

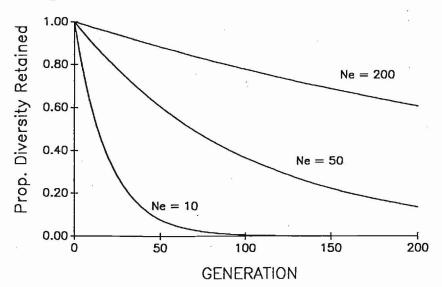


Figure 8. Loss of genetic diversity over 200 generation in populations with different effective sizes (N_e).

Generation Time. Genetic diversity is lost generation by generation, not year by year. Hence, species with longer generation times will have fewer opportunities to lose genetic diversity within the given period of time selected for the program. As a consequence, to achieve the same genetic objectives, MVP's can be smaller for species with longer generation times. Generation time is qualitatively the average age-specific survivorships and fertilities of the population which will vary naturally and which can be modified by management, e.g., to extend generation time.

<u>The Number of Founders</u> - A founder is defined as an animal from a source population that establishes a derivative population. To be effective, a founder must reproduce and be represented by descendants in the existing population. Technically, to constitute a full founder, an animal should also be unrelated to any other representative of the source population and non-inbred.

Basically, the more founders, the better, i.e., the more representative the sample of the source gene pool and the smaller the MVP required for genetic objectives. There is also a demographic founder effect; the larger the number of founders, the less likely is extinction due to demographic stochasticity. However, for larger vertebrates, there is a point of diminishing returns, at least in genetic terms. Hence, a common objective is to obtain 20-30 effective founders to establish a population. If this objective can not be achieved, then a program must do the best with what is available.

PRESERVATION OF 90% OF ORIGINAL GENETIC DIVERSITY FOR 200 YEARS

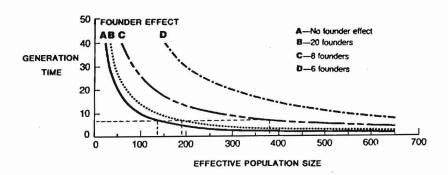


Figure 9. Interaction of number of founders, generation time of the species, and effective population size required for preserving 90% of the starting genetic diversity for 200 years.

Growth rate. The higher the growth rate, the faster a population can recover from small size, thereby outgrowing much of the demographic risk and limiting the amount of genetic diversity lost during the so-called "bottleneck". It is important to distinguish MVP's from bottleneck sizes.

Metapopulations and Minimum Areas

MVP's imply minimum critical areas of natural habitat, that may be difficult or impossible to maintain single, contiguous populations of the thousands required for viability.

However, it is possible for smaller populations and sanctuaries to be viable if they are managed as a single larger population (a metapopulation) whose collective size is equivalent to the MVP. Actually, distributing animals over multiple "subpopulations" will increase the effective size of the total number maintained in terms of the capacity to tolerate the stochastic problems. Any one subpopulation may become extinct or nearly so due to these causes; but through recolonization or reinforcement from other subpopulations, the metapopulation will survive. Metapopulations are evidently frequent in nature with much local extinction and recolonization of constituent subpopulations occurring.

Environmental Variation Catastrophes Demographic Variation POP Habitat Quality POP Human Impact Inbreeding Depression

Figure 10. The interaction between population 'patches' results in a Metapopulation structure. Conservation strategies must consider the spatial distribution of the patches and its effect on correlated extinctions and recolonization between patches.

METAPOPULATION

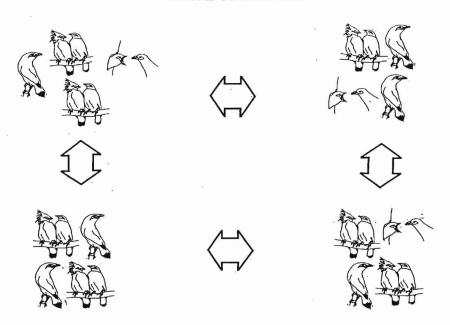


Figure 11. Multiple subpopulations as a basis for management of a metapopulation for survival of a species in the wild.

MANAGED MIGRATION AMONG POPULATIONS OF BALI MYNAH

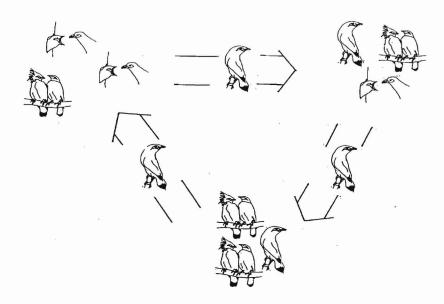


Figure 12. Managed migration among subpopulations to sustain gene flow in a metapopulation.

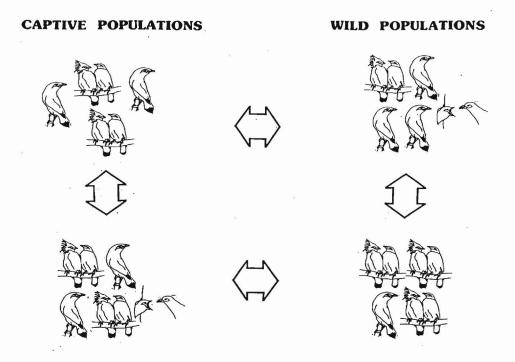


Figure 13. The use of captive populations as part of a metapopulation to expand and protect the gene pool of a species.

COMPARATIVE IMMIGRATION

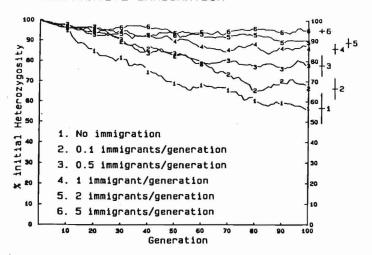


Figure 14. The effect of immigration from a large source population into a population of 120 breeding individuals. Each line represents the mean heterozygosity of 25 computer-simulated populations (or, equivalently, the mean heterozygosity across 25 non-linked genetic loci in a single population). Standard error bars for the final levels of heterozygosity are given at the right. Figure from Lacy 1987a.

A. ABSOLUTE SUBDIVISION

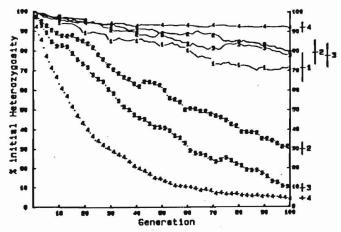


Figure 15. The effect of division of a population of 120 breeders into 1, 3, 5, or 10 isolated subpopulations. Dotted lines (numbers) indicate the mean within-subpopulation heterozygosities from 25 computer simulations. Lines represent the total gene diversity within the simulated metapopulation. Figure from Lacy 1987a.

MIGRATION AMONG 5 SUBPOPULATIONS

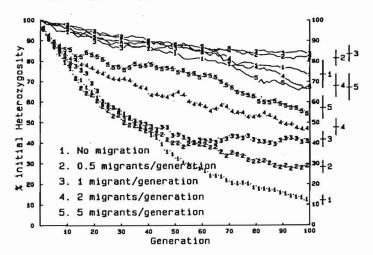


Figure 16. The effect of migration among 5 subpopulations of a population of 120 breeders. Dotted lines (numbers) indicate the mean within-subpopulation heterozygosities from 25 simulations. Lines represent the total gene diversity within the metapopulation. Figure from Lacy 1987a.

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KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 7 PVA GENERAL

The Population Viability Assessment Workshop: A Tool For Threatened Species Management

Tim W. Clark, Gary N. Backhouse, and Robert C. Lacy

Introduction

Population viability assessment (PVA) is a procedure that allows managers to simulate, using computer models, extinction processes that act on small populations and therefore assess their long-term viability. In both real and simulated populations, a number of interacting demographic, genetic, environmental, and catastrophic processes determine the vulnerability of a population to extinction. These four types of

extinction processes can be simulated in computer models and the effects of both deterministic and stochastic forces can be explored. In turn, the outcome of various management options, such as reducing mortality, supplementing the population, and increasing carrying capacity can also be simulated. Thus, PVA provides managers with a powerful tool to aid in assessing the viability of small populations and in setting target numbers for species recovery as a basis for planning and carrying out recovery programs. In addition, having performance-based management programs enables progress to be quantified and assessed. PVA also offers managers a powerful strategic planning and policy tool when vying for limited financial resources. This

paper describes a PVA workshop that used a stochastic computer simulation to model small populations of, and explore management options for, six threatened/endangered wildlife species in Victoria, Australia.

The Workshop

The workshop was co-sponsored by the Department of Conservation and Environment (DCE), Victoria, and the Zoological Board of Victoria (ZBV), in cooperation with the Chicago Zoological Society (CZS) and was held at the Arthur Rylah Institute for Environmental Research (DCE), Heidelberg, Victoria, from May 28 through June 1, 1990.

The objectives of the workshop were to: 1) examine the adequacy of data on the six threatened species; 2) simulate the vulnerability to extinction by using PVA; 3) examine outcomes of various management options to restore the species; 4) estimate population tar-



Mountain pygmy-possum

Photo by Ian McPherson

gets needed for recovery planning; 5) evaluate the potential of PVA as a teaching aid to illustrate extinction processes and management options.

The six species were: mountain pygmy-possum, Burramys parvus; leadbeater's possum, Gymnobelideus leadbeateri; eastern barred bandicoot, Perameles gunnii; long-footed potoroo, Potorous longipes; orange-bellied parrot, Neophema chrysogaster, and helmeted honeyeater, Lichenostomus melanops cassidix.

The 32 people attending the workshop represented experienced field biologists and wildlife managers with detailed knowledge of these and other threatened species. A month prior to the workshop all participants were provided with background reading material (e.g. Shaffer 1981, Brussard 1985, Samson 1985, Gilpin 1989, and Lacy and Clark 1990). A questionnaire on life-history parameters to be completed on each species as a basis for entering values into the computer was also pro-

vided. Following an introduction and overview of PVA, the participants formed teams and commenced work. Simulations, analyses, and discussions were ongoing over the next five days. The first week concluded with a report and review of each team's progress. During the following week, teams further refined their simulations and commenced preparation of a final report with management recommendations.

Population Viability Analysis: The Vortex Model

The workshop used a computer program, VORTEX, to simulate demographic and genetic events in the history of a small population (<500 individuals). VORTEX was written in the C programming language by

Robert Lacy for use on MS-DOS microcomputers. Many of the algorithms in VORTEX were taken from a simulation program, SPGPC, written in BASIC by James Grier (Grier 1980a, 1980b, Grier and Barclay 1988). See Lacy et al. 1989, Seal and Lacy 1989 and Lacy and Clark 1990 for earlier uses of VOR-TEX.

Life table analyses yield average long-term projections of population growth (or decline), but do not reveal the fluctuations in population size that

would result from variability in demographic processes. When a population is small and isolated from other populations of conspecifics, these random fluctuations can lead to extinction, even in populations that have positive population growth on average. Fluctuations in population size can result from several levels of stochastic effects. Demographic variation results from the probabilistic nature of birth and death processes. Therefore, even if the probability of an animal reproducing or dying is always constant, the actual number reproducing or dying within any time interval would vary according to the binomial distribution with mean equal to the probability of the event (p), and variance given by Vp = p*(1-p)/N. Demographic variation is thus intrinsic to the population and occurs in the simulation because birth and death events are determined by a random process (with appropriate probabilities). Environmental variation (EV) is the variation in the probabilities of reproduction and mortality that occur because of changes in the environment on an annual basis (or other timescales).

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, whether each adult female produces broods of size 0, 1, 2, 3, 4, or 5 during each year, and which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Mortality and reproduction probabilities are sex-specific. Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. Fecundity is assumed to be independent of age after an animal reaches reproductive age. The mating system can be specified to be either monogamous or polygynous. In either case, the user can specify that only a subset of the adult male population is in the breeding pool (the remainder being excluded perhaps by social factors). Those males in the breeding pool all have equal probability of siring offspring.

Each simulation is started with a specified number of males and females in each pre-reproductive age class and the breeding age class. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus. The user specifies the severity of inbreeding depression which is expressed in the model as a loss of viability in inbred animals. The computer program simulates and tracks the fate of each population and then produces summary statistics on: the probability of population extinction over specified time intervals; the mean time to extinction of those simulated populations that went extinct; the mean size of populations not yet extinct; and the levels of genetic variation remaining in any extant populations.

A population carrying capacity specified by the user is imposed by a probabilistic truncation of each age class if, after breeding, the population size exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity, as linear increases or decreases across a specified number of years.

VORTEX models environmental variation simplistically (which is both an advantage and disadvantage of simulation modelling), by selecting at the beginning of each year the population age-specific birth rates, age-specific death rates, and carrying capacity from distributions with means equal to the overall averages specified by the user, and with variances also specified by the user. Unfortunately, rarely do we have sufficient field data to estimate the fluctuations in birth and death rates, and in carrying capacity, for a wild population. The population would have to be monitored long enough to separate sampling error statistically from demographic variation in the number of births and deaths, from annual variation in the probabilities of these events. Such variation can be very important in determining the probability of extinction, yet we rarely have reasonable estimates for most populations of conservation concern. If data on annual variation are lacking, a user can try various values, or model the fate of the population in the absence of any environmental variation.

Endangered Species UPDATE

A forum for information exchange on endangered species issues December 1990 Vol. 8 No. 2

Alice Clarke and Joel Heinen...Editors
Dr. Terry Root.......Faculty Advisor
Jon Jensen......Staff Advisor

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Readers include a broad range of professionals in both scientific and policy fields. Articles should be written in an easily understandable style for a knowledgeable audience. Manuscripts should be 10-12 double spaced typed pages. For further information, contact the editors at the number listed below.

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Leadbeater's possum (Gymnobelideus leadbeateri) Photo by Jim Cooper

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VORTEX can model catastrophes as events that occur with some specified probability and which reduce survival and reproduction for one year. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (i.e. a binomial process is simulated). If a catastrophe occurs, the probability of breeding is multiplied by a severity factor that is drawn from a binomial distribution with a mean equal to the severity specified by the user. Similarly, the probability of survival for each age class is estimated in a similar manner.

VORTEX also allows the user to supplement or harvest the population for any number of years in each simulation. The numbers of immigrants and removals are specified by age and sex. VORTEX outputs the observed rate of population growth (mean of N[t]/N[t-1]) separately for the years of supplementation/harvest and for the years without such management, and allows for reporting of extinction probabilities and population sizes at whatever time interval is desired (e.g. summary statistics can be given at 5-year intervals in a 100-year simulation).

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Because it is a detailed model of population dynamics, often it is not practical to examine all possible factors and all interactions that may affect a population. The user, therefore, must specify those parameters that can be estimated reasonably, leave out of the model those that are thought not to have a substantial impact on the population of interest, and explore a range of possible values for parameters that are potentially important but very imprecisely known. A companion program, VORPLOTS, was used at the workshop to produce plots of mean population size, time to extinction, and loss of gene diversity from simulation results.

Equipment Required

VORTEX requires an MS-DOS microcomputer with at least 640K of memory. A math co-processor speeds up the program substantially. The

VORPLOTS plotting program produces files in the Hewlett Packard Graphics Language (HPGL), for use on an HP plotter or equivalent.

A Kodak Dataview EGA enabled projection of a computer display via an overhead projector onto a large screen so that all participants could observe demonstrations of VORTEX during initial training.

Computers were used during the daily sessions primarily for exploratory analyses with relatively few runs (100 or fewer) of a simulation; more extensive analyses were run overnight. A test with 100 runs would take from 15 minutes to 3 hours, depending on the machine used and the size of the population being simulated.

The Workshop Results

Each team documented its activities and provided a preliminary report of the simulations completed, conclusions, an assessment of the conduct of the workshop, and the usefulness of the PVA process. Results will be published in peer-reviewed scientific journals by each team.

All cases showed similar results. First, most species and populations were highly susceptible to local extinction. Any further habitat loss or fragmentation or reduction in population size and density would result in rapid extinction. Second, in all cases, more field data would have been help-Third, management options to stave off extinction were identified and results simulated. Options included strict habitat protection, enhancement of existing habitat or restoration of lost habitat, captive breeding, and reintroduction of animals to existing habitat patches in which the species has become extinct in recent decades or to newly created habitat. Various combinations of management strategies were recommended for future management. Fourth, the simulations demonstrated that if proactive conservation management had been undertaken even 5 to 10 years ago when populations and habitats were considerably larger, the task of present day managers would be much more tractable. And fifth, improved conservation management for all six

species is expected to result from the PVA exercise, enhanced research, and subsequent on-the-ground management. Three cases illustrate these conclusions: the mountain pygmy-possum (Mansergh et al. in prep.), eastern barred bandicoot (Myroniuk and Patrick in prep.), and orange-bellied parrot (Brown et al. in prep.).

Mountain Pygmy-Possum: The mountain pygmy-possum is a small marsupial restricted to alpine and subalpine (>1500m altitude) rock screes and boulderfields with heathlands. The species has been well studied and much information is available on its ecology (Mansergh 1989). Diet consists of invertebrates, seeds, and fruits. Breeding occurs from September to December, with litter size of 3 to 4. The young become independent by mid-January. Females can breed in their first year, and can live up to 9 years. An unusual feature of the life history of Burramys is the fact that sexes are segregated during the non-breeding season. The adult population is heavily biased towards females (6F:1M) because of the very high mortality experienced by males post-dispersal.

The current total population is estimated to be 2,300 breeding adults of which 80% are females. The species is regarded as vulnerable in Victoria and rare in New South Wales. The species is also susceptible to climatic changes associated with global warming.

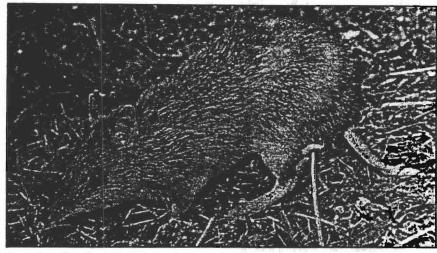
The mountain pygmy-possum exists as a number of discrete populations isolated from each other on mountain tops. A total of seven populations, ranging from 20-850 individuals (representing the situation in the wild) was modelled. High probabilities of extinction were observed in all small (<150 animals) populations at 25 and 50 years; this could account for the absence of the species from apparently suitable habitat within its range. The larger populations had a decreased likelihood of extinction. When modelled with a small but steady decrease in carrying capacity (1% per annum) such as could occur through climatic change with global warming, the probability of extinction increased greatly (to 45% in the case of the largest Victorian population of 850 individuals, over 50 years).

Disturbance to habitat and further fragmentation of populations would increase the likelihood of extinction.

Eastern Barred Bandicoot: The mainland population of this marsupial species was formerly distributed over about 23,000 sq km of volcanic grassland in western Victoria. This population has now declined to 200 or fewer individuals restricted to remnant habitat near Hamilton (Clark and Seebeck 1990). The species is polygynous, with females capable of breeding from 3 months of age and males from 4 months of age. Gestation lasts about 12 days, with litters comprised of 1 to 5 offspring (usually 2-3); young remain in the pouch about 55 days. Females are capable of producing several broods per year. In spite of the very high reproductive potential, the population is believed to be declining at about 25% per annum. Juvenile mortality at dispersal from the nest is very high (> 90% within the first year). The decline of the species is attributed to habitat modification from pastoral activities and predation from introduced predators, including the red fox (Vulpes vulpes) and the cat (Felis catus).

Wild and captive populations of the eastern barred bandicoot were simulated. Modeling the wild population using available data without any change to current management indicated a 100% probability of extinction within 25 years, with a mean time to extinction of 7.2 years (± 2.1). Doubling the carrying capacity and leaving mortality unchanged had negligible impact on the probability of extinction and increased the mean time to extinction by only 2 years. Doubling the carrying capacity. reducing mortality by 30% and supplementing the wild population with the liberation of captive-bred animals greatly enhanced prospects for survival of the wild population. Under this scenario the probability of extinction was reduced to 0% over 25 years with a mean final population size of close to the carrying capacity of 300 animals. Modeling the existing and proposed captive populations allowed investigation of a variety of scenarios. The existing captive population of 16 pairs has an extinction probability of 83% over 25 years, with a mean time to extinction of 21.5 years. Doubling the number of adult pairs decreased the extinction probability to 0% but the surviving population had very low genetic variability, and there is little potential to harvest juveniles for release into the

150-200 individuals. The orange-bellied parrot breeds in coastal southwest Tasmania in woodlands adjoining extensive sedgelands. After breeding, it migrates across Bass Strait to overwinter in coastal regions of southern main-



Eastern barred bandicoot

Photo by J. Seebeck

wild. Increasing the captive population to 62 adult pairs increased genetic variability and the potential to harvest juveniles without jeopardizing the captive population. Maintaining a captive population of 62 adult pairs (in two groups at separate locations to avoid catastrophe but managed as one population) and establishing two semi-captive populations with a capacity for 400 animals gave the best prospects for long term survival, maintenance of genetic variability, and production of sufficient offspring to consider reintroductions to suitable habitat within their former range. The exercise highlighted the need for a combination of management actions, rather than any single action, to prevent the almost certain extinction of the wild population under the existing management regime. Reduction of mortality by predator control and traffic management is essential for the survival of the eastern barred bandicoot. Captive management will be an important part of the recovery program, but with a more intensive program than that currently underway.

Orange-bellied Parrot: The biology and ecology of the orange-bellied parrot is comparatively well known (Loyn et al. 1986). The species is one of the rarest and most threatened birds in Australia, with a total population of

land Australia. The birds feed in a variety of coastal habitats including grassland, saltmarsh, and dune systems. showing strong preferences for particular habitats and food types in different parts of their winter range and at different times of the year. An estimated 40 breeding pairs annually produce a total of 50-70 juveniles. The orange-bellied parrot is considered endangered. Loss of coastal habitat for development and trapping for the aviculture trade are considered to be the primary causes of the species' past decline. Pressures for development on or adjacent to its main wintering areas and habitat alteration are now the main threats to its survival. A captive breeding program is now underway as part of a range of measures undertaken to ensure the future survival of the species.

Populations were modelled using the current carrying capacity (150), a reduced carrying capacity (50), and an increased carrying capacity (500). Simulations which involved varying mortality, capture, and supplementation rates of the wild population were run for all carrying capacities. Simulating the existing population using current data and management regimes indicated that the species would remain extant over the next 50 years at least, and stood a good chance of surviving for 100 years.

Reducing the carrying capacity to 50 under current conditions somewhat surprisingly did not increase the probability of extinction over 50 years, although genetic variability was greatly diminished. As would be expected, increasing the carrying capacity to 500 birds further reduced the prospects of extinction and greatly increased the genetic variability of the population. When modelled with an increased juvenile mortality rate (75% cf 50%), the population with the reduced carrying capacity showed a 70% probability of extinction within 50 years, while the current and increased carrying capacity populations showed extinction probabilities of 20% within that time. Imposing a capture and release captive breeding program on the populations only slightly decreased the extinction probability of the reduced carrying capacity, high mortality population, but greatly improved heterozygosity in the reduced carrying capacity, current mortality population. No extinctions occurred in the current and increased carrying capacity populations even at the high mortality levels, when simulated with supplementation from a captive breeding program. The simulations indicate several points. Juvenile mortality is of great significance to the health of the population. Any increase above the present rate of 50% greatly increases the probability of extinction, even with an enhanced habitat carrying capacity. The captive breeding program is an important back-up to the wild population, and will be extremely valuable if the wild population declines.

Evaluation of the Workshop

An evaluation was considered to be an important part of the workshop. All participants rated the background material supplied prior to the workshop as good to very good. Provision of background material was essential as very few participants had any prior experience with PVA. Organization was rated as very good to excellent by participants. The key to success was the large number of microcomputers available so that 2 to 3 people per computer was possible. Presentations were rated as very good to excellent.

The workshop format was considered to be a highly successful way of presenting PVA. PVA was considered to be a useful tool to aid threatened species management, providing its application and limitations were understood. PVA can focus attention on questions that should be addressed through additional research. PVA can be applied to well-studied taxa, and the general principles can be applied more widely to other taxa providing program characteristics are kept in perspective. All participants would recommend PVA as a management tool.

Conclusions

The PVA workshop proved a very useful way of quickly learning a new technique for threatened species management and conservation. PVA was applied to six species allowing a critical, quantitative analysis of extinction probabilities, as well as exploring management options to prevent species loss. PVA results will be used in forthcoming management plans and actions directed towards restoring these species to a status from which they will be relatively immune to extinction from random processes. In the future, it can be expected that PVA's will be carried out on additional endangered species to help manage their recovery.

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Author affiliations are as follows: T. Clark. Department of Conservation Biology, Chicago Zoological Society, Brookfield, IL, 60513, USA and School of Forestry and Environmental Studies, Yale University, New Haven, CN, 06511, USA; G. Backhouse. Wildlife Management Branch, Department of Conservation and Environment, PO Box 137, Heidelberg, Victoria, 3084, Australia.; R. Lacy. Department of Conservation Biology, Chicago Zoological Society, Brookfield, IL, 60513, USA.

POPULATION VIABILITY ANALYSIS AS A TOOL IN WILDLIFE MANAGEMENT: A REVIEW WITH REFERENCE TO AUSTRALIA.

DAVID B. LINDENMAYER

Department of Conservation and Environment Flora and Fauna Division, Wildlife Branch 123 Brown St., Heidelberg, VIC Australia 3084

TIM W. CLARK

Northern Rockies Conservation Cooperative
Box 2705, Jackson, WY 83001
and
School of Forestry and Environmental Studies
Yale University, New Haven, CT 06511

ROBERT C. LACY

Department of Conservation Biology Chicago Zoological Society, Brookfield, IL 60513

VIRGINIA C. THOMAS

Department of Conservation and Environment Flora and Fauna Division, Wildlife Branch 123 Brown St., Heidelberg, VIC Australia 3084

ABSTRACT/ Wildlife conservation policy for endangered species restoration follows a six phase process. Population viability analysis (PVA) can play a major contributing role in four of these. PVA is a technique in which extinction vulnerabilities of small populations are estimated using computer modeling to simulate an array of interacting factors. PVA benefits and limitations in wildlife decision and policy processes are reviewed. PVA permits decision makers to set time frames for management, estimate the required magnitude of restoration efforts, identify quantitative targets for species recovery and select, implement, monitor, and evaluate managment strategies. A limitation of PVA is that it can only simplistically model population dynamics, a problem which can be exacerbated by a paucity of biological data. This reduces accuracy of PVA and limits its applicability for rare species policy and management for which it is of greatest value. These problems may be overcome with more data and improved models. Benefits of PVA far outweigh its limitations and applications of the approach are most useful when integrated with decision analysis and completed within an adaptive management philosphy. We recommend that PVA be used to guide research programs, develop conservation strategies, and inform decision and policy making for for both endangered and non-endangered species because it can significantly improve many aspects of natural resource policy and management.

Key words: Population Viability Analysis, wildlife conservation and policy, Australia.

INTRODUCTION

The rapid and ongoing global loss of biodiversity is unprecedented (Wilson 1988). Nowhere is this loss more evident than in Australia (Kennedy 1990), one of the world's seven "megadiversity" countries (Economist 1988). Since European settlement in 1788, there has been an extraordinary rate of extinction (Recher and Lim 1990) and ecosystem destruction (Saunders and others 1987). In Australia, biodiversity conservation is recognized as an integral element of "sustainable development" (Ecologically Sustainable Working Group 1991) and Federal and State Government policies embody biodiversity conservation language (e.g., The National Conservation Strategy, [Anon 1982], State Conservation Strategy [Victorian Government 1987] and The Flora and Fauna Guarantee [Victorian Government 1988]).

If biodiversity conservation is to be achieved amongst growing and competing demands for natural resources in Australia and elsewhere, the sizes of viable populations and viable ecosystems must be estimated and policy prescriptions and management programs successfully instituted. Population Viability Analysis (PVA), a relatively new concept and technique, is a useful tool in meeting biodiversity conservation policy goals. Clark and others (1991, p.1) define PVA as "a procedure that allows wildlife managers to simulate, using computer models, extinction processes that act on small populations of organisms, and therefore to assess their long term viability."

Computer simulation models used in PVA require a range of input data including: 1) demographic attributes (e.g., age and sex-specific birth and death rates), 2) breeding system (degree of polygny), 3) ecology (e.g., the amount, spatial distribution and changes in the availability of habitat), and, 4) genetics (e.g., the response of the population to inbreeding, which is typically determined by the "genetic load" of deleterious alleles). PVA simulation programs then step through years or other time increments, determining the fate of each individual in the population at each stage of the life cycle (birth, reproduction, migration, disease, death etc.). Most life events, except aging, are probabilistic phenomena and the occurrence of events in the life of the simulated organism are determined by random sampling from probability distributions describing such events. These probabilities can be inter-dependent. For example, the probability of death can be a function of the genes inherited from the parents. PVA simulations track the fate of individuals through generations and provide an array of population statistics such as population size, sex ratio, age distribution and genetic variation. The fate of the population is simulated many times to give a frequency distribution of possible fates (e.g. extinction or survival).

In this paper we: 1) introduce the wildlife policy process and examine how it can be improved using PVA, 2) review the concept of PVA and the methods to apply it, and 3) assess the potential of PVA to improve wildlife and land-use policy, programs and management, including a review of its strengths and limitations with reference to Australian examples.

WILDLIFE CONSERVATION POLICY AND MANAGEMENT

Biodiversity and endangered species conservation is both a technical and a policy challenge. Tohe present biodiversity crisis stems from the failure of past natural resource, economic, and human population policies. All natural resource and endangered species conservation policies follow a "process" with predictable phases. PVA is directly relevant to several of these phases and can improve the overall policy process if utilized in appropriate ways and within pertinent phases.

The theoretical perspective of the policy process used here follows Lasswell (1971) and Brewer and deLeon (1983). Policy processes, whether in the management of biodiversity or other problems, are a product of many actions by many actors, each with potentially different interests, roles, information, and perspectives. The policy process undergoes predictable steps in which each phase is populated by somewhat different agencies and interest groups with different analytical and political agenda. The policy process is often not optimized for the system as a whole, because no one is in control of the overall system and because it is not always possible to determine optimality in any specific application (Ascher and Healy 1990).

The policy process can be divided into six phases (Brewer and deLeon 1983) and these can be seen clearly in attempts to manage biodiversity, endangered species, and natural resources. The phases are:

1) initiation: a problem is perceived, identified, and placed on the public agenda,

2) estimation: the problem is defined in more detail using expert analysis and technical considerations,

(3) selection: a policy response to the problem is formulated, debated, and authorised by a legitimate source,

(4) implementation: a program is developed and applied to the problem,

5) evaluation: ex post appraisal of the implementation effort and the original policy formulation, and

6) termination: discontinuation, revision, or succession of policy.

PVA can be used to improve all phases of the policy process, especially estimation, selection, implementation, and evaluation. The technique permits decision and policy makers to understand extinction as the result of a complex, but relatively predictable sequence of deterministic and stochastic events that may be prevented through the application of appropriate policy and management. As rare, vulnerable, and endangered species occur in a wide array of habitats and ecosystems, PVA can be useful to foresters, park managers, and a wide range of other people.

PVA is integral to the estimation phase because it enables relatively precise estimation of the likelihood of extinction and provides a basis for setting quantitative targets for species restoration. A host of management options and their expected costs and benefits can then be explored. PVA produces numerical targets in numbers of individuals and populations needed to prevent extinction. These targets are usually given in terms of a probability statement over a 25, 50, 100 or more years.

PVA is central to the selection phase because this is where the relative various programs can be compared and a decision is taken on a specific management course.

PVA is essential to the implementation phase because once a recovery target has been set, the size, resource, and organisational requirements of the program can be estimated and instigated. PVA permits a realistic assessment of the personnel, financial, technical, and institutional commitments required to restore and maintain a population.

PVA can be used in the evaluation phase to measure the performance of the restoration program and determine if policies, programs and recovery targets have been met. This is possible because PVA estimates numerical targets in terms of population sizes and numbers of populations needed to prevent extinction. Clark and Harvey (1988) evaluated an endangered species recovery program where a host of organizational problems significantly constrained the restoration effort.

In summary, PVA is central to the overall policy processes associated with endangered species restoration and biodiversity conservation. These policy processes can be significantly improved if PVA is explicitly used in these policy and programmatic processes.

THE POPULATION VIABILITY ANALYSIS CONCEPT: A REVIEW

Estimating the viability of populations

Modern conservation biology focuses on managing small populations and this requires estimating their viability (or vulnerability to extinction) so that appropriate management action can be taken. Shaffer (1981) noted that a range of factors make populations vulnerable to extinction. These do not operate in isolation (Burgmann and Neet 1989, Gilpin 1989, Figure 1). A classic example is the heath hen (Tympanuchus cupido cupido). Initially, hunting and human-induced habitat degradation dramatically reduced the species' distribution and abundance. The decline continued because of fires, windstorms, and unfavorable seasonal conditions. Later a combination of disease, inbreeding depression, reduced sexual vigor and an imbalanced sex ratio led to extinction (Simberloff 1986a). This example illustrates the complex interaction of both deterministic and stochastic (or random) forces in the extinction of a species population. Further, it shows that demographic, environmental, genetics, and episodic catastrophes are important in extinction processes. Another factor, social dysfunction, may also contribute to the vulnerability of small populations (Allee 1949, Soulé 1983, Ferson and Burgmann 1990).

Shaffer (1981) listed five approaches to estimate the cumulative impacts of various chance events on small populations:

- 1) Experimentation, where isolated populations are monitored over time, and the fate of each population is documented.
- 2) Biogeographic analyses, including studies of island biogeography (e.g., MacArthur and Wilson 1967, see Shafer 1991 for a comprehensive review) and patch dynamics (Levin 1976, Pickett and Thompson 1978).
- 3) Theoretical and analytical models, including models of population growth and change (e.g., Richter-Dyn and Goel 1972, Keiding 1975, Wright and Hubbell 1983, Reed and others 1986, Ewens and others 1987, Phillippi and others 1987). For example, Goodman (1987) developed a model that estimated the likelihood of persistence of populations based on their size and fluctuations in growth rate (e.g., Belovsky 1987, Kinniard and O'Brien 1991).
- 4) Genetic principles, where the size of a population required to ensure genetic "fitness" is estimated (Lehmkuhl 1984, Davey 1989).
 - 5) Simulation models, in which the fates of hypothetical populations are tracked in response to a suite of parameters (e.g., Salwasser and others 1984, Harris and others 1986, Marcot and Holthausen 1987, Grier and Barclay 1988, Doak 1989, Lacy and others 1989, Seal and Lacy 1989, Seal and others 1989, Burgmann and Gerard 1990, Ginzburg and others 1990, Lacy and Clark 1990). In this paper, PVA is regarded as those techniques which employ computer simulation models.

There are advantages and disadvantages of each approach (Shaffer 1981, Simberloff 1988), although Burgmann and others (1988) considered that island biogeography had little or no practical application to wildlife conservation because there were underlying limitations in the theory and its empirical application. However, Shafer (1991) provides an alternative view of the value of island biogeography. Thus, most or all of these approaches have the potential to improve the understanding of the biological processes leading to extinction, and to help identify appropriate conservation strategies (Clark and others 1990, Shaffer 1990). These five methods were applied to the endangered black-footed ferret (*Mustela nigripes*) by Groves and Clark (1986), Harris and others (1989), and Lacy and Clark (1989) to estimate population viability as basis for setting recovery targets and management needs.

Minimum Viable Populations (MVP) and Population Viability Analysis (PVA).

Shaffer (1981) noted that the probability of survival of a population was high if its numbers could be maintained above a certain size. This was termed a "minimum viable population" (MVP). Shaffer (1981, p.132) arbitrarily defined a MVP for any given species as one "having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental and genetic stochasticity, and natural catastrophes." Originally, it was implied that a population's MVP could be determined using PVA (Shaffer 1981). Today, it is understood there is no such thing as an MVP, per se. Instead, populations become increasingly vulnerable to extinction the smaller they are (Shaffer 1990, Ferson and Burgmann 1990).

Conceptually, MVP and PVA are intimately linked. PVA was developed to investigate the relative and cumulative impacts of various deterministic and stochastic influences on a given population (Lacy and others 1989). Many of the processes which effect small populations can and do interact (Brussard 1985). For example, a lack of genetic diversity, inbreeding depression, and reduced adaptability can lead to an even smaller population size, a lower probability of finding a mate, and increased inbreeding and reduced genetic variability (Marcot and Hollthausen 1987). Such a population will spiral toward extirpation in an "extinction vortex." Gilpin and Soulé (1986) described several types of vortices which reflect the different forms of interactions between stochastic factors. Brussard (1985), Seal and others (1989), and Thomas (1990) noted that the threshold size of a population needed for a species to remain above an extinction vortex would be an MVP.

The size of a viable population is not static (Usher 1987, Menges 1990) but will differ for any given species (Gilpin and Soulé 1986), the circumstances impinging on that organism at any given time (Fowler and MacMahan 1982), and place (Grumbine 1990). This is because vulnerability to extinction will be, in part, related to demographic attributes and other characteristics (Howe and others 1991) and some of these will vary with a plethora of factors, such as a changed disturbance regime (e.g., forest logging). This was recognized by Belovsky (1987) who noted that his application of the model developed by Goodman (1987) did not determine an MVP but emphasized that the probability of persistence would increase with population size. PVA may indicate that a particular population is not viable, although this does not imply that attempts to conserve it should be abandoned (Soulé 1987, Thomas 1990). A non-viable population will be one in urgent need of management to reduce its vulnerability to extinction (Kinniard and O'Brien 1991).

In summary, an application of PVA may allow the identification of the size of a population necessary for the survival of a given species, with a given probability, over a particular time span (e.g., 100 years), in a particular place, and under certain conditions (Ginzburg and others 1990). For example, Lacy and Clark (1990) used PVA to examine the vulnerability of a small population of the eastern barred bandicoot (*Perameles gunnii*) in western Victoria and concluded that it had a 91% probability of extinction within 15 years.

Examples of the use of PVA

PVA has been applied in North America, Australia, Asia, Africa, and Europe (Table 1) and the utility of the approach is evident in the growing use of the technique in wildlife management and attempts to conserve endangered species (Mace and Lande 1991). In North America, PVA has been used in studies of a wide range of species. Some of the most notable have been on the grizzly bear (*Ursus arctos horribilis*; Shaffer 1981, 1983, Shaffer and Samson 1985, Suchy and others 1985) and the northern spotted owl (*Strix occidentalis caurina*; Marcot

and Holthausen 1987, Lande 1988, Doak 1989, Thomas and others 1990). Other North American studies include PVA of plants, invertebrates, and all major vertebrate groups (Table 1).

PVA has been used only recently in Australia on the eastern barred bandicoot (Lacy and Clark 1990), greater glider (*Petauroides volans*; Possingham and others 1991), powerful owl (*Ninox strenua*; Possingham and others 1991), Leadbeater's possum (*Gymnobelideus leadbeateri*; Lindenmayer and others 1991), brush-tailed rock wallaby (*Petrogale pencilliata*; Hill 1991), orange-bellied parrot (*Neophema chrysogaster*), long-footed potoroo (*Potorous longipes*), helmeted honeyeater (*Lichenostomus melanops cassidix*), and mountain pygmy possum (*Burramys parvus*; Clark and others 1991).

THE RELATIVE MERITS AND LIMITATIONS OF POPULATION VIABILITY ANALYSIS.

The following discussion focuses on the relative strengths and weaknesses of PVA in relation to its implications for improved natural resource management and policy. These strengths and limitations will have different ramifications according to the policy phase in, and the purpose for which, PVA is applied.

Strengths of Population Viability Analysis

1) Explicit statement of species' biology and the identification of missing data.

PVA requires a review of a species' biology including demographics, environmental conditions, genetics, and catastrophes. This leads to explicit statements about what is known about a species and reveals those attributes for which values must be estimated. This assessment is an important first step in formulating strategies and objectives for research, conservation, and management. Once data weaknesses are identified, research can be planned to acquire missing information so that subsequent PVA can be based on a more complete dataset.

2) Synthesis of interacting factors and modeling trends in population behavior.

PVA produces an estimate of the relative impacts of a number of interacting factors on extinction. Estimates of the impacts of these factors would be difficult or almost impossible with PVA. This is important because: (1) the dynamics of populations may change according to their size and circumstances (Seal and others 1989, Berger 1990, Lindenmayer and others 1991), and, (2) a plethora of factors influence population behavior (see the example of *T.c.cupido* given above).

PVA allows trends in population behavior to be identified and quantified. Factors which may exert influence on such trends can be determined. Key questions can be addressed, such as: 1) What is the relationship between population size and population stability? And, 2) At what population size do stochastic events become important and which factors are most critical? An understanding of the processes leading to extinction can also have an important instructional role (Simberloff 1986a, Seal and others 1989, Clark and others 1990) and may provide information to prevent future extinctions.

Trends for declining populations can be identified early and the application of PVA may allow a "preventative management philosophy" where species are managed before they become endangered (Figure 1). This is useful as attempts to conserve small and declining populations can be expensive (Clark and Harvey 1988), difficult to organise (Clark and Westrum 1989), and are not guaranteed of success (Griffith and others 1989, Clark and Cragun 1991).

3) Identifies threatening processes.

PVA may identify previously unknown factors or anticipate the effects of known factors that threaten a population's viability (Lacy and Clark 1990). For example, PVA of the Puerto Rican parrot (Amazona vitatta) showed that a catastrophe could have decimate wild populations of the species (Lacy and others 1989). A hurricane struck Puerto Rico soon after PVA was completed, killing approximately half the birds in the wild flock.

The State Conservation Strategy (Victorian Government 1987, p.31) stated that it "will control and manage any activities threatening terrestrial plants and animals." Thus, the application of PVA can qualify and quantify the impact of a particular threatening process and hence assist Governments in meeting their aims to preserve biodiversity. It can also reveal if current policy and programs are meeting stated policy and management aims.

4) "Minimum critical area" and reserve design.

PVA has implications for determining the "minimum critical area" that is the size of an area needed to support a viable population of a given species (Soulé and Simberloff 1986, Conner 1988, Davey 1989). Wilcox (1984) in Shafer (1991, p.104) proposed a sequence of steps in defining such critical areas, viz: a) target taxon, b) minimum viable population, c) habitat requirements, and d) minimum critical area requirements. These important links between PVA and minimum critical areas are predicated on an understanding of several factors, including: a) the habitat and area requirements of wildlife, b) the spatial and temporal availability of suitable habitat, and c) the effectiveness of retained systems (e.g., wildlife corridors) in contributing to minimum critical areas (Lindenmayer and others 1991). Currently, the habitat requirements of most species are poorly understood (Simberloff 1986b), as are the area requirements for viable populations (Diamond 1978, Usher 1986). PVA may also be used in tandem with a range of other procedures to design and assess the adequacy of nature reserves (Wright and Hubbell 1983, Grumbine 1990, Ecologically Sustainable Development Working Group 1991), and the determine the impacts of various land uses on conservation values (Shaffer 1981, Reed and others 1988, Thomas 1990).

5) Highlights need for management.

PVA may play a central role in management planning, aid the implementation of existing policy and indicate that new policy and management are needed. The use of PVA as a "preventative" management tool is being considered in Australia by the Resource Assessment Commission (1991), Australian National Parks and Wildlife Service (Hill 1991) and Ecologically Sustainable Working Group (1991). In this context, the Resource Assessment Commission (1991, p. N11) states that "estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices ought to be an essential part of conservation planning." Similarly, Mace and Lande (1991) recommended using PVA to classify threatened species into "risk" categories.

6) Complements on-ground management and decision-making.

PVA must be integrated with, and not substituted for, other approaches to wildlife management and natural resource conservation. The technique should be an adjunct to detailed studies of key taxa including those potentially threatened by the exploitation of natural resources (Murphy and others 1990). These studies need to be carefully targeted to test hypotheses and quantify results. Simberloff (1988, p.50) correctly noted that "sound conservation science must be founded on autecological studies of individual systems." This view was supported by Burgmann and others (1988) in a detailed review of the use of extinction models. Such an approach is presently being used in several Australian endangered species restoration efforts (e.g., eastern barred bandicoot, Clark and Seebeck 1990).

The use of PVA, data collection, and monitoring and evaluation of management actions

are closely interlinked (Figure 2). These tasks need to be integrated, ongoing, and regularly updated in an adaptive management approach (Holling 1973, 1978, Clark and Seebeck 1990, Clark and others 1990), with each facet of such a framework providing feedback to the others (Clark 1989, Clark and Harvey 1988). This will allow more responsive and more effective conservation and management (Casey and others 1990). The needs for such management were highlighted by Holling (1973, p.21) who recognized a need to "devise systems that can absorb and accommodate future events in whatever unexpected form they may take."

Adaptive management is presently being applied in efforts to conserve the eastern barred bandicoot in western Victoria (Arnold and others 1990). Marcot and Holthausen (1987) recommended adoption of regularly re-evaluated management procedures for the conservation of the northern spotted owl. Clark and Harvey (1988) noted the value of a similar approach for the management of the remaining populations of the black-footed ferret. Adaptive management could also be accompanied by attempts to develop a standardized procedure for the use of PVA (Salwasser and others 1984, Mace and Lande 1991).

The consequences of management actions can be estimated using PVA (Shaffer 1990, Maguire and others 1990) and these can be made obvious to land managers. A useful example is provided Thomas and others (1990) in an investigation of the probability of extinction of the northern spotted owl. They demonstrated that proposed management strategies were inadequate and recommended new ones more likely to improve the probability of survival. Furthermore, the study identified a need for further studies of the dispersal behavior of the northern spotted owl.

PVA should be coupled with risk analysis (sensu Maguire 1991) to assist land managers to make decisions (Salwasser and others 1984, Maguire 1986, 1989, Maguire and others 1987, 1990, Gilpin 1989, Soulé 1989, Marcot in press). Several examples illustrate the value of combining PVA and decision analysis. Maguire and others (1987) integrated PVA and decision analysis to explore management options for Sumatran rhino (Dicerorhinus sumatrensis) conservation. Similar analyses have been completed for the black-footed ferret (Maguire 1989) and the eastern barred bandicoot (Maguire and others 1990). Soulé (1989) combined PVA and risk analysis in studies of the Concho water snake (Nerodia harteri paucimaculoota). Maguire and Lacy (1990) used decision analysis in studies of the captive management of tigers (Panthera tigris).

Both PVA and decision analyses can be useful in planning conservation strategies. This can be important, particularly given the cost and logistic requirements for species recovery programs (Clark and Harvey 1990, Clark and Westrum 1989, Murphy and others 1990) and the limited resources typically allocated for nature conservation. Thus PVA, in tandem with decision analyses, can assist in ranking tasks and allocating scarce resources (Soulé 1989, Maguire and others 1990). Without PVA, decision and policy makers and managers have few conceptual, explicit, and "objective" frameworks by which to assess the impacts of land-use decisions on the risks of extinction (Murphy and others 1990). Therefore, the use of PVA may reduce the potential for inappropriate, subjective, or partisan assessments of population vulnerability (Mace and Lande 1991).

7) Species recovery, reintroduction, and captive breeding programs.

PVA can be used to define a target number of animals for species recovery (Hill 1991), reintroduction, and captive breeding (Clark and others 1991). Lacy and Clark (1990) and Maguire and others (1990) illustrated this for the eastern barred bandicoot in western Victoria. In other cases, Seal and Lacy (1989), Lacy and others (1989) and Maguire and Lacy (1990) used PVA and decision analyses to explore the effectiveness of reintroduction and captive breeding programs for various endangered species. Thus, applications of PVA may be important in

developing endangered species recovery programs such as those required under the Australian National Strategy for the conservation of species and habitats threatened with extinction (Australian National Parks and Wildlife Service 1989) and the Flora and Fauna Guarantee (Victorian Government 1988). For example, PVA has been applied in the development of a species recovery program for the brush-tailed rock wallaby, *Petrogale pencilliata* (Hill 1991).

In conclusion, application of PVA can provide a suite of potential advantages for endangered species and natural resource management. Among these are an improved approach for research, species recovery and management, identifying endangering processes, setting and monitoring policy, making decisions, and taking management actions. PVA is most effective when coupled with decision analysis and applied within an adaptive management framework.

Limitations of Population Viability Analysis

1) Data intensive technique.

Comprehensive data on target species are required for PVA (Davey and Norton 1990). Such data are unavailable or incomplete for most species (Grumbine 1990), in particular those rare and endangered organisms that may urgently require PVA. Estimation of the values for these parameters requires considerable experience and must be based on a detailed knowledge of the biology of a species or attributes of related taxa (Simberloff 1988). PVA may be very time consuming, as there may be a myriad of parameters and many values within each parameter to be tested. It may take time to identify those factors that are important and therefore warrant thorough and further investigation.

The paucity of detailed biological, ecological, and genetic data for many taxa will make it difficult to estimate accurately their vulnerability to extinction (Davey and Norton 1990). More accurate estimates will be predicated on the collection of more comprehensive basic biological data.

2) Functional role of taxa.

PVAs focus on the probability of extinction of a species but they do not consider the "functional role" of species, or the inter-dependence of organisms, in ecosystems (Conner 1988). The reduction in size, or loss of populations can have major implications for important biological and ecological functions in ecosystems, such as pollination, seed dispersal, and nutrient cycling. On this basis, Conner (1988, p.82) believed that populations of organisms must be conserved in "sufficient abundance to be ecologically functional in their community."

However, the estimation of "ecologically functional populations" is presently not possible (Conner 1988). PVA is typically a single species approach to wildlife conservation (Soulé 1987, Shafer 1991). Ecosystem viability may be indicated by the viability of "bio-indicator", "keystone" "umbrella", and "mobile link" species (see Kohm 1990). Therefore, PVA may be most effective if focused on these species (Soulé 1987, Thomas 1990) but few data exist on such organisms (Ecologically Sustainable Working Group 1991). This approach assumes that the conservation of such organisms will also result in the conservation of a significant proportion of other species. Soulé (1987), Soulé and Kohm (1989), and Norton and Lindenmayer (In Press) discuss further the value of using various types of indicator species to conserve biodiversity.

3) Interactions between parameters.

PVA may not be able to incorporate all the potentially synergistic impacts of factors which influence actual populations (Soulé 1987, Lande 1988, Mace and Lande 1991). For example, changes in carrying capacity resulting from the loss of trees with hollows will reduce the area of suitable habitat available for Leadbeater's possum, (Lindenmayer and others 1990). This will, in turn, increase mortality among dispersing animals and further isolate remaining

subpopulations (Lindenmayer and others 1990). The incorporation of such synergistic interactions between parameters would provide more accurate estimates of the vulnerability of populations. This could be achieved by modifying the computer programs used in PVA. For example, a new version of the simulation model VORTEX (Lacy unpublished) as well as the programs FORPOP (Possingham and others 1991) and ALEX (Lindenmayer and Possingham In Press), can be used to investigate the viability of metapopulations and subpopulations and the importance of exchanges of individuals between such groups.

4) Simplification of population dynamics.

Population dynamics are more complex than can be simulated by computers. Computer programs necessarily include a large number of assumptions (Lindenmayer and others 1991) and simplistically model the response of organisms to catastrophes and environmental variation. Thus, PVA can provide only a relatively simple estimation of the actual dynamics of wild populations and caution should be used when interpreting and applying the results of PVA. PVA should, however, reflect general trends in population behavior (Soulé 1987).

More reliable estimates of PVA may be obtained with new, more detailed and comprehensive models together with better input data (Soulé 1987). Thus, it will be appropriate to repeat and upgrade a PVA for a particular taxon when new data and models become available. This is part of the "adaptive management" process described above (Figure 2).

5) Lack of a generic model

A suite of PVA models exist. Some of these include: GRIER (Grier 1980a), SPGPC (Grier 1980a, 1980b, Grier and Barclay 1988), GAPPS (Harris and others 1986), POPDYN (Cox 1988), SIMPOP (Lacy and others 1989, Seal and Lacy 1989, Lacy and Clark 1990), VORTEX (Seal and Lacy 1990, Clark and others 1991), RAMAS (Ferson and others 1988 in Ginzburg and others 1990, p.65), RAMAS/age (Ferson and Akcakaya 1990), RAMAS/space (Akcakaya and Ferson 1990), FORPOP (Possingham and others 1991), ALEX (Lindenmayer and Possingham In Press).

Each of these models have inherent strengths and limitations, some have unique features, and some are better suited to PVA analysis of particular taxa than others. For example, Samson (in Simberloff 1988, p.494) noted that the structure of the model POPDYN which was applied in a PVA of the gopher tortoise (Gopherus polyphemus) (Cox 1988) would preclude its use from studies of species such as the northern spotted owl that do not breed annually. In other examples, the models FORPOP (Possingham and others 1991) and ALEX (Lindenmayer and Possingham In Press) simulate populations dynamics within and between various patches of suitable habitat but take no account of genetics as a factor contributing to extinction.

Values for many parameters which influence population dynamics, particularly life-history and demographic attributes, are species-specific (Thomas 1990). Thus, estimates of vulnerability and viable population size will differ for each species and each location (Newmark 1986 in Soulé 1987 p.175, Belovsky 1987, Soulé 1987) and the modeling procedure used (Kinniard and O'Brien 1991). This was shown by Belovsky (1987) who demonstrated that the probability of extinction of mammals in residual montane environments varied according to a range of factors, including body size. These findings also indicate that not all species in a given area face the same probability of extinction (Burgmann and others 1988) and that strategies appropriate for the conservation of one species may be inadequate for others (Doak 1989). Hence, PVA will need to be completed for each species of concern (Soulé 1987) although some of the work required may be reduced by completing PVA for bio-indicators, keystone species and umbrella species.

Models selected for PVA may need to be modified to meet the particular requirements

of a given case study. For some studies, new models may need to be developed whereas in others several models may be used simultaneously. The choice of a model is dependent on the objectives of the study together with an understanding of the strengths and limitations, including the assumptions, which are implicit and explicit in each model (Simberloff 1988). Because of the unique problems inherent in many cases, we consider that it is unlikely that a generic model can be developed (Lindenmayer and others 1991). However, this does not detract from the value of PVA or the concepts and theory which underpin the approach.

CONCLUSIONS

Improving wildlife conservation and policy is, in part, dependent on using appropriate concepts and applied tools which permit: 1) early recognition of problems (initiation in the wildlife policy process), 2) accurate estimation of the size or extent of those problems, 3) selection of an appropriate solution, 4) successful implementation of solutions through various programs, 5) continuous evaluation of the original problem as well as the effectiveness and adequacy of implementation efforts. PVA can aid in all these phases of the restoration of endangered populations and in preventing currently relatively larger populations from being reduced and eventually endangered. In turn, PVA can help decision and policy makers understand the extinction process in general and hopefully conclude that large-scale biodiversity conservation is the best policy for conserving a nation's biological wealth (see Kohm 1990).

PVA adds a new and important dimension to the study, utilization and management of natural resources. Applications of the technique can: 1) yield information on trends in population behavior, 2) identify and assess the impacts of factors which influence the viability of populations, 3) provide an objective and explicit framework for assessing extinction risks, research, decision-making, and wildlife and land use management. PVA will be most effective if applied within an adaptive management framework (Figure 2).

PVA has a number of weaknesses. In particular, a simplified simulation of the behavior of populations and an array of assumptions that underpin its use (Lindenmayer and others 1991). These problems are often exacerbated by a lack of detailed biological information for target species, although this is not a weakness of the technique, per se. Many of these apparent limitations can be overcome with more detailed biological research together with efforts to improve and further refine computer simulation models. There is merit in future attempts to upgrade models for use in PVA because it is one of the few techniques capable of assessing the effects of various factors and management options on population vulnerability. This is important given the anticipated rise in the number of species facing extinction (Recher and Lim 1990) and growing pressure to exploit natural resources (Davey and Norton 1990).

In summary, we consider the benefits of PVA far outweigh the limitations of the technique and recommend that the approach be used in improving policies and programs aimed at managing natural environments and their biota.

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- Figure 1. A general extinction model showing the fragmentation of a population's distribution into smaller and more isolated patches and the role of systematic and random factors in this process (after Clark and others 1989, p. 4).
- Figure 2. A generalized model of interrelationships between PVA computer simulation models, data input and output, and management options and decision making.
- Table 1. Examples of Population Viability Analysis.



Captive Breeding Specialist Group

Species Survival Commission
IUCN - The World Conservation Union
U. S. Seal, CBSG Chairman

PHVA WORKSHOP PREPARATIONS

1991

OUTLINE

- 1. Introductions, briefing materials, and updates.
- 2. Outline of organization, preparations, conduct, and report of a PVA Workshop. Relationship to Captive Breeding Action Plans and SSP.
- 3. Preparation of the **Problem Statement and Agenda**. Examples: Key Deer, Tana River Primate Reserve, Mexican Wolf, Florida Panther, Bali Mynah, Javan Rhinoceros.
- 4. Selection of **Participants and Assignments**. Examples: Florida Panther, Whooping Crane, Javan Rhinoceros.
- 5. Preparation of the **Briefing Book**. Includes literature, field reports, surveys, taxonomy, captive population information, life history, **MAPS**, popular articles, recovery plans. Examples: African Wild Dog, Asian Rhinos, Bali Mynah, Ethiopia, Mexican Wolf.
- 6. Location, organization, and conduct of the **Workshop**. Isolation, resources, chairs, assignments, production of draft report.

- 7. Captive population data sets. Studbooks, masterplans, SPARKS, analyses. Demonstration of **SPARKS**. **GENES**, **CAPACITY** and pedigree analysis. Demographic analyses.
- 8. Wild population census and monitoring, mortality, and fertility data, life history information. Recovery plans, management plans, and published information. VORTEX and other software packages (GAPPS and RAMAS). Demonstration and discussion of assumptions.
- 9. Identification of scientific problem areas. Environmental variance and threats, protection, reproduction and nutrition, toxicology, disease, taxonomy, long term trends, Ne, inbreeding effects, rates of loss of heterozygosity, founder numbers, risks and their estimation, viable populations, recovery goals and their basis, introgression.
- 10. People problems. Political instability, agency agendas, wildlife biology traditions, turf protection, data ownership, field worker bonding to population and species, habitat vs species, community ecology vs species ecology, local animosities, development vs protection, animal rights, anti-zoo and captivity.
- 11. Production of final PVA Workshop Report. Completion of simulations. Responsibility for various segments of report. Translations. Maps and pictures. Editing and assembly. Printing and distribution costs.
- 12. Budgets, costs, funding, and contracts.
- 13. Overview and the next 5 years.
- 14. Reference materials.

PHVA WORKSHOPS

Preparation and Documentation Needs

1991

Information to be included in briefing book:

- 1. Bibliography preferably complete as possible and either on disk or in clean copy that we can scan into a computer file.
- 2. Taxonomic description and most recent article(s) with information on systematic status including status as a species, possible subspecies, and any geographically isolated populations.
- 3. Molecular genetic articles and manuscripts including systematics, heterozygosity evaluation, parentage studies, and population structure.
- 4. Description of distribution with numbers (even crude estimates) with dates of information, maps (1:250,000) with latitude and longitude coordinates.
- 5. Protection status and protected areas with their population estimates. Location on maps.
- 6. Field studies both published and unpublished agency and organization reports (with dates of the field work). Habitat requirements, habitat status, projected changes in habitat. Information on reproduction, mortality (from all causes), census, and distribution particularly valuable. Is the species subject to controlled or uncontrolled exploitation? Poaching?
- 7. Life history information particularly that useful for the modelling. Includes (sex specific where possible): adult body weight, age of first reproduction, mean litter or clutch size, interbirth interval, first year mortality, adult mortality, breeding structure (monogamous or polygamous in a given season), and seasonality of breeding.
- 8. Published or draft Recovery Plans (National or regional) for the wild population(s). Special studies on habitat, reasons for decline, environmental fluctuations that affect reproduction and mortality, and possible catastrophic events.
- 9. Regional and international studbooks hard copy and entered in SPARKS. If needed we (CBSG) will do the entry into SPARKS. Results of genetic and demographic analyses using software provided with SPARKS.

- 10. SSP and similar masterplans for the captive population.
- 11. Color pictures (slides okay) of species in wild and captivity suitable for use as cover of briefing book and final PVA document.

Plans for the Meeting:

- 1. Dates and location. Who will organize the meeting place and take care of local arrangements? Should provide living quarters and food for the 3 days in a location that minimizes outside distractions. Plan for meeting and working rooms to be available for the evening as well as the day. Three full days are needed for the workshop with arrival the day before and departure on the evening of the 3rd day or the morning after.
- 2. Average number of participants about 30 usually with a core group of about 15 responsible for making presentations. Observers (up to 20) welcome if facilities available but their arrangements should be their own responsibility. Essential that all with an interest in the species be informed of the meeting. Participants to include: (1) all of the biologists with information on the species in the wild should be invited and expected to present their data, (2) policy level managers in the agencies with management responsibility, (3) NGOs that have participated in conservation efforts, (4) education and PR people for local programs, (5) zoo biologists with knowledge of the species, (6) CBSG experts in population biology and needed areas of biological expertise (reproduction, nutrition, disease, behavior), and (7) local scientists with an interest in the species.
- 3. Preparation of briefing document. Compiled in collaboration with organizer and printed by CBSG. Usually prepare about 50 copies.
- 4. Funding primarily for travel and per diem during the meeting. Also preparation of briefing document and the PVA report. CBSG costs are for preparation of the 2 documents, travel of 3-4 people, and their per diem ranges from \$5,000 to 7,000.
- 5. Preparation of agenda and securing of commitments to participate, supply information, and make presentations needs to have one person responsible and to keep in contact with CBSG office on progress.
- 6. Meeting facilities need to include meeting room for group, break away areas, blackboard, slide projector, overhead projector, electrical outlets for 3+ computers, printer (parallel port IBM compatible), and photocopying to produce about 200-500 copies per day. Have food brought in for lunches. Allow for working groups to meet at night.



Species Survival Commission
IUCN - The World Conservation Union
U. S. Seal, CBSG Chairman

PREPARATIONS FOR PHVA PARTICIPANTS

The purpose of Population and Habitat Viability Assessment Workshops is to assess the risk of extinction of one or more species and their habitat. Then management scenarios are suggested and evaluated in terms of their effect on the risks of extinction. Simulation models, based upon data and information prepared for the workshop and the expertise and unpublished information brought to the workshop by researchers and managers, are used as a part of the risk assessment process.

The success of the Workshops very much depend upon information brought to the workshop by knowledgeable people. It frequently has not been published and in significant part may be the expertise acquired through long experience but no explicitly available in written form.

Important information (data and numbers wherever possible) that you might bring and be prepared to discuss is outlined below. We recognize the list is long but you should choose the topics for which you have data and expertise. An example of the kinds of report that are developed and the information that is used is provided as an example. Also several pages describing the process we follow for preparing for a workshop are attached. The specific scope of the present workshop is summarized in the attached Problem Statement, Goals, and Objectives.

Life history information on the individual species:

Mean age of first reproduction
Maximum and mean litter size
Interbirth interval
Number of females not producing young in a given year
Mortality in first year
Mortality of juveniles
Mortality of adults (by sex if known)
Sex ratio at birth and sex ratio of adults
Life expectancy

Population information:

Density dependent effects

Population size(s) and changes over time

Subpopulations - sizes and distribution (on a map)

Census history

Taxonomic status (evidence for phylogeographic differentiation, subspecies)

Data on inbreeding effects

Threats to the population (Poaching, land use, exotic species, climatic variation, unusual violent events, fire, disease, lack of legal protection, human population growth, global warming, pollutants, habitat removal)

Habitat and Protected Area Information:

- -Topographic map of areas and boundaries
- -Distribution and numbers of people living in area
- -Population projections
- -Human usage of area by resource, season, and intensity
- -Local attitudes towards area and key species (plant and animal)
- -Nature of legal protection
- -Budget and personnel involved in protection and management of area
- -Climatic data over time (rainfall and temperatures)
- -Possible effects of global warming
- -Natural features characteristics rivers, erosion,
- -Species list (especially endemics) and abundance data (dates)
- -Major floristic composition and projected successional events. Regeneration rates of key plant species (population biology approach)
- -Pollutants in environment that might have biological effects

Raw data from all years of collection is valuable for estimation of variance and the possible association of this variance with specific environmental events. Distribution of litter or clutch sizes is useful. For birds information on fertility, hatching, and fledging rates is useful. Data across years is even highly desirable.

We will help in any way possible. We particularly want and appreciate materials that can be included in the briefing book for the workshop. Please send the CBSG office any papers, manuscripts, bibliographies, and maps that you think will be useful. We also want copies of color slides of animals, plants, or area overviews that might use. We always try to use a color print for the cover of the briefing book and a map for the back cover.

POPULATION VIABILITY ANALYSIS DATA FORM - BIRDS

Species:
Species distribution:
Study taxon (subspecies):
Study population location:
Metapopulation - are there other separate populations? Are maps available?: (Separation by distance, geographic barriers?)
Specialized requirements (Trophic, ecological):
Age of first reproduction for each sex (proportion breeding):
a)Earliest:
b)Mean:
Clutch size (N, mean, SD, range):
Number fertile:
Number hatched:
Number fledged:
Laying Season:

Laying frequency (interclutch interval): Are multiple clutches possible? **Duration of incubation:** Hatchling sex ratio: Egg weights: Hatchling weights (male and female): Age(s) at fledging: Adult sex ratio: Adult body weight of males and females: Reproductive life-span (Male & Female, Range): Life time reproduction (Mean, Male & Female): Social structure in terms of breeding (random, pair-bonded, polygyny, polyandry, etc; breeding male and female turnover each year?): Proportion of adult males and females breeding each year:

Dispersal distance (mean, sexes): Migrations (months, destinations): Territoriality (home range, season): Age of dispersal: Maximum longevity: Population census - most recent. Date of last census. Reliability estimate.: Projected population (5, 10, 50 years).: Past population census (5, 10, 20 years - dates, reliability estimates): Population sex and age structure (young, juvenile, & adults) - time of year.: Fecundity rates (by sex and age class): Mortality rates and distribution (by sex and age) (neonatal, juvenile, adult); Population density estimate. Area of population. Attach marked map.: Sources of mortality-% (natural, poaching, harvest, accidental, seasonal?).:

Habitat capacity estimate (Has capacity changed in past 20, 50 years?).:
Present habitat protection status.:
Projected habitat protection status (5, 10, 50 years).:
Environmental variance affecting reproduction and mortality (rainfall, prey, predators, disease, snow cover ?).:
Is pedigree information available?:
Attach Life Table if available.
Date form completed:
Correspondent/Investigator:
Name:
Address:
Telephone:
Fax:

References:

Comments:

KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 8
VORTEX DOCUMENTATION

VORTEX:

A Computer Simulation Model for Population Viability Analysis

Robert C. Lacy
Department of Conservation Biology
Chicago Zoological Society, Brookfield, IL 60513 USA

Abstract < 1 page still to be written

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvest, habitat destruction, or competition or predation from invasive introduced alien species. Even if the original causes of decline are removed, however, once a population becomes small and isolated from any other populations of conspecifics additional forces, intrinsic to the dynamics of small populations, come into play and may drive the population to extinction (Clark and Seebeck 1990). Of particular impact on small populations are stochastic, or random probabilistic, processes. With the exception of aging, virtually all events in the life of an organism are stochastic. Mating, reproduction, gene transmission between generations, migration, disease, and predation can be described by probability distributions, with individual occurrences being sampling from these distributions. Because small samples display high variance around the mean or expectation, the fates of small wildlife populations can be determined more by random luck than by adaptation, or mean birth and death rates.

The stochastic processes impacting small populations have been usefully categorised into demographic stochasticity, environmental variation, catastrophic events, and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate, and sex ratio of a population even if the probabilities of birth and death remain constant. Demographic stochasticity would follow binomial distributions and will be important (the frequency of birth and death events and the sex ratio deviating far from the statistical expectation) only in populations that are smaller than a few tens of animals (ref.). Environmental variation is the fluctuation in the probabilities of birth and death that results from inconstancy of the environment. Weather, the prevalence of enzootic disease, the abundances of prey and of predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. Catastrophic variation is the extreme of environmental variation, but for both methodological and heuristic reasons rare catastrophic events can be usefully analysed separately from the environmental variation of more typical yearly or seasonal fluctuations. Catastrophes such as epidemic disease, hurricanes or other severe storms, large-scale fires, and floods are outliers in the distributions of environmental variation (see Fig. 1); they have quantitatively and sometimes qualitatively different impacts on wildlife populations (a forest fire is not just a very hot day); and they are often the cause of the final decline of wildlife populations to extinction. One of two populations of whooping cranes (Grus americana) was decimated by a hurricane in 194? and soon after went extinct. The only remaining population of black-footed ferrets (Mustela nigripes) was in the process of being eliminated by an outbreak of distemper when the last 18 ferrets were captured. [Good Australian example would be useful.]

Genetic drift, the cumulative, non-adaptive fluctuations in allele frequencies resulting from the random sampling of genes each generation, can impede the recovery or accelerate the decline of wildlife populations for several reasons. Inbreeding, not strictly a component of genetic drift but a correlate of it in small populations, has been documented to cause loss of fitness (decreased survival and fecundity, and increased susceptibility to disease and other environmental stresses) in a wide variety of species, including virtually all sexually

reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls et al. 1988; Lacy et al. in press). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation throughout a population that results from inbreeding and genetic drift will reduce the ability of the population to adapt to future changes in the environment (refs.).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals (inbreeding) and the population negatively impact demographic rates and also increase susceptibility to environmental perturbations and catastrophes, exacerbating the effects of these stochastic processes on population stability. Reduced population growth and greater fluctuations in numbers in turn accelerates genetic drift (Crow and Kimura 1970). The synergistic destabilising effects of stochastic process on small populations of wildlife has been described as an "extinction vortex" (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered one definition of a "minimum viable population" (MVP) (Brussard 1985; Seal et al. 1989 **** I need to check this ****; Thomas 1990). The estimation of MVPs or, more generally, the investigation of the probability of extinction of a population constitutes Population Viability Analysis (PVA) (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990).

The study of extinction-recolonisation dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991) all require an understanding of the multiple, interacting forces that contribute to extinction vortices. Because demographic and genetic processes in small populations are inherently unpredictable, the expected fates of wildlife populations will only be describable in terms of probability distributions (of population sizes, times to extinction, and amounts of genetic variation). Because the processes determining the dynamics of small populations are multiple and complex, analytical formulae for describing the probability distributions have been few (e.g., Goodman 1987; Lande 1988; Reed et al. 1988; Burgmann and Gerard 1990), and have incorporated only few of the threatening processes. No analytical model exists, for example, to describe the combined effect of demographic stochasticity and loss of genetic variation on the probability of population persistence.

A few studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g., Belovsky 1987; Griffith et al. 1989; Berger 1990; Thomas 1990), but presently only order of magnitude estimates can be provided for MVPs of vertebrates (Soulé ...), threatened species are by their rarity unavailable and inappropriate for collection of sufficient experimental data to determine MVPs precisely, and it is likely that the function relating extinction probability to population size will differ among species, localities, and times (Lindenmayer et al. in press).

Lacking adequate empirical data or theoretical and analytical models to allow prediction of the dynamics of populations of threatened wildlife species, various biologists have turned to computer simulation techniques for Population Viability Analysis. By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and which cumulatively determine the fates of populations. The focus is usually on detailed and explicit modelling of the specific forces impinging on a given population, place, and time of interest,

rather than on delineation of rules (which may not exist) that would apply generally to most wildlife populations. Computer programs available to PVA include: SPGPC (Grier 1980a, 1980b; Grier and Barclay 1988), GAPPS (Harris et al. 1986), POPDYN (Cox 1988), RAMAS (Ferson 1990 *** Check this ***; Akcakaya and Ferson 1990; Ferson and Akcakaya 1990), FORPOP (Possingham et al. 1991), ALEX (Lindenmayer and Possingham in press), and SIMPOP (Lacy et al. 1989; Lacy and Clark 1990) and its descendant VORTEX.

Lindenmayer et al. (in press) describe generally the use of computer simulation modelling for PVA, and discuss the strengths and weaknesses of the approach as a tool for wildlife management. In this paper, I present the PVA program VORTEX and describe its structure and capabilities. In an accompanying paper, Lindenmayer et al. present a PVA of Leadbeater's Possum (Gymnobelideus leadbeateri) using VORTEX. Previously, VORTEX (or SIMPOP) has been used in PVA to help guide conservation and management of the Puerto Rican Parrot (Amazona vittata) (Lacy et al. 1989), Javan Rhinoceros (Rhinoceros sondaicus) (Seal and Foose 1989), Sumatran Rhinoceros (???), Florida Panther (Felis concolor coryi) (Seal and Lacy 1989), Florida Key Deer (Odocoileus virginianus clavium) (Seal and Lacy 1990), Eastern Barred Bandicoot (Perameles gunnii) (Lacy and Clark 1990; Maguire et al. 1990), Lion Tamarins (Leontopithecus rosalia ssp.) (Ballou et al. 1991), Brush-Tailed Rock Wallaby (Petrogale pencillata pencillata) (Hill 1991), Red Wolf (Canis rufus) (Parker et al. 1991), Mountain Pygmy Possum (Burramys parvus), Leadbeater's Possum, Long-Footed Potoroo (Potorous longipes), Orange-Bellied Parrot (Neophema chrysogaster) and Helmeted Honeyeater (Lichenostomus melanops cassidix) (Clark et al. 1991), Spotted Tree Frog (Litoria Striped Legless Lizard (Delma impar), Red-Tailed Black Cockatoo (Calyptorhynchus magnificus magnificus), Malleefowl (Leipoa ocellata), Brolga (Grus rubicundus), and New Holland Mouse (Pseudomys novaehollandiae) (Backhouse et al. in press), Whooping Crane (Grus americana) (Seal et al. in press, a) Tana River Crested Mangabey () and Tana River Red Colobus () (Seal et al. in press, b), and Black Rhinoceros () (Seal et al. in press, c).

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations. Earlier versions of VORTEX were named SIMPOP, and then VORTICES. Many of the algorithms in VORTEX were drawn from the computer simulation program SPGPC (Grier 1980a, 1980b, Grier and Barclay 1988). VORTEX models population dynamics as discrete, sequential events (e.g births, mortality, catastrophes, carrying capacity truncation) that occur according to defined probabilities. The probabilities of events are modelled as constants or as random variables that follow specified distributions.

VORTEX simulates a population by stepping through the series of events that describe the typical life cycle of a sexually reproducing, diploid organism. The program was written originally to model mammalian and avian populations, but it has been used for modelling some species of reptiles and amphibians and could be used for fish, invertebrates and possibly even plants. VORTEX iterates life events on an annual cycle (although a user could model populations with "years" that are other than 12 months duration). The simulation of the population is then itself iterated to reveal the distribution of fates that the population might experience.

The program models demographic stochasticity by determining the occurrence of probabilistic events (reproduction, litter size, sex determination, death) with a pseudo-random number generator. The probabilities of mortality and reproduction are sex specific and pre-determined for each age class up to the age of breeding, beyond which it is assumed that reproduction and survival probabilities remain constant until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability (0.50 for most species) of an offspring being male. For each life event, if the random value sampled from a specified probability distribution falls above the mean value, the event is deemed to have occurred, thereby simulating a binomial process.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), based on the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value [binomial distributions are discrete and not all values of s are possible; $N = p(1 - p) / s^2$], then conducting N binomial trials (using sampling from the uniform 0-1 distribution) to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing any bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of male breeders might limit reproduction by females. In the polygamous model, only one adult male is required to allow breeding by females. In addition, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

The upper limits for population size within a habitat (the "carrying capacity") must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed during this truncation.

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation each demographic parameter (reproductive success, mortality rates, population carrying capacity) is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions; environmental variation in carrying capacity is modelled as a normal

distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and fluctuations in that mean due to environmental variation.

Data on the annual variation in birth and death rates is important in determining the probability of extinction, as it influences population stability. Unfortunately, this information is rarely available from field data. VORTEX allows a population to be modelled in the absence of any environmental variation, or any plausible range of variation that might be usefully examined. Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is likely to be important in the dynamics of a population. This can guide research priorities and indicate where management actions can ameliorate factors that put a population at risk.

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of that occurrence (i.e. a binomial process is simulated). Following a catastrophic event, the chance of survival and successful breeding for that simulated year is multiplied by a severity factor.

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring created is randomly assigned one of the alleles from each parent. Inbreeding depression which is modelled as a loss of viability during the first year amongst inbred animals.

The impacts of inbreeding on the population are determined by using one of two models available within VORTEX: a Recessive Lethals model and a Heterosis model. In the Recessive Lethals model each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele somewhere in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multi-locus model an individual could be homozygous for several lethal alleles simultaneously. By virtue of the death of individuals that are homozygous for lethal alleles, the lethal alleles would be removed slowly by natural selection during the generations of a simulation. This would reduce the genetic variation present in the population (relative to the case with no inbreeding depression), but would also lessen the subsequent probability that inbred individuals would be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many wildlife species, as the median number of lethal equivalents per diploid genome that is estimated for mammalian populations is approximately three (Ralls et al. 1988).

In the Heterosis model, all homozygotes have reduced fitness compared with heterozygotes. Juvenile survival is modelled according to the logarithmic model developed by Morton *et al.* (1955):

ln(S) = A - BF

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the

absence of inbreeding, and B is a measure of the rate at which survival decreases with inbreeding. B is termed the number of "lethal equivalents" per haploid genome (2B is the number of lethal equivalents per diploid genome), because it estimates (half) the number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due to recessive lethal alleles. A population with the level of inbreeding depression of one lethal equivalent per diploid genome may have one recessive lethal allele per individual (as in the RECESSIVE LETHAL model, above); it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some combination of recessive deleterious alleles which equate in effect with one fully lethal allele per individual.

Inbreeding effects may result not from the expression of fully recessive deleterious alleles in inbred organisms, but rather (or also) because of superior fitness of heterozygotes (heterozygote advantage or "heterosis"). Unlike the situation with fully recessive deleterious alleles, natural selection cannot remove deleterious alleles at heterotic loci, because all alleles are deleterious when homozygous (relative to the heterozygote fitness). Thus the effects of inbreeding are unchanged during the repeated generations of inbreeding.

In addition to simulating the stochastic effects of demographic variation, environmental variation, catastrophes, and genetic drift, VORTEX also can incorporate several deterministic processes. Reproduction can be specified to be density-dependent. The function relating the percent of adult females breeding each year to the total population size is modelled as a fourth-order polynomial (providing a close fit to virtually any plausible density dependence curve). Populations can be supplemented or harvested for any number of years in each simulation. The numbers of additions and removals are specified according to the age and sex of animals. Trends in the carrying capacity can also be modelled in VORTEX. These are specified as an annual percentage change. Thus, a reduction in habitat carrying capacity is incorporated in VORTEX as a linear decrease rather than a geometric decline.

VORTEX can model up to 25 populations, with specification of each pairwise migration rate (probability of an individual moving from one population to another). The probability of an animal migrating between any two populations is independent of the age and sex of the animal. Because of between-population migration and managed supplementation, populations can be recolonised.

In summary, VORTEX is able to simulate many of the processes which influence the size, behaviour and viability of a population. The program tracks the fate of populations and the output contains a summary of: (1) the probability of the extinction during at each specified interval (e.g. every 10 years during a 100 year simulation), (2) the median time to extinction (if at least 50% of the population went extinct in at least 50% of the simulations), (3) the mean time to extinction of those simulated populations that became extinct, and, (4) the mean size of, and genetic variation within, extant populations. Standard deviations across simulations and standard errors of the mean are reported for the probability of extinction [given by $SE(p) = p \times [1-p]/(\sqrt{n})$, in which the frequency of extinction was p over n simulated populations], population size, and the measures of genetic variation. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Input can be either from the keyboard or from an input file. In the case of keyboard data entry, an input file with the entered values is created for possible modification and later

use. An example of the output from VORTEX is given in Appendix 1.

VORTEX is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc., Lombard, Illinois, U.S.A.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. The program calls many functions specific to the Lattice compiler, but most have direct counterparts in the function libraries provided with other popular C compilers. Copies of the compiled program, the source code, and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, MN 55124, USA. The programs have been tested by a variety of workers, but the program cannot be guaranteed to be without errors. Each user retains the responsibility for the assuring that the program does what is intended.

Sequence of Program Flow

- (1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century (Lattice function).
- (2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of iterations. (See sample output, Appendix 1).
- (3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

 $N_{max} = (K + 3s) \times (1 + L)$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max} . If this occurs then the program will give an error message and abort.

- (4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it been adjusted downward because of limiting memory often will not hamper the analyses. Except for limitations imposed by the size of the computer memory (VORTEX can use extended memory, if available), the only limit to the size of the analysis is that no more than 25 populations exchanging migrants can be simulated.
- (5) Expected mean growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow standard cohort life-table analyses (ref). Generation time and the expected stable age distribution are also estimated. The life-table estimations assume no limitation by carrying capacity, no limitation of mates, and no loss of fitness due to inbreeding depression, and the estimate of growth rate assumes that the population has already reached the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the mean values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

- (6) Iterative simulation of the population proceeds via steps 7 through 26 below. For exploratory modelling, 100 iterations is usually sufficient to reveal gross trends among sets of simulations with different input parameters. For more precise examination of population behaviour under various scenarios, 1000 or more simulations should be used to minimise standard errors around mean results.
- (7) The starting population is assigned an age and sex structure. The user can specific the exact age-sex structure of the starting population, or can specify a total initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed all to be unrelated. Thus, inbreeding can occur in second and later generations.
- (8) Two unique alleles at a hypothetical genetic locus are assigned to each individual in the starting population. The simulation therefore uses an infinite alleles model of genetic variation, with each immigrant individual (due to supplementation of the population by management) bringing in two new alleles. The subsequent fate of genetic variation is tracked by reporting the number of extant alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by $H_e = 1 \Sigma(p_{12})$, in which p_1 is the frequency (proportion) of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has a heterozygosity of 1.0 at the hypothetical locus, only inbred animals can become homozygous, and the probability that an individual is homozygous is equal to the inbreeding coefficient of that individual.
- (9) The user specifies one of three options for modelling the effect of inbreeding: (a) no effect of inbreeding on fitness, i.e. all alleles are selectively neutral, (b) each founder individual has one unique lethal and one unique non-lethal allele (Recessive Lethals option), or (c) first-year survival of each individual is exponentially related to its inbreeding coefficient (Heterosis option). The first case is clearly an optimistic one, as almost all diploid populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977, Falconer 1981). Each of the two methods of modelling inbreeding depression are perhaps still optimistic, in that inbreeding is assumed to impact only first-year survival. The third option allows, however, for the user to specify the severity of inbreeding depression in juvenile survival.
 - (10) The years of the simulation are iterated via steps 11 through 25 below.
- (11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).
- (12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions (for birth and death rates) or a normal distribution (for carrying capacity), with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variation in reproduction and

mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, the new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) for the year is determined by first incrementing or decrementing the base (year 1) carrying capacity by the amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with appropriate mean and standard deviation.

- (13) Birth rates and survival rates for the year are adjusted to model catastrophes (if any are determined to have occurred in that year of the simulation).
- (14) Breeding males are selected for the year. For each male of breeding age, the male is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding age males specified to be breeding.
- (15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.
- (16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal A, and another existing animal, B, is $\mathbf{r}_{AB} = 0.5 * (\mathbf{r}_{MB} + \mathbf{r}_{PB})$ in which \mathbf{r}_{U} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $\mathbf{F} = \mathbf{r}_{MP}$, and the relationship of an animal to itself is $\mathbf{r}_{AA} = 0.5 * (1 + F)$. (See Ballou 1984 for a detailed description of this method for calculating inbreeding coefficients.)
- (17) The survival or death of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the HETEROSIS model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome. If the RECESSIVE LETHALS model is used, all offspring that are homozygous for the lethal allele (half of all founder alleles are recessive lethals) are killed.
- (18) The age of each animal is incremented by 1, and any animal exceeding the maximum age is killed.
- (19) If more than one population is being modelled, migration among populations is occurs stochastically with specified probabilities.
- (20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and killed. If the number to be harvested do not exist for any age-sex class, the program continues (without completing the harvest) but reports that the harvest was incomplete.

- (21) Dead animals are removed from the computer memory to make space for future generations.
- (22) If population supplementation is to occur in a particular year, new individuals of the specified age-class are created. Each immigrant is assigned two unique alleles, one of which will be a recessive lethal in the RECESSIVE LETHALS model, and each immigrant is assumed to be genetically unrelated to all other individuals in the population.
- (23) The population growth rate is calculated as the ratio of the population size in the previous year to the current size.
- (24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to (N K)/N, so that the expected population size after the additional mortality is K.
- (25) Summary statistics on population size and genetic variation are tallied and reported. A simulated population is determined to be extinct if either sex has no representatives.
 - (26) Final population size and genetic variation are determined for the simulation.
- (27) Summary statistics on population size, genetic variation, probability of extinction and mean population growth rate are calculated across iterations and output.

Assumptions underpinning VORTEX

It is impossible to simulate the complete range of complex processes and dynamics typical of a wild populations. As a result there are necessarily a range of mathematical and biological assumptions which underpin any PVA program. Some of the more important assumptions in VORTEX include:

- (1) Survival probabilities are density independent when the population size is less then carrying capacity. Additional mortality imposed when the population exceeds K affects all age and sex classes equally.
- (2) The relationship between changes in population size and genetic variability are examined for only one locus. Thus, potentially complex interactions between genes located on the same chromosome are ignored. Such interactions (e.g., linkage disequilibrium) are typically associated with genetic drift in very small populations, but it is unknown if, or how, they would affect population viability.
- (3) All animals of reproductive age have an equal probability of breeding. This ignores the likelihood that some animals within a population will have a greater probability of breeding successfully, and breeding more often, than other individuals. If breeding is not at random among those in the breeding pool, then decay of genetic variation and the consequent inbreeding will occur more rapidly than in the model, perhaps further destabilising the population.
- (4) The life-history attributes of a population (birth, death, harvesting, supplementation etc) are modelled as a sequence of discrete and therefore seasonal events. However, such events are typically continuous through time and the model therefore ignores the possibility that they may be aseasonal or only partly seasonal.

- (5) The genetic effects of inbreeding on a population are determined in VORTEX using one of two possible models: the Recessive Lethals model and the Heterosis model. Both models have attributes likely to be typical of some populations but these will vary between species (Brewer et al. 1990). Given this, it is probable that the impacts of inbreeding will fall between the effects of these two models. Inbreeding is assumed to depress only one component of fitness, first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased disease susceptibility or decreased ability to adapt to environmental change are not modelled.
- (6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity. This assumes that animals continue to breed until they die.
- (7) A simulated catastrophe will have an effect on a population only in the year that the event occurs.
 - (8) Migration rates among populations are independent of age and sex.
- (9) Complex, inter-species interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator-prey interactions cannot be modelled by VORTEX.

Discussion

Uses and Abuses of Simulation Modelling for PVA

Computer simulation modelling is a tool that can allow crude estimation of the probability of population extinction, and the mean population size and amount of genetic diversity, from data on diverse interacting processes that are too complex to be integrated intuitively (mental models) and for which no analytic solutions presently, or are likely to soon, exist. The technique focusses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest, and can only be as good as the data and the assumptions fed into the model (Lindenmayer et al. in press). Yet the use of even simplified computer models for PVA will provide more accurate predictions about population dynamics than the even more crude techniques available previously, such as calculation of expected population growth rates from life tables. For the purpose of estimating extinction probabilities, methods that assess only deterministic factors are almost certain to be inappropriate, because populations near extinction will commonly be so small that random processes predominate over deterministic ones. The suggestions by Mace and Lande (1991) that population viability be assessed by the application of simple rules (e.g., a taxon be considered Endangered if the total genetically effective population size is below 50 or the total census size below 250) should be followed only if knowledge is insufficient to allow more accurate quantitative analysis. Moreover, such preliminary judgements, while often important in stimulating appropriate corrective measures, should signal, not obviate, the need for more extensive investigation and analysis of population processes, trends, and threats.

At least a handful of good population simulation models are available for PVA (see Introduction). They differ in capabilities, assumptions, and ease of application; ease of application being related to the number of simplifying assumptions and inversely related to the flexibility and power of the model. It is unlikely that a single or even a few simulation models will be appropriate for all PVAs. The VORTEX program has some capabilities not found in many other population simulation programs, but is not as flexible as are a few others (e.g., GAPPS: Harris et al. 1986). VORTEX is user-friendly enough to be used by those with relatively little understanding of population biology and extinction processes. This is both an advantage and a disadvantage.

VORTEX, like most other models in use, was designed to represent the life history typical of many larger vertebrates (primarily reptiles, mammals, and birds), with slow reproduction and long lifespans. Although it could and has been used for highly fecund vertebrates and invertebrates, it is awkward to use in such cases (e.g., it requires complete specification of the percent of females producing each possible clutch size), and computer memory limitations often hamper analyses. Unfortunately, it is just such taxa that are the most effected by stochastic processes, show the greatest fluctuations in population numbers, and likely have the greatest minimum viable population sizes.

Because many of the processes being simulated are stochastic, a PVA can never specify what will happen to a population. Rather, PVA can provide estimates of probability distributions describing possible fates of a population. The ultimate fate of a given population may happen to fall at the extreme tail of such a distribution, even if the processes and

probabilities are assessed precisely. Therefore, it will be often be impossible to empirically test the accuracy of PVA results by monitoring of one or a few threatened populations of interest. (Presumably, if even a single population followed a course that was well outside of the range of possibilities predicted by a model, that model could be rejected as inadequate. Often, however, the range of plausible fates generated by PVA is quite broad.)

Simulation programs can be checked for internal consistency (e.g., does the simulation model predict the same average long-term growth rate, in the absence of inbreeding depression and other confounding effects, as does a life table calculation? [VORTEX does.]). Beyond this, some confidence in the accuracy of a simulation model can be obtained by comparing observed fluctuations in population numbers to those generated by the model, thereby comparing a data set consisting of perhaps tens to hundreds of data points to model results. For example, from 1938 through 1991, the wild population of whooping cranes had grown at a mean (geometric) rate of 4.1%, with annual fluctuations in the growth rate of SD = 13.8% (Seal et al. in press). Life table analyses of the whooping crane predict a mean population growth rate of 4.9%. Simulations using VORTEX predicted a mean population growth rate of 4.6% into the future, but just 3.1% annual growth, with an SD of 11.2%, if the simulations were started with the 18 cranes present in 1938 rather than the 146 cranes in 1991. (The lower predicted growth rate when started from a smaller size reflects the effects of inbreeding and perhaps imbalanced sex ratios among breeders in the simulation, factors that are not considered in the life table calculations.) The closeness of the observed mean population growth rate to the rates in the simulated populations lends support for the accuracy of the estimated birth and death parameters. The simulation model, when started with 18 individuals, slightly under-predicted the mean growth rate and final population size after 52 years (108 + 91 SD), but the observed final size of the population (146 at the beginning of 1991) was well within the range observed among simulations. The model also slightly underpredicted the annual fluctuations in population growth (11.2% vs. 13.8% SD). This may reflect a lack of full incorporation of all aspects of stochasticity into the model (e.g., the observed rate of catastrophe years, 14%, was greater than the modelled rate, 10%), or may simply reflect the sampling error inherent in stochastic phenomena. Because the data fed into the model necessarily derive from analysis of past trends, however, such retrospective analysis should be viewed as little more than a check of consistency. As another confirmation of consistency, both deterministic calculations and the simulation model project an overwintering population consisting of 12% juveniles (less than 1 year old), while the observed frequency of juveniles at the wintering grounds in Texas has averaged 13%.

Convincing evidence of the accuracy, precision, and usefulness of PVA simulation models would require the comparison of the distribution of fates of many replicate populations to model predictions. Such a test probably cannot be conducted on any endangered species, but could and should be examined in experimental non-endangered populations.

Directions for Future Development of PVA Models

Continuous time models
Better handling of r-selected life histories
Cross-validation of programs
Other?

Appendix 1 - Sample output from VORTEX.

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C:\LACY>vortex
 Welcome to VORTEX
 Written by R.C. Lacy
     Department of Conservation Biology
     Chicago Zoological Park
     Brookfield, IL 60513
 Version 4.1, 20 August 1991
 Input file name? (CR for keyboard)
 Output file name? (S for screen)
 PARROT
 Do you want data files produced for plotting? N
 Do you want the full table printed (first five runs only)? N
 How many times do you want the simulation repeated? 20
 How many years do you want the simulation to run? 100
 At what time interval do you want extinction reports? 10
How many populations do you want to model? 2
Enter migration rates from Population 1 to ...
  Population 2: .01
 Enter migration rates from Population 2 to ...
  Population 1: .005
Do you want EV(reproduction) to be correlated with EV(survival)? N
How many types of catastrophes do you want to model? 2
Do you want to incorporate inbreeding depression? Y
You can choose either a general HETEROSIS model, in which selection
    against homozygotes does not remove the genetic load, but which allows
    for user-defined number of lethal equivalents, or a
    RECESSIVE LETHALS model in which each founder starts with
    one unique, recessive lethal allele (and a unique, dominant non-lethal),
    and in which selection against homozygotes for the lethal alleles
    removes those alleles from the population.
Do you want a general HETEROSIS model (specify H) or a
    RECESSIVE LETHALS model (specify L)? H
How many lethal equivalents per diploid genome in the population? 3.2
-Monogamous (M) or polygynous (P) breeding? M
At what age do females normally begin breeding? 4
At what age do males normally begin breeding? 4
What is the maximum age, beyond which all animals die? 30
```

```
What is the sex ratio (proportion males) at birth? 0.5
What is the maximum number of young per litter? 2
Input parameters for population 1:
Is reproductive success density dependent? N
In an average year ...
  what percent of adult females produce 0 young? 60
  what percent of adult females produce 1 young? 35
  what percent of adult females produce 2 young? 5
You have specified that 40.00 percent of adult females produce young
  in an average year
What is the SD in this percent females of producing litters due to EV? 10
What is the percent mortality of females between ages 0 to 1? 50
    What is the SD in the above mortality due to EV? 10
What is the percent mortality of females between ages 1 to 2? 10
    What is the SD in the above mortality due to EV? 3
What is the percent mortality of females between ages 2 to 3? 5
    What is the SD in the above mortality due to EV? 2
What is the percent mortality of females between ages 3 to 4? 5
    What is the SD in the above mortality due to EV? 2
What is the annual percent mortality of adult females (4 <= age <= 30)? 2
    What is the SD in the above mortality due to EV? 1
What is the percent mortality of males between ages 0 to 1? 50
    What is the SD in the above mortality due to EV? 10
What is the percent mortality of males between ages 1 to 2? 10
   What is the SD in the above mortality due to EV? 3
What is the percent mortality of males between ages 2 to 3? 5
   What is the SD in the above mortality due to EV? 2
What is the percent mortality of males between ages 3 to 4? 5
   What is the SD in the above mortality due to EV? 2
What is the annual percent mortality of adult males (4 <= age <= 30)? 2
   What is the SD in the above mortality due to EV? 1
```

```
Enter the probability of catastrophe type 1 (as a percent): 10
Enter the severity of type 1 catastrophes as a multiplicative effect.
Note: 0 = total catastrophe, 1 = no effect.
    Severity with respect to reproduction? 0.8
    Severity with respect to survival? 0.9
Enter the probability of catastrophe type 2 (as a percent): 3
Enter the severity of type 2 catastrophes as a multiplicative effect.
Note: 0 = total catastrophe, 1 = no effect.
    Severity with respect to reproduction? 0
    Severity with respect to survival? 0.5
Are all adult males in the breeding pool? N
What percent of the adult males in the breeding pool? 70
Do you want the starting population to reflect the stable age distribution? Y
How many animals are in the initial population? 80
What is the carrying capacity of population 1? 250
    What is the SD in K due to EV? 0
Is there a trend projected in the carrying capacity? (Y or N) Y
Over how many years is the carrying capacity expected to change? 20
What percent annual increase (positive) or decrease (negative) is projected? -1
Do you want to harvest the population 1? N
Do you want to supplement population 1? N
Input parameters for population 2:
Is reproductive success density dependent? N
In an average year ...
  what percent of adult females produce 0 young? 50
  what percent of adult females produce 1 young? 40
  what percent of adult females produce 2 young? 10
You have specified that 50.00 percent of adult females produce young
  in an average year
What is the SD in this percent females of producing litters due to EV? 10
What is the percent mortality of females between ages 0 to 1? 40
```

```
What is the SD in the above mortality due to EV? 10
What is the percent mortality of females between ages 1 to 2? 10
    What is the SD in the above mortality due to EV? 5
What is the percent mortality of females between ages 2 to 3? 5
    What is the SD in the above mortality due to EV? 3
What is the percent mortality of females between ages 3 to 4? 5
    What is the SD in the above mortality due to EV? 3
What is the annual percent mortality of adult females (4 <= age <= 30)? 5
    What is the SD in the above mortality due to EV? 3
What is the percent mortality of males between ages 0 to 1? 50
    What is the SD in the above mortality due to EV? 10
What is the percent mortality of males between ages 1 to 2? 10
    What is the SD in the above mortality due to EV? 3
What is the percent mortality of males between ages 2 to 3? 5
    What is the SD in the above mortality due to EV? 2
What is the percent mortality of males between ages 3 to 4? 5
    What is the SD in the above mortality due to EV? 2
What is the annual percent mortality of adult males (4 <= age <= 30)? 5
    What is the SD in the above mortality due to EV? 2
Enter the probability of catastrophe type 1 (as a percent): 10
Enter the severity of type 1 catastrophes as a multiplicative effect.
Note: 0 = total catastrophe, 1 = no effect.
    Severity with respect to reproduction? 0.7
   Severity with respect to survival? 0.9
Enter the probability of catastrophe type 2 (as a percent): 3
Enter the severity of type 2 catastrophes as a multiplicative effect.
Note: 0 = total catastrophe, 1 = no effect.
   Severity with respect to reproduction? 0
   Severity with respect to survival? 0.5
Are all adult males in the breeding pool? Y
```

```
Do you want the starting population to reflect the stable age distribution? Y
How many animals are in the initial population? 25
What is the carrying capacity of population 2? 125
   What is the SD in K due to EV? 0
Is there a trend projected in the carrying capacity? (Y or N) Y
Over how many years is the carrying capacity expected to change? 20
What percent annual increase (positive) or decrease (negative) is projected? +1
Do you want to harvest the population 2? N
Do you want to supplement population 2? N
Warning: Memory may be insufficient to do heterosis calculations
PARROT: Run 1 .....
      Population 1 extinction at year 67.....
   Population 2: Final size 4
   Meta-population: Final size 4
PARROT: Run 2 ......
      Population 1 extinction at year 78.....
      Population 1 recolonized at year 84.....
   Population 1: Final size 2
   Population 2: Final size 42
   Meta-population: Final size 44
PARROT: Run 3 .....
      Population 2 extinction at year 50.....
      Population 2 recolonized at year 55..
      Population 2 re-extinction at year 56....
      Population 2 recolonized at year 59......
      Population 2 re-extinction at year 67......
      Population 2 recolonized at year 76.....
      Population 2 re-extinction at year 91.....
   Population 1: Final size 16
   Meta-population: Final size 17
PARROT: Run 4 .....
      Population 2 extinction at year 33.....
      Population 1 extinction at year 74.
      Meta-population extinction at year 74...............
Population 2 extinction at year 86.....
      Population 1 extinction at year 91.....
      Meta-population extinction at year 95.....
PARROT: Run 6 ......
   Population 1: Final size 9
   Population 2: Final size 47
   Meta-population: Final size 56
PARROT: Run 7 .....
      Population 2 extinction at year 81......
      Population 1 extinction at year 88.
      Meta-population extinction at year 88.....
PARROT: Run 8 .....
   Population 1: Final size 43
   Population 2: Final size 34
   Meta-population: Final size 77
```

	C.1
PARROT: Run 9	
Population 2 extinction at year 94	П
Population 1: Final size 5 Meta-population: Final size 7	11
PARROT: Run 10	
Population 2 extinction at year 53	
Population 1 extinction at year 79.	11
Meta-population extinction at year 79	7.3
PARROT: Run 11	
Population 1 extinction at year 94	П
Population 2: Final size 50	1.)
Meta-population: Final size 51	
PARROT: Run 12	
Population 2 extinction at year 66	
Population 1 extinction at year 77	1.2
Meta-population extinction at year 80	Π
PARROT: Run 13	11
Population 1 extinction at year 96	
Population 2 extinction at year 97	
Meta-population: Final size 4	1.7
PARROT: Run 14	2.7
Population 1: Final size 31	
Population 2: Final size 48	
Meta-population: Final size 79	15
PARROT: Run 15	- 1
Population 1 extinction at year 87	
Population 1 recolonized at year 92	11
Population 1: Final size 2	1.1
Population 2: Final size 3	
Meta-population: Final size 5	
PARROT: Run 16	
Population 1: Final size 10	
Population 2: Final size 24	
Meta-population: Final size 34	1
PARROT: Run 17	7 7
Population 1 extinction at year 30	
Population 2: Final size 4	
Meta-population: Final size 4	11
PARROT: Run 18	
Population 1: Final size 27	
Population 2: Final size 23	11
Meta-population: Final size 50	5 1
PARROT: Run 19	
Population 1: Final size 58	
Population 2: Final size 24	11
Meta-population: Final size 82	
PARROT: Run 20	
Population 1 extinction at year 47	11
Population 1 recolonized at year 54	F. J.
Population 1 re-extinction at year 57	_
Population 1 recolonized at year 65	П
Population 1 re-extinction at year 79	
Population 2 extinction at year 85.	
Meta-population extinction at year 85	T1
Do you want to run another simulation? N	11
	1 1
C:\LACY>	
	-1

VORTEX -- simulation of genetic and demographic stochasticity PARROT Fri Nov 08 10:44:53 1991 2 population(s) simulated for 100 years, 20 runs Migration matrix: 1 0.9900 0.0100 2 0.0050 0.9950 HETEROSIS model of inbreeding depression with 3.20 lethal equivalents per diploid genome First age of reproduction for females: 4 Age of senescence (death): 30 Sex ratio at birth (proportion males): 0.5000 Population 1: Reproduction is assumed to be density independent. 60.00 (EV = 10.00 SD) percent of adult females produce litters of size 0 35.00 percent of adult females produce litters of size 1 5.00 percent of adult females produce litters of size 2 50.00 (EV = 10.00 SD) percent mortality of females between ages 0 and 1 10.00 (EV = 3.00 SD) percent mortality of females between ages 5.00 (EV = 2.00 SD) percent mortality of females between ages 2 and 3 5.00 (EV = 2.00 SD) percent mortality of females between ages 3 and 4 2.00 (EV = 1.00 SD) percent annual mortality of adult females $(4 \le age \le 30)$ 50.00 (EV = 10.00 SD) percent mortality of males between ages 0 and 1 10.00 (EV = 3.00 SD) percent mortality of males between ages 1 and 2 5.00 (EV = 2.00 SD) percent mortality of males between ages 2 and 3 5.00 (EV = 2.00 SD) percent mortality of males between ages 3 and 4 2.00 (EV = 1.00 SD) percent annual mortality of adult males $(4 \le age \le 30)$ EVs may have been adjusted to closest values possible for

EV in mortality will be correlated among age-sex classes

but independent from EV in reproduction.

binomial distribution.

Frequency of type 1 catastrophes: 10.000 percent with 0.800 multiplicative effect on reproduction and 0.900 multiplicative effect on survival

Frequency of type 2 catastrophes: 3.000 percent with 0.000 multiplicative effect on reproduction and 0.500 multiplicative effect on survival

Monogamous mating; 70.00 percent of adult males in the breeding pool.

Initial size of Population 1:

Females

(set to reflect stable age distribution) Age 1 Total Males

Carrying capacity = 250 (EV = 0.00 SD) with a 1.000 percent decrease for 20 years.

Deterministic population growth rate (based on females, with assumptions of

no limitation of mates and no inbreeding depression):

r = 0.016lambda = 1.016R0 =1.251 Generation time for: females = 13.87 males = 13.87

Stable age distribution:	Age class	females	males
beable age albertbacton.	-		
	0	0.072	0.072
	1	0.035	0.035
	2	0.030	0.030
	3	0.027	0.027
	4	0.025	0.025
	5	0.023	0.023
	6	0.022	0.022
	7	0.021	0.021
	8	0.019	0.019
	9	0.018	0.018
	10	0.017	0.017
	11	0.016	0.016
	12	0.015	0.015
	13	0.014	0.014
	14	0.013	0.013
	15	0.013	0.013
	16	0.012	0.012
	17	0.011	0.011
	18	0.010	0.010
	19	0.010	0.010

20	0.009	0.009
21	0.009	0.009
22	0.008	0.008
23	0.008	0.008
24	0.007	0.007
25	0.007	0.007
26	0.006	0.006
27	0.006	0.006
28	0.006	0.006
29	0.005	0.005
30	0.005	0.005

Ratio of adult (>= 4) males to adult (>= 4) females: 1.000

Population 2:

Reproduction is assumed to be density independent.

50.00 (EV = 10.00 SD) percent of adult females produce litters of size 0

40.00 percent of adult females produce litters of size 1 10.00 percent of adult females produce litters of size 2

40.00 (EV = 10.00 SD) percent mortality of females between ages 0 and 1

10.00 (EV = 5.00 SD) percent mortality of females between ages 1 and 2

5.00 (EV = 3.00 SD) percent mortality of females between ages 2 and 3

5.00 (EV = 3.00 SD) percent mortality of females between ages 3 and 4

5.00 (EV = 3.00 SD) percent annual mortality of adult females (4 <= age <= 30)

50.00 (EV = 10.00 SD) percent mortality of males between ages 0 and 1

10.00 (EV = 3.00 SD) percent mortality of males between ages 1 and 2

5.00 (EV = 2.00 SD) percent mortality of males between ages 2

5.00 (EV = 2.00 SD) percent mortality of males between ages 3 and 4

5.00 (EV = 2.00 SD) percent annual mortality of adult males (4 \leq age \leq 30)

EVs may have been adjusted to closest values possible for binomial distribution.

EV in mortality will be correlated among age-sex classes but independent from EV in reproduction.

Frequency of type 1 catastrophes: 10.000 percent with 0.700 multiplicative effect on reproduction and 0.900 multiplicative effect on survival

Frequency of type 2 catastrophes: 3.000 percent with 0.000 multiplicative effect on reproduction and 0.500 multiplicative effect on survival Monogamous mating; all adult males in the breeding pool.

Initial size of Population 2:

(set to reflect stable age distribution) Age 1 Total 11 Males Females

Carrying capacity = 125 (EV = 0.00 SD) with a 1.000 percent increase for 20 years.

Deterministic population growth rate (based on females, with assumptions of

no limitation of mates and no inbreeding depression):

r = 0.033 lambda = 1.033 R0 = 1.475 Generation time for: females = 11.89 males = 11.89

15	Stable age distribution	0 1 2 3 4 5 6 7 8 9 10 11 12 13	females 0.089 0.051 0.043 0.038 0.035 0.031 0.028 0.025 0.022 0.020 0.018 0.016 0.014 0.013 0.012	males 0.089 0.042 0.036 0.032 0.029 0.026 0.023 0.021 0.019 0.017 0.015 0.013 0.012 0.011
10				
11 0.016 0.013 12 0.014 0.012 13 0.013 0.011 14 0.012 0.010 15 0.010 0.009 16 0.009 0.008 17 0.008 0.007 18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004				
12 0.014 0.012 13 0.013 0.011 14 0.012 0.010 15 0.010 0.009 16 0.009 0.008 17 0.008 0.007 18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004				
13				
14 0.012 0.010 15 0.010 0.009 16 0.009 0.008 17 0.008 0.007 18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004		12	0.014	
15 0.010 0.009 16 0.009 0.008 17 0.008 0.007 18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004		13	0.013	0.011
16 0.009 0.008 17 0.008 0.007 18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004		14	0.012	0.010
17 0.008 0.007 18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004		15	0.010	0.009
18 0.007 0.006 19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004		16	0.009	0.008
19 0.007 0.006 20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004			0.008	
20 0.006 0.005 21 0.005 0.004 22 0.005 0.004 23 0.004 0.004				
21 0.005 0.004 22 0.005 0.004 23 0.004 0.004		19		
22 0.005 0.004 23 0.004 0.004				
23 0.004 0.004				
24 0.004 0.003				
		24	0.004	0.003

```
0.003
                                            0.003
                                 26
                                                        0.002
                                            0.003
                                 27
                                            0.003
                                                        0.002
                                 28
                                            0.002
                                                        0.002
                                 29
                                            0.002
                                                        0.002
                                 30
Ratio of adult (>= 4) males to adult (>= 4) females: 0.833
Population1
                          0, P[E] = 0.000
     N[Extinct] =
     N[Surviving] = 20, P[S] = 1.000
     Population size =
                                                 4.78 SE,
                                                              21.38 SD)
                                      69.30 (
     Expected heterozygosity = Observed heterozygosity = Number of extant alleles =
                                                0.001 SE,
                                                              0.004 SD)
                                      0.986 (
                                                0.000 SE,
                                                              0.000 SD)
                                      1.000 (
                                                 4.81 SE,
                                                              21.49 SD)
                                      90.10 (
     N[Extinct] =
                          0, P[E] = 0.000
     N[Surviving] =
                          20, P[S] = 1.000
     Population size =
                                      62.35 (
                                                 6.37 SE,
                                                              28.47 SD)
     Expected heterozygosity = Observed heterozygosity = Number of extant alleles =
                                      0.972 (
                                                0.004 SE,
                                                              0.020 SD)
                                                0.004 SE,
                                                              0.019 SD)
                                      0.992 (
                                      62.35 (
                                                 5.55 SE,
                                                              24.81 SD)
     N[Extinct] =
                          1, P[E] = 0.050
     N[Surviving] =
                          19, P[S] = 0.950
                                                              28.82 SD)
     Population size =
                                                 6.61 SE,
                                      54.00 (
     Observed heterozygosity = Number of extert
                                      0.955 (
                                                0.008 SE,
                                                              0.036 SD)
                                      0.987 (
                                                0.009 SE,
                                                              0.038 SD)
     Number of extant alleles =
                                      44.89 (
                                                 4.39 SE,
                                                              19.15 SD)
     N[Extinct] =
                          1, P[E] = 0.050
     N[Surviving] =
                         19, P[S] = 0.950
     Population size =
                                      41.11 (
                                                 8.39 SE,
                                                              36.58 SD)
     Expected heterozygosity = 0.930 (
Observed heterozygosity = 0.965 (
                                                0.016 SE,
                                                              0.068 SD)
                                                0.017 SE,
                                                              0.075 SD)
     Number of extant alleles =
                                      30.05 (
                                                 3.48 SE,
                                                              15.15 SD)
     N[Extinct] =
                          2, P[E] = 0.100
     N[Surviving] =
                         18, P[S] = 0.900
     Population size =
                                                 8.92 SE,
                                                              37.86 SD)
                                      38.50 (
     Expected heterozygosity = 0.912 (
Observed heterozygosity = 0.962 (
                                                0.019 SE,
                                                              0.079 SD)
                                                0.017 SE,
                                                              0.071 SD)
     Number of extant alleles =
                                      24.44 (
                                                 3.50 SE,
                                                              14.85 SD)
     N[Extinct] = 2, P[E] = 0.100
```

0.003

0.003

25

Year 10

Year 20

Year 30

Year 40

Year 50

Year 60

```
N[Surviving] =
                        18, P[S] = 0.900
     Population size =
                                   35.39 (
                                             8.62 SE,
                                                        36.55 SD)
     Expected heterozygosity =
                                            0.037 SE,
                                   0.872 (
                                                        0.157 SD)
     Observed heterozygosity =
                                   0.933 (
                                            0.037 SE,
                                                        0.155 SD)
     Number of extant alleles =
                                   20.50 (
                                             3.32 SE,
                                                        14.10 SD)
Year 70
     N[Extinct] =
                       2, P[E] = 0.100
     N[Surviving] = 18, P[S] = 0.900
     Population size =
                                   23.78 (
                                             5.88 SE,
                                                        24.96 SD)
     Expected heterozygosity =
                                   0.846 (
                                            0.034 SE,
                                                        0.142 SD)
     Observed heterozygosity =
                                   0.941 (
                                                        0.122 SD)
                                            0.029 SE,
     Number of extant alleles =
                                   16.39 (
                                             2.89 SE,
                                                        12.28 SD)
Year 80
                        7, P[E] = 0.350
     N[Extinct] =
     N[Surviving] =
                       13, P[S] = 0.650
     Population size =
                                   31.08 (
                                             7.85 SE,
                                                        28.31 SD)
     Expected heterozygosity =
                                   0.874 (
                                            0.023 SE,
                                                        0.082 SD)
     Observed heterozygosity =
                                   0.920
                                         (
                                            0.023 SE,
                                                        0.082 SD)
     Number of extant alleles =
                                  17.54 (
                                             3.38 SE,
                                                        12.18 SD)
Year 90
     N[Extinct] =
                       8, P[E] = 0.400
     N[Surviving] =
                       12, P[S] = 0.600
     Population size =
                                  24.42 (
                                             7.06 SE,
                                                        24.45 SD)
     Expected heterozygosity =
                                  0.855 (
                                            0.023 SE,
                                                        0.079 SD)
     Observed heterozygosity =
                                  0.885
                                            0.034 SE,
                                                        0.119 SD)
     Number of extant alleles =
                                                        10.07 SD)
                                  14.42 (
                                             2.91 SE,
Year 100
     N[Extinct] =
                       10, P[E] = 0.500
                       10, P[S] = 0.500
     N[Surviving] =
     Population size =
                                  20.30 (
                                             6.01 SE,
                                                        19.01 SD)
     Expected heterozygosity =
                                  0.753 (
                                            0.087 SE,
                                                        0.276 SD)
     Observed heterozygosity =
                                            0.096 SE,
                                  0.845
                                                        0.305 SD)
     Number of extant alleles =
                                  11.60 (
                                             2.85 SE,
                                                        9.01 SD)
In 20 simulations of 100 years of Population1:
  10 went extinct and 10 survived.
This gives a probability of extinction of 0.5000 (0.1118 SE),
  or a probability of success of
                                          0.5000 (0.1118 SE).
12 simulations went extinct at least once.
Median time to first extinction was 91 years.
Of those going extinct,
    mean time to first extinction was 75.67 years (5.69 SE, 19.70
SD).
4 recolonizations occurred.
```

Mean time to recolonization was 6.50 years (0.65 SE, 1.29 SD).

```
2 re-extinctions occurred.
Mean time to re-extinction was 8.50 years (5.50 SE, 7.78 SD).
Mean final population for successful cases was 20.30 (6.01 SE,
19.01 SD)
                                     Total
                       3
                           Adults
   Age 1
                                     10.30
                                           Males
    0.50
            0.70
                    0.20
                            8.90
                            8.70
                                     10.00
                                           Females
    0.60
            0.30
                    0.40
Without harvest/supplementation, prior to carrying capacity
truncation,
  mean lambda was 0.9796 (0.0032 SE, 0.1332 SD)
Final expected heterozygosity was
                                      0.7531 ( 0.0874 SE,
0.2763 SD)
Final observed heterozygosity was
                                      0.8449 ( 0.0965 SE,
0.3051 SD)
Final number of alleles was
                                       11.60 (
                                                 2.85 SE,
9.01 SD)
*************************
*****
Population2
Year 10
     N[Extinct] =
                       0, P[E] = 0.000
     N[Surviving] =
                       20, P[S] = 1.000
     Population size =
                                 35.10 (
                                           3.56 SE,
                                                      15.91 SD)
     Expected heterozygosity =
                                          0.005 SE,
                                 0.960 (
                                                      0.022 SD)
     Observed heterozygosity =
                                 1.000 (
                                          0.000 SE,
                                                      0.000 SD)
     Number of extant alleles =
                                 37.70 (
                                           2.59 SE,
                                                      11.57 SD)
Year 20
     N[Extinct] =
                       0, P[E] = 0.000
                      20, P[S] = 1.000
     N[Surviving] =
     Population size =
                                 43.60 (
                                           6.03 SE,
                                                      26.98 SD)
     Expected heterozygosity =
                               0.947 (
                                          0.007 SE,
                                                     0.029 SD)
     Observed heterozygosity = 0.987 (
                                          0.008 SE,
                                                      0.035 SD)
     Number of extant alleles =
                                 33.80 (
                                           2.99 SE,
                                                      13.36 SD)
Year 30
    N[Extinct] =
                       0, P[E] = 0.000
    N[Surviving] =
                      20, P[S] = 1.000
     Population size =
                                 41.15 (
                                           5.08 SE,
                                                      22.72 SD)
     Expected heterozygosity =
                                 0.939 (
                                          0.005 SE,
                                                      0.024 SD)
    Observed heterozygosity =
                                 0.969 (
                                          0.010 SE,
                                                      0.044 SD)
    Number of extant alleles =
                                 29.15 (
                                           2.29 SE,
                                                      10.25 SD)
Year 40
    N[Extinct] =
                      1, P[E] = 0.050
```

```
N[Surviving] =
                         19, P[S] = 0.950
      Population size =
                                    38.05 (
                                                           25.42 SD)
                                               5.83 SE,
     Observed heterozygosity =
      Expected heterozygosity =
                                    0.933 (
                                              0.005 SE,
                                                           0.021 SD)
                                    0.980 (
                                              0.005 SE,
                                                           0.024 SD)
     Number of extant alleles =
                                    24.21 (
                                               1.99 SE,
                                                           8.66 SD)
Year 50
     N[Extinct] =
     N[Extinct] = 2, P[E] = 0.100
N[Surviving] = 18, P[S] = 0.900
                        2, P[E] = 0.100
     Population size =
                                                           36.58 SD)
                                    38.61 (
                                               8.62 SE,
                                    0.905 (
     Expected heterozygosity =
                                              0.012 SE,
                                                           0.049 SD)
     Observed heterozygosity =
                                    0.979 (
                                              0.006 SE,
                                                           0.026 SD)
     Number of extant alleles =
                                    20.39 (
                                               2.60 SE,
                                                           11.04 SD)
Year 60
     N[Extinct] = 2, P[E] = 0.100
N[Surviving] = 18, P[S] = 0.900
     Population size =
                                    30.00 (
                                               5.77 SE,
                                                           24.50 SD)
     Expected heterozygosity =
                                    0.883 (
                                              0.014 SE,
                                                           0.059 SD)
     Observed heterozygosity =
                                    0.973 (
                                              0.008 SE,
                                                           0.033 \text{ SD})
     Number of extant alleles =
                                    17.17 (
                                               2.49 SE,
                                                           10.55 SD)
Year 70
     N[Extinct] =
                        4, P[E] = 0.200
     N[Extinct] = 4, P[E] = 0.200

N[Surviving] = 16, P[S] = 0.800
     Population size =
                                               7.07 SE,
                                                           28.29 SD)
                                    36.19 (
     Expected heterozygosity =
                                    0.864 (
                                              0.018 SE,
                                                           0.071 SD)
     Observed heterozygosity = 0.956 (
                                                           0.046 SD)
                                              0.011 SE,
     Number of extant alleles =
                                    15.87 (
                                               2.71 SE,
                                                           10.84 SD)
Year 80
                        3, P[E] = 0.150
     N[Extinct] =
     N[Surviving] = 17, P[S] = 0.850
                                                          27.07 SD)
     Population size =
                                    30.76 (
                                               6.57 SE,
     Expected heterozygosity =
                                                          0.148 SD)
                                    0.809 (
                                              0.036 SE,
     Observed heterozygosity =
                                    0.886 (
                                              0.036 SE,
                                                           0.148 SD)
     Number of extant alleles =
                                                          10.40 SD)
                                    13.76 (
                                               2.52 SE,
Year 90
                        6, P[E] = 0.300
     N[Extinct] =
     N[Surviving] = 14, P[S] = 0.700
                                    33.00 (
                                              10.39 SE,
                                                           38.87 SD)
     Population size =
     Expected heterozygosity = Observed heterozygosity =
                                    0.829 (
                                              0.029 SE,
                                                           0.109 SD)
                                    0.902 (
                                              0.022 SE,
                                                           0.082 SD)
     Number of extant alleles =
                                               2.69 SE,
                                                           10.05 SD)
                                    13.64 (
Year 100
     N[Extinct] =
                        9, P[E] = 0.450
     N[Surviving] = 11, P[S] = 0.550
                                    27.55 (
                                               5.48 SE,
     Population size =
                                                          18.19 SD)
                                                          0.121 SD)
     Expected heterozygosity =
     expected neterozygosity =
Observed heterozygosity =
                                    0.816 (
                                              0.037 SE,
                                    0.881 (
                                              0.034 SE,
                                                          0.114 SD)
     Number of extant alleles =
                                    11.91 (
                                              2.10 SE,
                                                          6.98 SD)
```

```
In 20 simulations of 100 years of Population2:
  9 went extinct and 11 survived.
This gives a probability of extinction of 0.4500 (0.1112 SE),
                                         0.5500 (0.1112 SE).
  or a probability of success of
9 simulations went extinct at least once.
Of those going extinct,
    mean time to first extinction was 71.67 years (7.41 SE, 22.24
SD).
3 recolonizations occurred.
Mean time to recolonization was 5.67 years (1.76 SE, 3.06 SD).
3 re-extinctions occurred.
Mean time to re-extinction was 8.00 years (4.04 SE, 7.00 SD).
Mean final population for successful cases was 27.55 (5.48 SE,
18.19 SD)
               2
                       3
                          Adults
                                    Total
   Age 1
                           9.55
                                    12.82
                    1.18
                                           Males
    0.91
            1.18
                                    14.73
    1.36
            1.18
                    1.64
                          10.55
                                           Females
Without harvest/supplementation, prior to carrying capacity
truncation,
  mean lambda was 1.0039 (0.0038 SE, 0.1599 SD)
Final expected heterozygosity was
                                      0.8160 ( 0.0366 SE,
0.1214 SD)
Final observed heterozygosity was
                                      0.8809 ( 0.0343 SE,
0.1138 SD)
Final number of alleles was
                                       11.91 (
                                                 2.10 SE,
6.98 SD)
***************************
*****
 ****** Meta-population Summary ******
Year 10
    N[Extinct] =
                       0, P[E] = 0.000
    N[Surviving] =
                      20, P[S] = 1.000
    Population size =
                                104.40 (
                                           5.76 SE,
                                                      25.77 SD)
                               0.989 (
    Expected heterozygosity =
                                          0.001 SE,
                                                      0.003 SD)
    Observed heterozygosity =
                                1.000 (
                                          0.000 SE,
                                                      0.000 SD)
    Number of extant alleles = 121.95 (
                                           5.22 SE,
                                                      23.36 SD)
Year 20
    N[Extinct] =
                       0, P[E] = 0.000
    N[Surviving] =
                      20, P[S] = 1.000
```

```
Population size =
                                  105.95 (
                                              9.83 SE,
                                                         43.98 SD)
     Expected heterozygosity = 0.981 (
                                             0.002 SE,
                                                         0.008 SD)
     Observed heterozygosity =
                                   0.991 (
                                             0.003 SE,
                                                         0.016 SD)
     Number of extant alleles =
                                              5.67 SE,
                                   85.90 (
                                                         25.37 SD)
Year 30
     N[Extinct] =
                        0, P[E] = 0.000
     N[Surviving] =
                        20, P[S] = 1.000
     Population size =
                                   92.60 (
                                             10.23 SE,
                                                         45.75 SD)
     Expected heterozygosity =
     Observed heterozygosity =
                                   0.967
                                             0.005 SE,
                                                         0.023 SD)
                                   0.978 (
                                             0.008 SE,
                                                         0.038 SD)
     Number of extant alleles =
                                   60.95 (
                                             5.17 SE,
                                                         23.11 SD)
Year 40
     N[Extinct] =
                        0, P[E] = 0.000
     N[Surviving] =
                        20, P[S] = 1.000
     Population size =
                                   75.30 (
                                            12.25 SE,
                                                         54.78 SD)
     Expected heterozygosity =
                                   0.948
                                            0.011 SE,
                                                         0.051 SD)
     Observed heterozygosity =
                                   0.968
                                            0.013 SE,
                                                         0.057 SD)
     Number of extant alleles = 43.05 (
                                             4.18 SE,
                                                         18.69 SD)
Year 50
     N[Extinct] =
                        0, P[E] = 0.000
     N[Surviving] = 20, P[S] = 1.000
     Population size =
                                   69.65 (
                                            15.55 SE,
                                                         69.56 SD)
     Observed heterozygosity = Number of extent
                                   0.927 (
                                            0.014 SE,
                                                         0.062 SD)
                                   0.965 (
                                            0.013 SE,
                                                         0.056 SD)
     Number of extant alleles =
                                                         18.14 SD)
                                   32.40 (
                                             4.06 SE,
Year 60
     N[Extinct] =
                        0, P[E] = 0.000
     N[Surviving] = 20, P[S] = 1.000
     Population size =
                                                         54.54 SD)
                                   59.05 (
                                            12.20 SE,
     Expected heterozygosity = 0.889 (
Observed heterozygosity = 0.941 (
                                            0.034 SE,
                                                         0.151 SD)
                                            0.033 SE,
                                                         0.145 SD)
     Number of extant alleles =
                                   25.80 (
                                             3.68 SE,
                                                         16.45 SD)
Year 70
                       0, P[E] = 0.000
     N[Extinct] =
     N[Surviving] = 20, P[S] = 1.000
     Population size =
                                   50.70 (
                                            10.84 SE,
                                                         48.48 SD)
     Expected heterozygosity =
                                                         0.119 SD)
                                   0.872 (
                                            0.027 SE,
     Observed heterozygosity =
                                   0.945 (
                                            0.017 SE,
                                                         0.077 SD)
     Number of extant alleles =
                                   20.80 (
                                             3.37 SE,
                                                         15.05 SD)
Year 80
     N[Extinct] =
                        3, P[E] = 0.150
     N[Surviving] =
                       17, P[S] = 0.850
                                   54.94 (
     Population size =
                                            12.72 SE,
                                                         52.46 SD)
     Expected heterozygosity = 0.871 (
Observed heterozygosity = 0.899 (
                                                         0.100 SD)
                                            0.024 SE,
                                            0.026 SE,
                                                         0.109 SD)
     Number of extant alleles =
                                   20.06 (
                                             3.42 SE,
                                                         14.11 SD)
```

Year 90

```
5, P[E] = 0.250
     N[Extinct] =
     N[Surviving] =
                      15, P[S] = 0.750
                                                      48.08 SD)
     Population size =
                                 50.67 (
                                          12.41 SE,
                                          0.023 SE,
     Expected heterozygosity =
                                 0.864 (
                                                      0.089 SD)
     Observed heterozygosity =
                                 0.907 (
                                          0.022 SE,
                                                      0.086 SD)
                                           3.28 SE,
                                                      12.68 SD)
                                 17.80 (
     Number of extant alleles =
Year 100
                       6, P[E] = 0.300
     N[Extinct] =
     N[Surviving] =
                       14, P[S] = 0.700
                                                      30.08 SD)
     Population size =
                                 36.71 (
                                           8.04 SE,
                                                      0.141 SD)
                                          0.038 SE,
     Expected heterozygosity =
                                 0.813 (
                                          0.042 SE,
                                                      0.157 SD)
     Observed heterozygosity =
                                 0.872 (
     Number of extant alleles =
                                 13.86 (
                                           2.70 SE,
                                                      10.10 SD)
In 20 simulations of 100 years of Meta-population:
  6 went extinct and 14 survived.
This gives a probability of extinction of 0.3000 (0.1025 SE),
                                         0.7000 (0.1025 SE).
  or a probability of success of
6 simulations went extinct at least once.
Of those going extinct,
    mean time to first extinction was 83.50 years (3.04 SE, 7.45
SD).
No recolonizations.
Mean final population for successful cases was 36.71 (8.04 SE,
30.08 SD)
   Age 1
               2
                      3
                          Adults
                                    Total
    1.07
            1.43
                    1.07
                          14.14
                                    17.71
                                           Males
    1.50
            1.14
                    1.57
                          14.79
                                    19.00
                                          Females
Without harvest/supplementation, prior to carrying capacity
 mean lambda was 0.9845 (0.0027 SE, 0.1170 SD)
Final expected heterozygosity was
                                      0.8128 ( 0.0376 SE,
0.1408 SD)
Final observed heterozygosity was
                                      0.8723 ( 0.0421 SE,
0.1574 SD)
Final number of alleles was
                                       13.86 (
                                                 2.70 SE,
10.10 SD)
*************************************
```

PVA SIMULATIONS - BASIC SCENARIOS CATASTROPHES POPULATION PARAMETERS II REMOVALS **PROJECTIONS** I INBRD YRS λ G FRQ **SVRT** FRQ **SVRT** TOT# YRS K M_x P(E) T_{E} POP. HE

KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 9
GENETIC BACKGROUND

Loss of Genetic Diversity from Managed Populations: Interacting Effects of Drift, Mutation, Immigration, Selection, and Population Subdivision

ROBERT C. LACY

Department of Conservation Biology Chicago Zoological Society Brookfield, Illinois 60513

Abstract: A computer simulation program was used to examine interacting effects of genetic drift, mutation, immigration from outside populations, directional and balancing selection, and population subdivision on the loss of genetic variability from small, managed populations. Stochastic events were simulated with a pseudo-random number generator, and the genetic variation (expected beterozygosity) within and between populations was monitored in 25 populations for 100 generations.

Genetic drift was the overriding factor controling the loss of genetic variation. Mutation has no noticeable effect on populations of the size typically managed in zoos and nature preserves. Immigration from a large source population can strikingly slow, halt, or even reverse the loss of genetic variation, even with only one or a few migrants per generation. Unless selection is stronger than commonly observed in natural populations, it is inefficient in countering drift when population sizes are on the order of 100 or fewer. Subdivided populations rapidly lose variability from within each subpopulation but retain variation across the subpopulations better than does a panmictic population.

These results suggest that population managers should be concerned with the variation-depleting effects of genetic drift, perhaps almost to the exclusion of consideration of selection and mutation. Drift can be countered by the introduction of very occasional immigrants or, less effectively, by division of the managed population into smaller breeding groups that interchange enough migrants to prevent unacceptably deleterious inbreeding within each subpopulation.

Resumen: A través de un programa de simulación por computadora se examinaron los efectos interactivos de la deriva génica, las mutaciones, la inmigración de poblaciones externas, la selección balanceada y direccional, y la subdivisión de poblaciones pequeñas sujetas a manejo, debido a la pérdida de variabilidad genética. Se simularon eventos estocásticos con un generador de números pseudo-azarosos y se estudió la variación genética intra e interpoblacional (beterocigosis esperada) en 25 poblaciones durante 100 generaciones.

La deriva génica fue el factor predominante que controló la pérdida de variación genética. Las mutaciones no tuvieron un efecto notable en poblaciones del tamaño típico manejado en zoológicos y áreas protegidas. La inmigración proveniente de otras poblaciones más grandes puede asombrosamente disminuir, detener ó invertir la pérdida de variación genética, aún con la influencia de sólo uno o pocos migrantes por generación. Cuando el tamaño de las poblaciones es del orden de 100 individuos ó menos, no es necesario evaluar la deriva génica, a menos que la selección sea más fuerte que la comunmente observada en poblaciones naturales. Las poblaciones divididas pierden rápidamente su variabilidad intra-subpoblacional, pero retienen una mayor variación intersubpoblacional que las poblaciones panmiticas.

Los resultados sugieren que los manejadores de poblaciones deben estar más atentos a la disminución de la variación genética producida por la deriva génica, que a las mutaciones ó a la selección natural. La deriva génica puede invertirse con la introducción de migrantes ocasionales, ó (aunque menos efectivamente) a través de la división de las poblaciones manejadas en pequeños grupos de crianza que puedan intercambiar migrantes para prevenir cruzamientos deletéreos dentro de cada subpoblación.

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Introduction

As natural habitats disappear and populations of organisms within remaining natural areas are increasingly exploited, many species are reduced to small, remnant populations occupying what is left of the habitat. Populations being propagated in zoos and intensively managed wildlife parks represent an extreme in these respects, at times being the last hope for survival of a species. By virtue of careful management, captive populations can be largely freed from the hazards of predation, inadequate nutrition, severe weather, disease, and difficulty in finding mates. Thus, smaller and more stable populations can be maintained in zoos or closely managed nature preserves than would persist in more natural environments.

Yet small populations of organisms lose genetic diversity over time. In the absence of any deterministic or directional forces on gene frequencies (selection, migration, mutation), frequencies of alleles follow a random walk process ("genetic drift") due to the random sampling of genes during transmission from one generation to the next. The random sampling of a small number of genes at each new generation results in greater fluctuations in gene frequencies than does the sampling of a larger number of genes. Therefore, small populations will tend to lose genetic variation by genetic drift more rapidly than will larger populations. The ultimate fate of any sexual population lacking mechanisms to restore genetic variation would be fixation of one allele at each genetic locus throughout the genome.

An immediate effect of the depletion of genetic variability is increasing homozygosity of the individuals in the population. Although the causes are still debated (Crow 1948, Lerner 1954, Clarke 1979, Frankel 1983), it has been widely recognized that increases in homozygosity often lead to lower viability and fecundity ("inbreeding depression") (Falconer 1981, Ralls & Ballou 1983).

Over a longer time scale, although the harmful effects of inbreeding on individuals may diminish as deleterious recessive genes are removed from the population by selection (Lynch 1977, Templeton & Read 1983), the population as a whole loses the evolutionary flexibility conferred by genetic diversity (Selander 1983). Without genetic variation between individuals on which natural selection can act, a population cannot adapt to changing environments and is vulnerable to new predators, diseases, parasites, climatic conditions, and competitors, and to changing foodsupplies.

For captive populations the loss of evolutionary flexibility may be especially rapid and particularly hazardous to long-term survival. The combined effect of rapid genetic drift in small captive populations and strong directional selection for survival in a novel captive environment might quickly deplete genetic variation.

The relative lack of predators and abundance of food and shelter might lead to a relaxation of many selective pressures to which wild populations would be exposed. Yet the restoration of genetic variation by mutation following this relaxation of selection for traits formerly under stringent selection is a very slow process—probably too slow to be of consequence in current efforts toward the preservation of species. For a given genetic locus, only one new mutation per thousand generations would be expected in a typical captive population of 100 to 1000 individuals. The rapid rate of habitat alteration is not likely to slow, so the species harbored by zoos will need considerable adaptive flexibility (evolutionary, physiological, and behavioral) if they are ever again to thrive in a noncaptive setting.

If zoos (or wildlife preserves and parks) are to propagate long-term viable populations, and especially if they are to contribute to the preservation of species diversity. they will have to manage their populations in such a way as to minimize, halt, or even reverse the decline in genetic variability that occurs in captive populations. Large breeding populations, exposed to varied environments, will maintain genetic variation and evolutionary flexibility, better than will smaller populations in less varied habitats (Levins 1968, Hedrick et al. 1976, Lacy 1982). With finite resources, however, allocation of space and facilities for one species necessarily limits space allocated to others. Efforts are needed to determine how best to manage captive breeding populations so as to make optimal use of those resources set aside for each species.

One approach to understanding how varied evolutionary forces effect genetic variation in small populations, and how populations can be managed to make those forces work toward the goals of captive management instead of against them, is to use computers to simulate the complex interactions of factors impinging on hypothetical populations. Computer models share with analytical theoretical approaches the property that results are dependent upon necessarily incomplete representations of natural processes. Models may be sensitive to incorrect assumptions, and important factors may have been omitted. Yet, for studying the effects of variables that can be well-defined, and for examining interactions among those variables, computer simulations can provide answers that may not be intuitive and that may not be readily obtainable by mathematical analysis. Moreover, many of the analytical models in the literature and many of the intuitive concepts about genetic diversity in small populations have been inadequately if at all examined by simulations. Unlike many analytical models, computer simulations do not make approximations that depend on the range of parameters for accuracy. The order-of-magnitude approximations of many analytical treatments are often not sufficiently informative for population managers.

In this paper I describe a general computer simulation model used to examine the effects of population size, mutation, immigration, selection, and population subdivision, and their interactions, on the maintenance of genetic variability in small, managed populations. Many of these factors have been examined before, either analytically or by simulation models, but the disparity among the models used to examine these factors makes comparisons of the effects, and of the resulting recommendations, difficult. Finally, because models are built on simplifying assumptions, the robustness of the conclusions derived from any model (including those presented here) should be verified by alternative approaches before they are put into practice.

Methods

A computer simulation program was written in the C programming language for use on microcomputers using the MS-DOS (Microsoft, Inc.) operating system. Results were output numerically via a printer and graphically via a Hewlett-Packard 7475A plotter.

To simulate the fate of two alleles at a genetic locus, the program

- Prompts the user to input the number of populations to be simulated, number of generations, population size, genotype fitnesses, forward and backward mutation rates, frequency of immigration into the population from an outside population, number of subpopulations into which the total population is fragmented, and migration rate between subdivisions.
- 2. Creates a population (composed of several subpopulations, if specified in step 1) of diploid individuals, assigning two alleles to each individual with probability 0.5 that each allele is of one type (say, "A") rather than the other ("a"). (Probabilistic events in the simulation are determined to occur when a real number drawn at random from a uniform distribution from 0 to 1 is less than the specified probability.)
- 3. Selects two parents at random from each (sub)population. Each parent is used for that mating with a probability equal to the fitness assigned to its genotype relative to the fitness of the most fit genotype. If a parent is not used, a replacement is drawn at random from the (sub)population, and then that newly chosen parent is in turn kept or discarded with probability determined by its relative fitness.
- Randomly selects one allele from each of the two parents and assigns that allele pair to an offspring.
- Replaces the offspring with a migrant from another subpopulation, with probability equal to the mi-

- gration rate between subpopulations. The migrant has a genotype that is drawn at random from the pool of genotypes present in the other subpopulations.
- 6. Replaces the individual with an immigrant from an outside population, with probability equal to the specified outside immigration rate. The immigrant has a genotype randomly drawn from a gene pool in which the two allelic variants are equally frequent (as in the starting population).
- Allows each of the two alleles of the individual to mutate to their respective alternate form, with probabilities equal to the specified mutation rate.
- Repeats steps 3 through 7 (for each subpopulation)
 as often as is necessary to create a new generation
 of the specified size.
- 9. Calculates allele frequencies and percent "expected" heterozygosity within each subpopulation, that is, the heterozygosity that would be observed if the subpopulation were in perfect Hardy-Weinberg equilibrium. The expected heterozygosity (calculated as 2pq, in which p and q are the frequencies of the two alleles) is twice the binomial variance in allelic frequencies in the population (Crow & Kimura 1970). The program also calculates allele frequencies averaged over subpopulations and from these overall allele frequencies calculates the "total heterozygosity" or "gene diversity" that would be present in the population if it were in Hardy-Weinberg equilibrium (mating at random with no subdivision) (Nei 1973, 1977). The total heterozygosity reflects both withinsubpopulation heterozygosity and any betweensubpopulation genetic differentiation. If all subpopulations are genetically alike, then the total heterozygosity will be equal to the (also equal) heterozygosities of the subpopulations. If subpopulations are genetically quite distinct, then the total heterozygosity will be much larger than is the average within-subpopulation heterozygosity, and it is the heterozygosity that would be present in a single randomly breeding population with the same amount of genetic diversity (strictly, the same total variance in alleles) as is present across the subpopulations.
- Repeats steps 3 through 9 for the specified number of generations, beginning each generation with the offspring from the previous generation.

Thus, the program simulates genetic processes in a constant size, randomly breeding population of sexually reproducing hermaphrodites with discrete generations. An individual can mate with itself, but is no more likely to do so than to mate with any other given individual. One important way in which the modeled population deviates from reality is the randomness of breeding within

the (sub)populations. In almost any real population, mate selection, polygamy, and sex-biased dispersal and mortality lead to deviations from panmixia. If these factors can be estimated for a population under study, then the "effective population size" can be calculated and a conversion made between the real population and the ideal populations presented in generalized models such as this. The effective size of a population is the size of an idealized monoecious population with random union of gametes, that would lose heterozygosity at the same rate as the observed population (Wright 1969). Thus, in the simulated (sub)populations, the actual population size is also the effective population size.

The lack of separate sexes and the self-compatibility are atypical of most captive populations, but the genetic behavior of such a population is almost indistinguishable from that of a population with separate sexes. A few simulations were run with the constraint that an individual could not mate with itself, and the results did not differ from simulations without such a constraint. Excluding self-fertilization has the same effect as consideration of separate sexes; either increases the genetically effective population size by 0.5 individuals (Wright 1969). The exclusion of sib-mating, as is commonly observed in wild populations (Ralls et al. 1986) and is often an intent of captive breeding programs, results in an effective population of just two greater than the idealized population modeled here (Wright 1969). An unequal sex ratio or nonrandom mating (producing a variance in family sizes that is greater than Poisson) can reduce the effective size to a fraction of the total population size (Crow & Kimura 1970, Ryman et al. 1981). In captive populations, these causes of low effective population size can be minimized (Flesness 1977, Denniston 1978). In fact, if family sizes are equalized, effective population approaches twice the real population size (Crow & Kimura 1970).

I monitored genetic diversity in the simulations using expected heterozygosities, both average within-subpopulation heterozygosity and the total (within- and between-subpopulation) heterozygosity that would be observed if all subpopulations were mixed at random and the genotypes were in Hardy-Weinberg proportions. Genetic diversity could have been expressed as the number of alleles present ("allelic diversity"), as in the simulations of Allendorf (1986) and the analytical models of Fuerst and Maruyama (1986). For several reasons heterozygosity is the more common measure of genetic diversity, but both measures yield important insights. Being proportional to genetic variance, the expected heterozygosity is also proportional to the short-term response to selection on that genetic locus (Fisher's Fundamental Theorem of Natural Selection: Fisher 1958). Long-term response to selection, however, is more dependent upon the alleles present in the population than on initial frequencies or heterozygosity (Allendorf 1986).

Unlike allelic diversity, the estimation of expected heterozygosity from a sample of a population is not highly dependent upon the sample size observed. Also, the fate of allelic diversity in a population is quite dependent upon the starting conditions (numbers and frequencies of alleles: Allendorf 1986), whereas heterozygosity decays at a steady average rate regardless of the initial allele frequencies in the population (Crow & Kimura 1970).

Results

Figure 1 shows the fate of heterozygosity in 25 simulated populations of 120 individuals across 100 generations. (A population size of 120 will be used frequently in this paper as a standard of comparison.) The only force leading to changes in gene frequencies and heterozygosities in Figure 1 is random genetic drift. All genotypes were assigned the same fitness, there was no mutation or immigration, and mating was random.

The stochastic nature of genetic transmission is apparent in the simulated populations, even though the populations are not unrealistically small for captive or even wild populations of large vertebrates. Three of the 25 populations lost all heterozygosity at the genetic locus within 100 generations (i.e., one of the two allelic variants was lost, the other was fixed), and yet six populations had virtually the same allele frequencies and heterozygosities after 100 generations as they had at the outset. The average heterozygosity in these 25 simulated populations after 100 generations was 58.25 percent of the initial value (SE = 7.19%), not significantly different from the 66 percent predicted from the commonly used equation for the loss of heterozygosity by random drift $H_{\rm c} = (1 - 1/[2N_{\rm c}])^2 H_0$

GENETIC DRIFT -- VARIATION AMONG RUNS

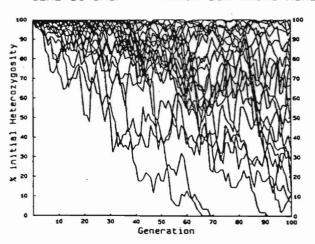


Figure 1. Percent beterozygosity retained across 100 generations in 25 simulated populations of 120 randomly mating individuals each.

in which N_c is the effective population size, and H_0 and H_t are heterozygosities at generations 0 and t, respectively.

Throughout the remainder of this paper, heterozygosities averaged across 25 simulated populations will be shown for each set of conditions discussed. The average behavior of the 25 simulations can represent the fate of a given genetic locus across 25 populations, or the fate of 25 genetic loci within one population. The relative smoothness of average heterozygosities shown in all subsequent figures should not obscure the fact that underlying the average heterozygosities are fates of individual populations that are as diverse as those shown in Figure 1. Results revealed by simulations are thus the "expected" behavior of a population only in a statistical sense: They should not be used to predict the behavior of a particular gene of interest. For example, only a few populations in Figure 1 were left with fractions of the initial heterozygosity close to the theoretical prediction of 66 percent.

Effect of Population Size

Figure 2 compares average heterozygosities of 25 simulated populations of various sizes and shows the effect of population size on the rate at which genetic drift depletes variation. Mean heterozygosities after 100 generations did not vary significantly from the theoretical values of 90.5 percent, 81.2 percent, 65.9 percent, 43.3 percent, 28.4 percent, and 8.0 percent that are expected

COMPARATIVE POPULATION SIZES

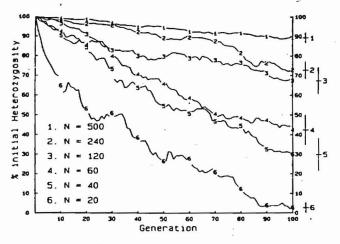


Figure 2. Percent beterozygosity retained in populations of 20, 40, 60, 120, 240, or 500 randomly mating individuals. Each line in this and all subsequent figures represents the average of 25 simulated populations. Means and standard errors of the final beterozygosities are indicated at the right. Except when otherwise specified, all subsequent figures are based on simulated populations of 120 animals.

for populations of size 500, 240, 120, 60, 40, and 20, respectively. Standard errors of the mean heterozygosities across these 25 simulated populations of each size (SE = 2.73%, 4.58%, 6.86%, 7.75%, 8.48%, and 2.79%, respectively) approximate the theoretical standard errors for heterozygosities remaining after 100 generations of drift (2.43%, 4.35%, 6.60%, 8.00%, 7.66%, and 4.79%; equation from Bulmer 1985).

Putting the loss of genetic variability into a perspective that is meaningful for a species or population of interest can be difficult. The history of inbreeding in a population (Lynch 1977) and the need to adapt to changing environments will affect the loss of heterozygosity that a population can withstand (Selander 1983). To provide some benchmarks, note that inbreeding of 1 percent per generation is considered by animal breeders to have negligible effect (Franklin 1980) and that many human societies prohibit marriages between relatives that would produce offspring with inbreeding coefficients of 6.25 percent or more. (Inbreeding reduces heterozygosity by 1% per 1% increase in the inbreeding coefficient, and losses of heterozygosity due to any kind of population structure are often measured by inbreeding coefficients or F-statistics [Wright 1965, Jacquard 1975]). Experimental populations have responded to artificial selection for more than 75 generations (Falconer 1981), suggesting that sufficient variability exists to allow "adaptation" even after genetic variation has been considerably depleted. Such experimental populations do not cope simultaneously with the diversity of selective constraints that are faced by natural populations, however, and clearly the many species that have gone extinct did not adapt sufficiently and rapidly to changing environments.

Mutation *

The ultimate source of new genetic variability is mutation, although recombination, migration, and selection can increase variability within a population by reshuffling existing alleles within and between populations and by changing allele frequencies. Figure 3 shows the effects of mutation on heterozygosity within populations of 120 individuals. Mutation can counter the effects of drift, but not at rates of mutation that are observed in any real population. Mutation rates typically range from 10-8 to 10-4 per gene per generation in eukaryotes and from 10-6 to 10-4 in mammals (Hedrick 1983, Strickberger 1985). Only at mutation rates greater than 10⁻³ did new mutation noticeably counter drift in the simulations. (The increased heterozygosity with $m = 10^{-4}$ in Figure 3 was due to chance, not the effects of mutation; note that the higher mutation rate of 10-3 had no effect on heterozygosity.)

In part, the minimal effect of mutation in the simulations results from the very high heterozygosity (50%)

COMPARATIVE MUTATION

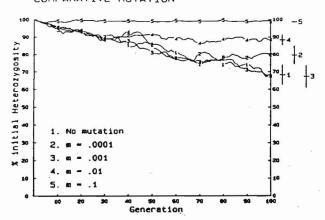


Figure 3. Percent beterozygosity retained in populations with equal forward and backward mutation rates of 0, 10^{-4} , 10^{-3} , 10^{-2} , or 10^{-1} per generation.

at generation 0. New variation introduced by mutation increases additively, independent of current heterozygosity, while drift leads to a geometric decrease in heterozygosity, the loss being proportional to extant heterozygosity. After heterozygosity reaches a low value, further loss due to drift will have diminished to the rate of gain by mutation: The population will be in mutationdrift equilibrium. For a population of 120 animals with a mutation rate of 10⁻⁵, mutation-drift balance is reached when heterozygosity drops to 0.0048, about 1 percent of the initial value in the simulations and about an order of magnitude lower than is commonly observed in natural populations of vertebrates. (In an ideal population such as the one modeled, mutation-drift equilibrium is reached when $H = 4N_m/(1 + 4N_m)$ [Crow & Kimura 1970].)

Immigration

For a captive or otherwise isolated population of a species that retains relatively large populations elsewhere, immigration of individuals from the large source-population constitutes a mechanism, similar to mutation, for reintroduction of genetic variability. Immigration differs in several important respects from mutation, however. Immigration rates can be much greater than are mutation rates. Moreover, immigration is often under control of a population manager. Most importantly, genetic variants introduced into a population by immigration act to restore alleles that formerly existed in the captive population or the ancestral stock from which it was derived.

Effects on heterozygosity of immigration from a hypothetical, genetically unchanging, source-population into a population of 120 individuals are shown in Figure 4. Given the standard errors observed around final heterozygosities, there is no evidence that an immigration

COMPARATIVE IMMIGRATION

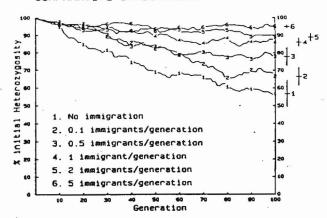


Figure 4. Percent beterozygosity retained in populations receiving an average of 0, 0.1, 0.5, 1, 2, or 5 immigrants per generation from an infinitely large source population with allele frequencies equal to those of the initial populations.

rate of 0.1 immigrants or less per generation causes a biologically significant effect.

Immigration rates as low as 0.5 immigrants per generation, obtainable for many captive propagation efforts, strikingly reduce the loss of variability from small populations. Although it is not obvious in Figure 4, the immigration causes genetic variation to approach an asymptote: The farther from the initial state a population becomes, the greater the restorative effect of immigration. Therefore, immigration can bring a formerly isolated and considerably divergent population back toward the genetic condition of the source population.

Because the degree to which immigration restores heterozygosity is dependent upon the extent to which the population has diverged from the source population, the effect of immigration is much greater on smaller populations than on larger populations. With moderate rates of immigration, the long-term (asymptotic) genetic fate of a population is almost independent of population size (Fig. 5).

Selection

Three types of selection were modeled: directional selection in which one homozygote has superior fitness to the other and the heterozygote has intermediate fitness, balancing selection in which the heterozygote has superior fitness and the two homozygotes have equal fitness, and disruptive selection in which the heterozygote has inferior fitness and the two homozygotes have equal fitness. As expected, under strong selection (Fig. 64: relative fitnesses of 1.0:0.8:0.6 for directional selection; 0.8:1.0:0.8 for balancing selection; and 1.0:0.8:1.0 for disruptive selection), balancing selection maintains allele frequencies and heterozygosity,

1 IMMIGRANT PER GENERATION

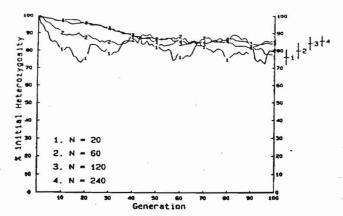


Figure 5. Percent beterozygosity retained in populations of size 20, 60, 120, or 240 receiving 1 immigrant per generation from a source population.

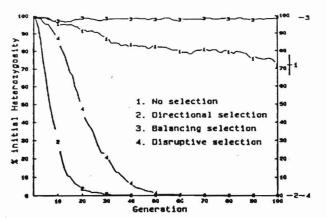
while directional and disruptive selection rapidly fix one allele in each population and thereby deplete genetic variation. Under symmetrical disruptive selection, about half the populations are fixed for one allele and half are fixed for the other. All populations were fixed for the selectively favored allele under directional selection.

Fitness differentials of 20 percent are probably rare, although such strong natural selection has been reported for some polymorphic traits (Endler 1986). Under more moderate selection (relative fitness of 1.0:0.95:0.90 for directional selection; 0.95:1.0:0.95 for balancing selection; and 1.0:0.95:1.0 for disruptive selection), the trends in heterozygosity are the same, but diminished (Fig. 6B). Over five to 10 generations, a 5 percent fitness differential has little effect on levels of genetic variation. Weak selection pressures (Fig. 6C, relative fitnesses of 1.0:0.99:0.98 for directional selection; 0.99:1.0:0.99 for balancing selection; and 1.0:0.99:1.0 for disruptive selection) affect heterozygosities, but the effects are hardly discernible over the background noise of random drift. This is in accord with analytical results of Kimura (1955), Robertson (1962), and others (Crow & Kimura 1970, Wright 1969) that show that selection is effective over random genetic drift when the product of the effective population size and the selection coefficient is much greater than one.

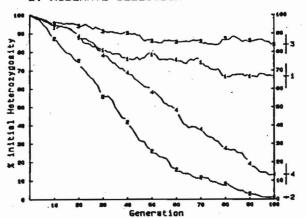
Population Subdivision

Captive populations are often fragmented into partially or wholly isolated subpopulations, each consisting of a breeding population held by a zoo or a group of zoos in close geographical proximity or in close cooperation. One effect of this subdivision is to allow genetic differentiation to develop between subpopulations, as a result of genetic drift or differential selection on the subpopulations inhabiting different environments (Chesser et

A. STRONG SELECTION



B. MODERATE SELECTION



C. WEAK SELECTION

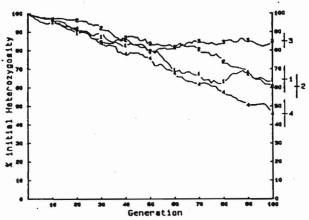


Figure 6. Percent beterozygosity retained in populations subjected to no selection, balancing selection, disruptive selection, or directional selection. (A) strong selection (relative fitnesses of 0.8:1.0:0.8, 1.0:0.8:1.0, and 1.0:0.8:0.6); (B) moderate selection (relative fitnesses of 0.95:1.0:0.95, 1.0:0.95:1.0, and 1.0:0.95:0.90); (C) weak selection (relative fitnesses of 0.99:1.0:0.99, 1.0:0.99:1.0, and 1.0:0.99:0.98).

al. 1980). Furthermore, because the subpopulations are necessarily smaller than is the total population and because each subpopulation would occupy a narrower range of habitats than does the total population, two processes that deplete genetic variation will be enhanced in isolated subpopulations relative to a panmictic population. Genetic drift will inevitably be greater in fragmented subpopulations; and while heterogeneous selection on large populations utilizing diverse habitats can maintain genetic variation (Levene 1953, Levins 1968, Hedrick et al. 1976, Taylor 1976, Lacy 1982), directional selection on isolated subpopulations for traits advantageous in narrow habitats would deplete variation (Karlin 1982).

Figure 7 illustrates the effect of dividing a population of 120 individuals into one, three, five, or 10 fully isolated breeding units. Average within-subpopulation het-

erozygosities (shown by points unconnected by lines) are strikingly diminished when the population is fragmented, while total gene diversity within and between subpopulations (points connected by lines) is better maintained by population subdivision.

Total gene diversity in a highly fragmented population asymptotes at a high level. In each generation some of the variation formerly present within each subpopulation is converted to variance between populations as the subpopulations randomly diverge. This between subpopulation variation is then protected from further decay due to genetic drift. When subpopulations become totally inbred (no heterozygosity within subpopulations), total variation is fixed at a level equal to the between-subpopulation genetic variation. Maintenance of total variation in simulated populations depends on the persistence of each subpopulation at a constant size,

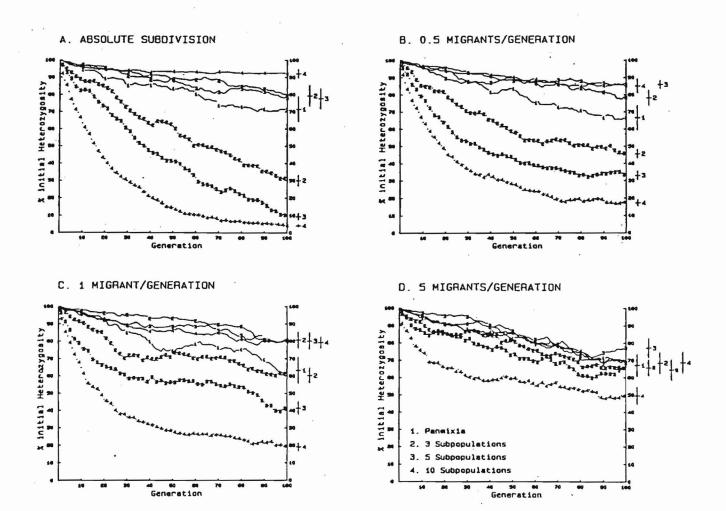


Figure 7. Percent heterozygosity retained within subpopulations (points and numbers not connected by lines) and total heterozygosity retained within and between subpopulations (points connected by lines) in populations of total size 120 divided into 1, 3, 5, or 10 subpopulations. (A) no migration between subpopulations; (B) 0.5 inter-subpopulation migrants per generation; (C) 1 migrant per generation; (D) 5 migrants per generation.

however. If some subpopulations were to go extinct, some between-population diversity would be lost with them.

Subpopulations need not be totally isolated. As few as 0.5 inter-subpopulation migrants per generation (over all subpopulations, not per subpopulation) will reduce inbreeding within subpopulations (compare within-subpopulation heterozygosities in Fig. 7B to those in 7A). Higher rates of migration between subpopulations (Fig. 7C and 7D) bring both the within-subpopulation heterozygosities and the total gene diversities closer to the heterozygosity expected under panmixia. Theoretical analyses (Wright 1969) and simulations (not shown) demonstrate that the effect of migration between populations on preventing divergence among subpopulations is dependent upon the number of migrants per generation, and independent of total population size.

Migration reintroduces genetic variation to subpopulations, causing within-subpopulation heterozygosities to level out after an initial rapid decline. (As was the case for immigration from an external population, migration between subpopulations only becomes effective after populations have diverged and lost variability.) By preventing subpopulations from becoming fixed with different genetic compositions, migration also prevents the subdivided population structure from retaining large total gene diversity. Under high rates of migration (Fig. 7D) subdivided populations do not retain within-subpopulation variation as well as do panmictic populations, nor do they retain measurably more total variation.

Figure 8 compares the effects of different rates of migration between subpopulations of a population divided into five breeding units of 24 individuals. Increasing migration lessens inbreeding within subpopulations, though not until generation 10 or beyond. Very low levels of migration perhaps actually increase total genetic variation maintained relative to the no migration case, while higher rates of migration bring total heterozygosity down.

Interaction Between Selection and Population Subdivision By augmenting genetic drift within subpopulations, subdivision alters the effectiveness of selection on small populations. Strong directional selection usually overwhelms genetic drift (Fig. 9A), even in highly subdivided populations. (About 1 percent of subpopulations of 12 individuals will be fixed for an allele strongly opposed by selection.) With more moderate selection, genetic drift within subpopulations prevents selection from being wholly effective (Fig. 9B). Among subpopulations of 12 individuals each, an average of 22 percent became fixed for the allele whose homozygote had 10 percent lower fitness than did the other homozygote. The selectively disadvantageous allele also remained longer within subpopulations of 24 and 40 individuals (five and three

MIGRATION AMONG 5 SUBPOPULATIONS

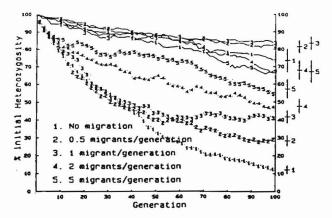


Figure 8. Percent beterozygosity retained within subpopulations (points not connected by lines) and total beterozygosity retained within and between subpopulations (points connected by lines) in populations divided into 5 subpopulations with an average of 0, 0.5, 1, 2, or 5 inter-subpopulation migrants per generation.

subpopulations, respectively) than it did within a panmictic population of 120. Weak directional selection (not shown), with only minor effects on a panmictic population, had no effect on the fate of alleles in subdivided populations.

The heterozygosity-preserving effects of balancing selection are also diminished by drift within small sub-populations (Figs. 9C and 9D). Balancing selection slows, but does not stop, fixation of alleles in small subpopulations, therefore also countering potential advantages of population subdivision. Rather than maintaining total heterogeneity by furthering between-subpopulation genetic differentiation, subdivision of a population under balancing selection causes a greater loss of total heterozygosity than would occur if the population were panmictic.

Discussion

Flesness (1977), Denniston (1978), Chesser et al. (1980), Allendorf (1983), Chesser (1983), Fuerst and Maruyama (1986), and Foose et al. (1986) have made recommendations about the optimal genetic management of captive populations. The simulations presented here provide further basis for making decisions about the genetic management of small populations. The goal of presenting simulations is not to prescribe a population size and structure to be used in the management of all populations: The opportunities, constraints, and goals of captive propagation programs are too diverse to permit such broad recommendations. Simulations, however, can help

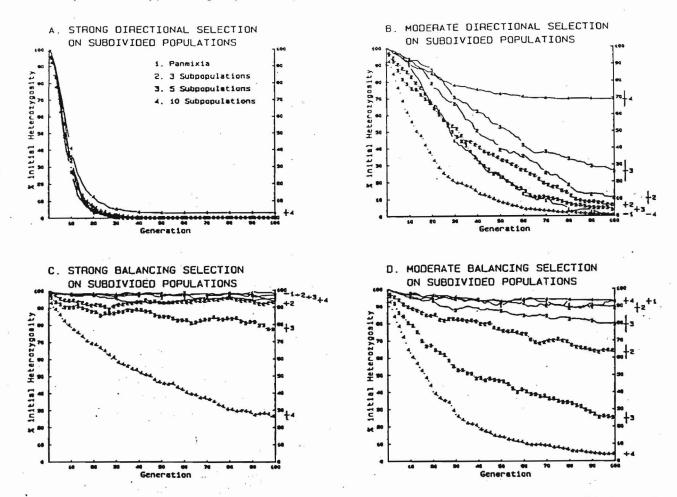


Figure 9. Percent beterozygosity retained within fully isolated subpopulations (points not connected by lines) and total beterozygosity retained within and between subpopulations (points connected by lines) in populations divided into 1, 3, 5, or 10 subpopulations subjected to selection. (A) strong directional selection (relative fitnesses of 1.0:0.8:0.6, except for total beterozygosity in 10 subpopulations, all beterozygosities have mean and standard error zero by generation 50); (B) moderate directional selection (relative fitnesses of 1.0:0.95:0.90); (C) strong balancing selection (relative fitnesses of 0.95:1.0:0.95).

to define the effects that different management strategies will have on the genetic constitution of a population. With such knowledge, management plans can become tailored, informed attempts to achieve the long-term genetic goals of captive propagation.

Genetic drift is commonly the most powerful evolutionary force acting on small populations, so, to a first approximation, management concerns can be focused solely on effects of drift. Under stringent conditions of selection and/or population structure, imposed artificially or naturally, other evolutionary forces can overcome the stochastic effects of drift. Genetic drift is a sampling phenomenon, and thus can be most effectively contolled by keeping large (effective) breeding populations. In unmanaged populations, many individuals contribute little or nothing to future generations, and careful management of a population is usually necessary

to assure that the genetically effective population size is not greatly smaller than the censused population (Foose 1977, Flesness 1977, Foose et al. 1986). Chesser (1983) points out that increases in the effective population size by demographic management may not be sufficient to slow drift adequately, and even suggests that "exclusive focus on population size can have disastrous results for the management of genetic resources." He then paradoxically discusses various means of managing the demography of a population to increase the effective population size (by managing migration between subpopulations) and thereby decrease inbreeding.

Mutation can reasonably be ignored as an evolutionary force in small captive populations. For example, a captive population of 100 individuals is unlikely to experience a mutation in any individual at more than 10 percent of its genetic loci over 100 generations. More-

over, the minor additional variation inserted into a captive population by mutation over any timespan of human interest is likely to be counterproductive for the goal of preserving the genetic uniqueness of a population.

One approach to the question of what size captive population is needed to preserve sufficient variability for long-term viability is to determine the number that would maintain adequate heterozygosity when at mutation-drift equilibrium. For example, Franklin (1980) suggested that a population of 500 would be sufficiently large to be in mutation-drift balance for adequate variability of quantitative (polygenic) traits. (Franklin's estimate was based on papers by Lande [1976] and others that suggested mutation could maintain considerable variation for quantitative traits under moderate stabilizing selection. Turelli [1984] questioned Lande's conclusions, showing that with somewhat different [and perhaps more realistic] assumptions about mutation rates, phenotypic effects of mutation, and the intensity of selection. mutation is much less capable of maintaining variation in a selected trait.) Franklin's estimate has often been proposed as a guideline for management of endangered species (e.g., Soulé & Wilcox 1980, Frankel & Soulé 1981, Schonewald-Cox et al. 1983) and has been applied to management plans for the Siberian tiger (Foose & Seal 1981, Foose 1983).

The use of a mutation-drift equilibrium model, or perhaps any equilibrium model, for the management of small captive populations may be misguided, however. At equilibrium, heterozygosity remains constant, but the genome does not. Allelic losses still occur due to drift, but those alleles are replaced by new, generally different mutations. In a natural population, most new mutations are lost by drift, a few increase to sufficient frequencies to be subject to the positive or negative force of selection, and the population slowly evolves. In a captive environment, such changes also occur, but selection is likely to be very different from that experienced by a population living in a more natural habitat. While in mutation-drift equilibrium, a captive population may be rapidly evolving into something quite different genetically from what it was initially. Unless captive propagation seeks to create domesticated stocks or to make specific changes in the genetic make-up of a population, genetic captive-management plans should aim for a cessation of evolutionary processes to the extent possible. (Planned genetic alteration of a population might occasionally be necessary to assure survival in captivity or other highly modified environments, and this consideration may override concerns about preservation of an unaltered population [Templeton & Read 1983, Foose et al. 1986].)

For assessing success in preserving the genetic characteristics of a population, captive management plans should be concerned with the loss of the variation present in the founding population. The consensus that arose from the 1984 Front Royal conference to strive for a

retention of 90 percent of heterozygosity for 200 years (Soulé et al. 1986) reflects a recognition of the non-equilibrium nature of genetic management of captive populations.

Fuerst and Maruyama (1986) also stressed the lack of equilibria in early generations of captive breeding, pointing out that most rare alleles present in natural populations would not be sampled when a small number of founders is obtained to begin captive breeding, or would be lost within the first few generations of captivity. Because rare alleles are lost during bottlenecks much more rapidly than is heterozygosity, Fuerst and Maruyama (1986) recommend that emphasis be placed on the preservation of allelic diversity and, therefore, that larger founding populations than those suggested by studies of heterozygosity will be needed. Unfortunately, except for short-term captive propagation plans, it is unlikely that sufficient wild stock can be obtained and sufficient captive stock maintained to give much hope for the preservation of rare alleles. Managers of very small populations may be forced to focus efforts on minimizing the deleterious consequences of severe loss of heterozygosity.

If a large wild population exists and can be used to supplement the captive population, periodic immigration (capture of new founder stock) can drastically reduce drift of the captive population away from the genetic characteristics of the wild population. As few as one immigrant per two generations would be beneficial, and five or more immigrants per generation would virtually halt genetic drift within the captive population. Immigration into very small populations is especially effective (and important), as loss of genetic variability is almost independent of population size when immigrants are introduced at a rate of one or more per generation. A population of only 20 individuals that receives an immigrant per generation retains almost as much genetic variability as does a population an order of magnitude larger. Because immigration reverses extant genetic differentiation between captive and source populations, sporadic immigration at the same long-term average rate can be just as effective as is a regular schedule of immigration in maintaining a population close to its initial state.

For an endangered species, there may be no large source-population available. If the captive population is much larger than is the wild population (as with Siberian tigers), migration into the wild population from the captive population can help to maintain genetic variability in an endangered wild population that otherwise might experience excessive inbreeding. If both the wild and captive populations are small, migration between them could give to both some of the advantages of a population size equal to their combined numbers (see results and discussion concerning population subdivision).

Selection can deplete, maintain, or even augment genetic variation, yet magnitudes of selection likely to act on populations not under artificial selection are not ef-

fective when populations are of a size typical of captive populations. The inefficiency of selection in the face of rapid genetic drift suggests that some concerns and some hopes of captive propagation are unlikely to be realized. The altered environment of captivity creates new selective pressures not experienced by a natural population, and releases the captive population from selective constraints experienced by the wild counterpart. Unless some traits are strongly deleterious or advantageous in a captive environment (causing perhaps a 10% differential in mortality between those individuals with the traits and those without), response to selection for "captive" traits is unlikely to be apparent amid random fluctuations in allele frequencies. Inadvertent and unavoidable selection for domestication has probably not produced "zoo species" in which genetic characteristics important to survival in the wild have been selected away. (Behavioral changes in captive populations are much more likely to cause problems for reintroduction programs.)

Unfortunately, the inefficiency of selection also means that drift will often fix deleterious alleles by chance in small captive populations. Genetic variants poorly adapted to either a captive or wild habitat may become prevalent in long-term captive populations. If continued survival and propagation of a species seems threatened by genetic changes occurring in the captive population, it may be necessary to impose strong artificial selection for a zoo-adapted, domesticated animal.

By dividing a captive population into several subpopulations (management units for breeding loans, trades, and sales), more of the genetic variability originally present in the founding stock can be maintained overall. The genetic cost of population subdivision is increased inbreeding within each subpopulation, and greater divergence of individual subpopulations from the genetic characteristics of the founders (Chesser et al. 1980, Chesser 1983).

The frequency of movement of animals between captive populations determines whether a species is managed as one interbreeding population or a number of more or less isolated subpopulations. An often-cited (e.g., Spieth 1974, Frankel & Soulé 1981, Hedrick 1983, Foose et al. 1986) theoretical result is that when the number of migrants per generation much exceeds one, the subdivided population behaves as though it were panmictic (Moran 1962). As shown in Figure 7D and Figure 8. however, five migrants per generation are not sufficient to bring the population to effective panmixia. Even 20 migrants per generation were not sufficient to prevent fully loss of genetic diversity within, and divergence among, subpopulations (simulations not shown). Allendorf and Phelps (1981) found that 10 migrants per generation were insufficient to prevent significant divergence among subpopulations in their very similar computer model of genetic drift in subdivided populations. The difference between 20 and "greater than one" may not be important to the theoretical results, but it certainly has meaning to the population manager.

Fuerst and Maruyama (1986) considered the fate of allelic diversity in subdivided populations. Pointing out that rare alleles are likely to be lost in small populations (even if substantial heterozygosity remains), and that most subpopulations would retain only the common alleles of the source population, they suggested that population subdivision is not beneficial to the preservation of allelic diversity. To the contrary, a subdivided population structure may be the only way to preserve allelic diversity in small populations. In the absence of balancing selection, eventually all alleles but one would be lost at each genetic locus of an isolated population. The probability that a neutral allele will be retained is equal to its initial frequency. Thus, a neutral allele with initial frequency in the source population of 0.01 has a 1 percent chance of being sampled and retained in any population. If 10 subpopulations are maintained, the probability that at least one will retain a rare allele is about 10 times the probability that a single panmictic population would retain the allele. (In the extreme, a clonally reproducing organism, with as many subpopulations as individuals, would never lose allelic diversity so long as all lines were maintained.)

Even in the first few, nonequilibrial, generations, a subdivided population will retain allelic diversity better than would a panmictic population. The probability that a rare allele is initially sampled from the wild population is not dependent upon how founders are partitioned into breeding groups for production of future generations. After the initial sampling, rare alleles will be present at much higher frequencies in those subpopulations where they exist than they would have been in a panmictic population, and this helps protect them from random loss. Mathematically, the probability of loss from a randomly mating population in any one generation is (I p)2N, in which p is the allele frequency and 2N is the number of alleles in the population. The probability of loss in any one generation from all k equal-size subpopulation is

$$(1 - p_1)^{2N/k} \cdot (1 - p_2)^{2N/k} \cdot \dots \cdot (1 - p_k)^{2N/k}$$

$$= [(1 - p_1) \cdot (1 - p_2) \cdot \dots \cdot (1 - p_k)]^{2N/k}$$

$$= [geometrical mean of (1 - p_i)]^{2N},$$

in which p_i is the frequency of the allele in subpopulation i. The frequency of any allele in the panmictic population will be equal to the arithmetic mean frequency across the subpopulations, $([1-p_1)+(1-p_2)+\dots+(1-p_k)]^{/k}=(1-p))$, and thus the probability of loss from the panmictic population is [arithmetic mean of $(1-p_i)$]^{2N}. The goemetric mean of a series of numbers is smaller than or equal to the arithmetic mean. Thus the probability of loss from all subpopulations is always less than the probability of loss from the one panmictic

population. Contrary to Fuerst and Maruyama (1986), perhaps the most beneficial result of population subdivision is the greater conservation of allelic diversity.

Population subdivision also slows the genetic response of a population to selection because it increases genetic drift within subpopulations where selection would act. By inhibiting directional selection, subdivision will help maintain variability and will slow inadvertent domestication of captive stocks. (If whole subpopulations were selectively eliminated after subpopulations have diverged [between-population selection], perhaps with the intent of eliminating less successful stocks, there would be considerable loss of genetic diversity.) Although not modeled here, different selection pressures among subpopulations can also maintain genetic variability (reviewed by Hedrick et al. 1976, Karlin 1982).

To the extent that balancing selection (favoring heterozygotes within each population) maintains genetic variability (an issue under much debate among evolutionary biologists), the increased drift that occurs with subdivision will push populations away from equilibria maintained by balancing selection and thereby cause loss of adaptive genetic variability. The disruption of balanced equilibria by drift is simply a restatement, in causal terms, of the deleterious effects of inbreeding ("inbreeding depression") in subdivided populations. Concern about the reduced efficacy of balancing selection should be tempered, however, by the realization that natural selection on captive populations is probably quite different from natural selection on wild populations. Polymorphisms maintained by balancing selection in the wild may not be protected by balancing selection in captive populations.

Chesser et al. (1980) suggested a management scheme for using subdivision to maximize balancing selection in order to preserve polymorphism in small populations. In examining equilibrium models of polymorphism, they point out that polymorphism can be maintained indefinitely in a small population only if there is strong balancing selection. They proposed to let subpopulations become partially inbred, so that the general heterosis (hybrid vigor) produced with subsequent migration would result in temporary strong balancing selection on the genome. If there is much variation that is not strongly adaptive in a captive environment, however, or if the time scales of conservation goals are finite (on the order of tens to perhaps hundreds of generations), then practices aimed at slowing evolutionary processes are probably more desirable.

Slatkin (1981) presented both analytical and simulation analyses of the efficacy of selection in a subdivided population with migration between subpopulations. He found that when migration is low (less than about 0.5 per generation), the ultimate result of selection (probability of fixation of a favored allele) is quite similar to the case of minimal migration; when migration is much above one per generation, the ultimate response was usually similar to the case of a paramictic population. The times to fixation (i.e., the rate of response rather than the ultimate result of selection) always increased with decreasing migration between subpopulations. Thus, as would be expected from the simulation results presented here, increasing isolation of the subpopulations slowed the rate of evolutionary change.

Allendorf (1983) recommended a management strategy of 1 migrant per generation among isolated nature reserves, pointing out that low levels of migration prevent the total loss of alleles from local populations, while not preventing adaptive genetic divergence. My simulations suggest that that level of migration might be advantageous among small captive populations also, although the costs and benefits of subdivision of captive populations are perhaps somewhat different from those for populations managed in nature reserves. Random genetic divergence between subpopulations allows for better maintenance of alleles and total gene diversity, but local adaptation of subpopulations resulting from differential selection might be an unfortunate consequence of captive propagation programs aimed at eventual restoration of diverse gene pools in more natural habitats. (As pointed out above, however, I see selection as relatively inefficient in small subdivided populations.) Also, while Allendorf emphasizes preventing the total loss of allelic variants from populations, I worry more about potentially severe losses of heterozygosity and any consequent loss of fitness. Reintroduced populations and augmented remnant wild populations will need both allelic diversity and moderate levels of heterozygosity to become securely reestablished.

The value of population subdivision to captive propagation depends considerably on the time scale for which captive management goals are set. The genetic cost of subdivision occurs primarily in early generations, as inbreeding is especially rapid over the first 10 to 20 generations. The benefit of improved maintenance of total variability and the ability of between-subpopulation migration to reduce inbreeding both become apparent only after 10 to 20 generations, because both are dependent upon genetic divergence of subpopulations. For shortterm management plans, there would be no genetic advantage to subdivision of the population, although isolation of smaller breeding groups may be important in the prevention of catastrophic disease outbreaks. For very long-term management (30 or more generations). the optimal management plan might be to subdivide the captive population into units of perhaps 20 breeding individuals each and then carefully to regulate inter-unit migration at the lowest level that does not lead to unacceptably deleterious effects of inbreeding. Apparently

more concerned about the effects of inbreeding, Foose et al. (1986) recommended keeping subpopulations sizes greater than 25, and preferably between 50 and 100. Unfortunately, the maximum acceptable level of inbreeding almost certainly differs among species. Currently, information does not exist for any species that would allow accurate determination of the degree of inbreeding that would jeopardize long-term survival.

Population subdivision is reversible, however, up to the point that one or more subpopulations go extinct. If a preliminary plan for subdivision seemed not to be producing desired results, subpopulations could be merged to produce a panmictic population that almost always would be more diverse genetically than it would have been had it never been subdivided. Unfortunately, such a reconstituted panmictic population, while high in genetic diversity and with allele frequencies approximating those in the founders, may be rather different from the ancestral stock with respect to genetic linkage relationships. On the other hand, if a captive population is kept panmictic there is no way to recover genetic variants that are lost by drift without introducing new founder stock from the wild.

Perhaps the biggest difficulty in a management plan centered around a divided breeding population lies in administration. Moderate levels of migration cancel the genetic benefits of subdivision, and more quickly so than the genetic costs of inbreeding are removed. For population subdivision to be a useful management tool, movement of animals between breeding units must be strictly controlled. Two or three unplanned movements per generation could turn genetic benefits into costs. For example, a highly subdivided population (10 subpopulations of 12 individuals each) with high migration rates (5 to 10 migrants per generation over the total population) will suffer effects of moderate inbreeding within subpopulations and yet likely retain no more total gene diversity than would a panmictic population. Unfortunately, many captive breeding programs currently result in just such a population structure. Given the primitive state of knowledge about the effects of population subdivision, management plans need to be carefully monitored and revised when necessary.

A preliminary attempt has been made to use computer simulations to explore some genetic consequences of evolutionary forces acting on managed populations. Much more detailed examination of the genetics of small populations is possible by computer simulation. There is perhaps a greater need at this point, however, to obtain empirical data on genetic responses by particular species of interest. If possible, work should focus on developing generalizations that allow prediction of the genetic behavior of a population based on knowledge of its biology and the biology of taxonomically and ecologically similar organisms. As empirical data on the effects of in-

breeding, the importance of genetic variation to captive and wild populations, and the factors maintaining or depleting variation are gathered, computer modeling can focus on factors of most importance, using appropriate parameters. Computer models such as the one presented here can be useful almost immediately in the comparison of possible alternative management plans being considered for species propagated in captivity.

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Estimates of Lethal Equivalents and the Cost of Inbreeding in Mammals

KATHERINE RALLS

Department of Zoological Research National Zoological Park Smithsonian Institution Washington, D.C. 20008, U.S.A.

JONATHAN D. BALLOU

Department of Zoological Research National Zoological Park Smithsonian Institution Washington, D.C. 20008, U.S.A.

ALAN TEMPLETON

Department of Biology Washington University St. Louis, Missouri 63130, U.S.A.

Abstract: The costs of inbreeding in natural populations of mammals are unknown despite their theoretical importance in genetic and sociobiological models and practical applications in conservation biology. A major cost of inbreeding is the reduced survival of inbred young. We estimate this cost from the regression of juvenile survival on the inbreeding coefficient using pedigrees of 40 captive mammalian populations belonging to 38 species.

The number of lethal equivalents ranged from -1.4 to 30.3, with a mean of 4.6 and a median of 3.1. There was no significant difference between populations founded with wild-caught individuals, a mixture of wild-caught and captive-born individuals, and individuals of unknown origin. The average cost of a parent-offspring or full sibling mating was 0.33, that is, mortality was 33% higher in offspring of such matings than in offspring of unrelated parents. This is likely to be an underestimate.

Resumen: Los costos de procreación en consanguinidad en poblaciones naturales de mamíferos son desconocidos a pesar de su importancia teórica en los modelos genéticos y sociobiológicos y en sus aplicaciones prácticas para la biología de la conservación. Uno de los costos mayores de la procreación en consanguinidad es la disminución en la sobrevivencia de las crías consanguíneas. Estimamos este costo por medio de la regresión de la sobrevivencia juvenil en el coeficiente de procreación en consanguinidad utilizando pedigrís de 40 poblaciones de mamíferos en cautiverio pertenecientes a 38 especies.

El número de equivalentes letales varió de -1.4 a 30.3, con una media de 4.6 y una mediana de 3.1. No bubo diferencia significativa entre poblaciones formadas a partir de individuos silvestres capturados, a partir de una mezcla de individuos silvestres capturados, y a partir de individuos de orígen desconocido. El costo promedio del apareamiento de padre-cría o bermanos completamente consanguíneos fue de 0.33, es decir, la mortalidad fue 33% más alta en las crías de tales apareamientos que en las crías de especies no relacionadas. Es probable que este cálculo sea una subestimación

Introduction

Many studies of laboratory, domestic, and zoo animals have documented reduced survival and fecundity of inbred young (Wright 1977; Ralls & Ballou 1983; Sausman 1984; Templeton & Read 1984). Inbreeding depression is thus a major concern in the management of small populations, and estimates of the cost of inbreeding are of considerable importance to conservation biology.

However, inbreeding can increase an individual's inclusive fitness by producing young that share more of its genome. Thus, when inbreeding has little or no genetic cost, there should be strong selective advantage for inbreeding as well as recognition and cooperation among kin (Wilson 1976; May 1979). The cost of inbreeding is therefore of theoretical importance as well.

Calculations of the total cost of inbreeding in natural populations would involve considering the effects of inbreeding on several components of fitness. However, the "cost of inbreeding" that appears in a variety of theoretical models (Dawkins 1976; Bengtsson 1978; Parker 1979; Smith 1979; Feldman & Christiansen 1984) is defined solely in terms of the survival of inbred young relative to non-inbred young. There are almost no estimates of this quantity in natural populations of mammals (Packer 1979).

We estimate this cost from pedigrees of 40 captive mammalian populations belonging to 38 species.

Methods

Morton, Crow, & Muller (1955) developed a log model for estimating the cost of inbreeding from the rate at which juvenile survival decreases with increasing amounts of inbreeding. Specifically,

$$S = e^{-(A + BF)}$$
 (1)

where S is the proportion of individuals surviving to some age, F is the inbreeding coefficient, A is considered a measure of death due to environmental causes and the genetic damage expressed in a randomly mating population, and B is a measure of the rate at which survival decreases with increasing inbreeding.

Makov & Bittles (1986) evaluated the use of this and several other equations to estimate effects of inbreeding in humans. They found that many different models could adequately detect significant inbreeding effects; however, different models resulted in different values of A and B. Because of the limited range of inbreeding levels in available data from human populations (F = 0-0.125), they were unable to determine which equation most adequately modeled data on inbreeding effects in humans. They suggested that different equations could more effectively be evaluated in animal populations with wider ranges of inbreeding levels.

We evaluated the log transformed equation (1) and two other equations, using several of our largest data sets with relatively wide ranges of inbreeding levels (F = 0-0.5). The two additional equations were

$$S = A + B(F) \tag{2}$$

$$\arcsin\sqrt{S} = A + B(F)$$
 (3)

where S, A, B, and F are the same values as in equation (1). Model 2 was used because it represents the simplest linear relationship between the variables. Model 3 (angular transformation) was used since it is often recommended for estimating proportions (Sokal & Rohlf 1969). Weighted least squares regression, with a small sample size correction (Templeton & Read 1984), was used to estimate the parameters for each of the models. The total percentage of variation explained by the equation (R²) was used to evaluate which model best fitted the data.

When analyzing pedigrees of zoo animals, care must be taken to distinguish inbreeding depression from hybridity effects or "outbreeding depression" (Templeton & Read 1984; Templeton et al. 1986). We therefore carried out the analysis developed for this purpose by Templeton & Read (1984) on those pedigrees with adequate sample sizes but found no evidence of outbreeding depression (Templeton & Read 1984; unpublished data).

Inbreeding coefficients (F) were calculated for each animal in each pedigree, relative to the founders of the population. Methods for calculating F from pedigree data are given by Ballou (1983). F is the probability that the two alleles present at a given locus are "identical by descent"—that is, are derived by replication of a single allele from a common ancestor. F ranges from 0 in a non-inbred individual to 1.0 in a completely inbred (homozygous) individual (Crow & Kimura 1970). The effect of inbreeding is often less severe in individuals with inbred ancestors (Bowman & Falconer 1960; Lorenc 1980; Templeton & Read 1984), but we were unable to exclude them from the analysis because this eliminated all levels of inbreeding except F = 0.25 in many pedigrees

Levels of inbreeding varied among pedigrees (Table 1). For each level of inbreeding represented in a particular pedigree, we calculated the proportion of animals that survived to a criterion age. This was 180 days for the larger species and one-half the age at sexual maturity for the smaller ones (Table 2). Ideally, studies of the relationship between inbreeding and juvenile mortality should be based upon the total mortality before reaching reproductive age (Cavalli-Sforza & Bodmer 1971), but we were unable to follow many individuals for this period because zoo animals are often transferred to other institutions before reaching reproductive age. Considering survival to a criterion age less than repro-

Table 1. Comparison of models used for estimating cost of inbreeding.

SPECIES ^a Short bare-tailed opossum	Maximum	Comparison of R ² Values MODEL					
	Inbreeding level	Log (1)	Linear (2)	Arcsin (3)			
	.328	.80	.79	.77			
Elephant shrew	.125	.05	.06	.07			
Golden lion tamarin	.375	.35	.26	.26			
Greater galago	.250	.17	.14	.13			
Maned wolf	.312	.77	.83	.83			
Bush dog	.500	.02	.00	.00			
Pygmy hippopotamus	.375	.45	.55	.55			
Dorcas gazelle	.375	.64	.66	.63			

^a Scientific names listed in Table 2.

ductive maturity tends to underestimate the cost of inbreeding, as inbred mortality increases more rapidly than non-inbred mortality with increasing age in some species (Ralls, Brugger, & Glick 1980; unpublished data).

Results

Table 1 shows the results of the three models applied to eight of the largest data sets. R² values were highest for the Linear model (2) in 2 populations, highest for the Arcsin model (3) in 2 populations, and highest for the log model (1) in 4 populations. As Makov and Bittles (1986) concluded, no one model was clearly better than the others; R² values ranged over only a few percentage points across the models.

The log transformed model (1) has been used extensively in the literature to estimate number of lethal equivalents and is the theoretically expected model, if it is assumed that genetic and environmental influences are independent of each other with respect to survival (Morton, Crow & Muller 1955). Use of this model also facilitates comparisons with A and B values already published in the literature. We therefore selected it for all subsequent analyses.

Estimates for A and B are shown in Table 2. Values of A ranged from 0.03 to 1.11 with a mean of 0.33 and a median of 0.32. Values for B ranged from -0.68 to +15.16, with a mean of +2.33 and a median of +1.57(Fig. 1). Of the 40 populations, 36 had positive slopes, which clearly indicates an overall trend towards higher levels of juvenile mortality with increasing inbreeding coefficients (Sign test, P < .001). This relationship was statistically significant—that is, the slope of the line was significantly greater than zero—in only 9 (23%) of the populations. However, most of our sample sizes were small and distributed over only a few levels of inbreeding. The statistical power to detect slopes significantly: greater than zero was therefore limited. Considering only those populations in which the relationship between inbreeding and survival is significant would be

likely to greatly overestimate the average cost of inbreeding in mammals. Limiting the analysis to only those species with relatively large data sets increases the power of the statistical comparisons but reduces the number of species that can be analyzed. Only 10 species had more than five levels of inbreeding and total sample sizes over 100. Six of these 10 had slopes significantly different from zero; the average B value was 1.98, with a median of 1.64. These B values did not differ significantly from those in the overall data set (Mann-Whitney U test, P > 0.05).

The distributions of B by order are shown in Figure 2. Median values were between one and two except for the Carnivora. There were no statistically significant differences between average B values in populations founded with wild-caught individuals ($\bar{x} = 2.57$, n = 18), a mixture of wild-caught and captive individuals ($\bar{x} = 2.42$, n = 11), and individuals of unknown origin ($\bar{x} = 1.95$, n = 10) (Kruskal-Wallis Test, P = 0.88).

The number of lethal equivalents per gamete lies between B and A but is usually very close to B (Cavalli-Sforza & Bodmer 1971; Crow & Kimura 1970). The number per zygote or individual is twice the number per gamete, thus our estimates of the average number of lethal equivalents per individual are twice the values of B in Table 2, with a mean of 4.6 and a median of 3.1. We estimated the cost of inbreeding for matings between first-degree relatives (parents and their offspring or full siblings) by solving equation (1) for each species using F = 0 and F = 0.25 to obtain the predicted survivorship at these levels of inbreeding. The cost of inbreeding (i) at F = 0.25 is then equal to

$$i = 1 - \left[\frac{\text{Survivorship at F} = 0.25 : e^{-(A + .25B)}}{\text{Survivorship at F} = 0 : e^{-(A)}} \right]$$
$$= 1 - e^{-.25B}. \tag{4}$$

The average cost of inbreeding between first degree relatives, calculated by averaging the costs across all populations, was 0.33 (Table 2). Solving equation (4)

Table 2. The cost of inbreeding in 40 mammalian populations.

TAXON	Survival to Age (Days)	N	Founder ^a Type	No. of Inbred	Model	Estimates	Model	Cost of Inbreeding ^c	Data Source
				Levels	Α	В	R ²	at $F = 0.25$	
MARSUPIALIA	75	25.	597		0.03	0 (26	0.00	10	National Zon
Short bare-tailed opossum (Monodelphis domestica)	75	251	W	6	0.03	0.43 ^b	0.80	.10	National Zoo
Parma wallaby	180	17	w	5	0.32	1.69	0.47	.34	National Zoo
(Macropus parma)		-,			5-				
NSECTIVORA									
Elephant shrew	21	218	w	7	0.28	2.12	0.05	.41	National Zoo
(Elephantulus rufescens)									
PRIMATES	100	22	397	2	0.22	2.22	0.00	42	National 700
Black spider monkey (Ateles fusciceps	180	23	W	3	0.23	2.22	0.88	.43	National Zoo
robustrus)									
Saddle-backed tamarin	180	233	U	2	1.11	1.86	_	.37	Monell Chemical
(Saguinus fuscicollis)	200	-33	Ü	-		1.00		.57	Senses Center
lliger's saddle-backed	180	406	U	4	0.40	7.92	0.40	.82	Rush-Presbyterian
tamarin									St. Luke's Medica
(Saguinus f. illigeri)									Center
Golden lion tamarin	180	974	w	18	0.54	2.15 ^b	0.35	.42	1984 Studbook
(Leontopithecus r. rosalia)			4						
Ring-tail lemur	180	53	M	4	0.34	0.13	0.01	.03	Oregon Primate
(<i>Lemur catta</i>) Black lemur	180	12	397	•	0.50	2 =0			Research Center
(Lemur macaco)	180	43	w	3	0.52	2.78	0.87	.50	Oregon Primate
Brown lemur	180	136	М	6	0.32	9.17	0.94	.90	Research Center
(Lemur fulvus)	100	130	141	U	0.52	9.17	0.94	.90	Oregon Primate Research Center
Greater galago	180	251	М	29	0.45	1.69b	0.17	.34	Oregon Primate
(Galago c. crassicaudatus)		-,-		-/	0.17	2.07	0.27	.5.	Research Center
Melanotic galago	180	54	M	4	0.36	0.48	0.19	.11	Oregon Primate
(Galago c argentatus)									Research Center
Crab-eating macaque	180 .	237	U	3	0.37	0.29	0.56	.07	New England Prima
(Macaca fascicularis)									Research Center
Celebes black ape	180	86	U	3	0.38	2.84	0.70	.51	Oregon Primate
(Macaca nigra)	100	2/=		,		5 2 2		22	Research Center
Chimpanzee (Pan troglodytes)	180	247	U	4	0.35	1.05	0.67	.23	Yerkes Primate
RODENTIA									Center
Climbing rat	45	49	U	5	0.22	014	0.03	0.4	N
(Tylomys nudicaudus)	4)	47	U)	0.23	-0.14	0.02	04	National Zoo
Wied's red-nosed rat	30	23	w	2	0.05	15.16		.98	National Zoo
(Wiedomys pyrrborbinos)	30	-5	••	2	0.07	13.10	_	.90	National Zoo
Rock cavy	90	132	U	3	0.12	0.77	0.87	.18	National Zoo
(Kerodon rupestris)							0.07		THEOLOGIC LOO
alt-desert cavy	90	17	w	2	0.08	7.21	_	.34	National Zoo
(Dolichotis salinicola)									
couchi	135	36	U	5	0.30	2.20	0.17	.42	National Zoo
(Myoprocta pratti)		-							
Soris	75	53	U	6	0.26	1.15	0.33	.25	National Zoo
(Octodontomys gliroides)	60	1/1	59/	,		th		2.7	
(Cercomys cunicularus)	60	161	W	4	0.10	0.94^{b}	0.91	.21	National Zoo
CARNIVORA									
laned wolf	180	338	M	4	0.52	-0.68	0.77	10	1002 (- 41 - 1
(Chrysocyon brachyurus)	100	330	141	7	0.52	-0.08	0.77	19	1983 Studbook
ush dog	180	176	W	9	0.54	0.24	0.02	.06	1002 Studbook
(Speothos venaticus)		-,-		,	0.71	0.21	0.02	.00	1983 Studbook
umatran tiger	180	427	M	12	0.49	0.01	0.00	.003	1983 Studbook
(Panthera tigris sumatrae)								.505	-, -, -, -, -, -, -, -, -, -, -, -, -, -
ERISSODACTYLA									
ebra	180	50	U	2	0.30	1.56	-	.32	National Zoo
(Equus burchelli)									¥
RTIODACTYLA	B. 100	, I				200		9	
ygmy hippopotamas	180	419	w	12	0.33	1.59 ^b	0.45	.33	1982 Studbook
(Choeropsis liberiensis)									

Table 2. Continued

TAXON	Survival to		Founder ^a Type	No. of Inbred Levels	Model Estimates		Model	Cost of Inbreeding	Data
	Age (Days)	N			A	В	R^2	at F = 0.25	Source
Reeves muntjac (Muntiacus reevesi)	180	75	М	9	0.19	1.20	0.37	.26	National Zoo
Eld's Deer (Cervus eldi thamin)	180	24	M	2	0.31	7.57	_	.85	National Zoo
Pere David's Deer (Elapburus davidianus)	180	39	С	7	0.17	0.63 ^b	0.74	.15	National Zoo
Reindeer (Rangifer tarandus)	180	50	w	4	0.32	4.20	0.71	.65	National Zoo
Giraffe (Giraffa camelopardalis)	180	19	w	2	0.29	2.24	-	.43	National Zoo
Kudu (Tragelaphus strepsiceros)	180	25	w	2	0.37	-0.03	_	01	National Zoo
Bongo (Tragelaphus eurycerus)	180	74	w	3	0.23	-0.55	0.74	15	1984 Studbook
Gaur (Bos gaurus)	180	182	w	6	0.18	0.51	0.36	.12	Hinz & Foose, 1982
Scimitar-horned oryx (Oryx dammab)	180	81	М	2	0.09	4.63	_	.69	National Zoo
Wildebeest (Connochaetes taurinus)	180	42	w	11	0.33	0.28	0.02	.07	National Zoo
Dik-dik (Madogua kirki)	180	20	М	3	0.80	0.59	0.12	.14	National Zoo
Dorcas gazelle (Gazella dorcas)	180	143	М	15	0.34	1.85 ^b	0.64	.37	National Zoo
Spekes gazelle (Gazella spekei)	30	64	w	5	0.22	3.08 ^b	0.92	.54	Templeton & Read, 1983
•		Mean	:		0.33	2.33		0.33	
		Media	an:		0.32	1.57		0.33	
			r Quartile:		0.23	0.45		0.09	
			r Quartile:		0.39	2.81		0.47	

^a Founder Type: W = All founders wild-caught.

using the average B value (2.3) results in a cost of inbreeding of 0.44. However, the statistic of interest here is the estimate of the expected value of the cost of inbreeding rather than the cost of inbreeding calculated from the expected value of B. We therefore base our discussion on an average cost of inbreeding of 0.33. The distribution of the cost of inbreeding between first degree relatives is shown in Figure 3.

Discussion

The costs of inbreeding varied widely among captive populations. This is not surprising since one would expect populations to differ in their level of susceptibility to inbreeding. However, in many cases, the models fit the data very poorly and only a small proportion of the variance was explained. These variable results probably reflect the heterogeneous data used for the analysis. The available data for the populations surveyed differed in sample size and the range and number of levels of inbreeding. Nevertheless, these results do provide data on the costs of inbreeding and number of lethal equivalents in a wide variety of captive populations and allow analyses of general trends and patterns.

The median number of estimated lethal equivalents for the captive mammalian populations we examined was 3.1. This figure is similar to estimates for other animal populations. Humans (May 1979), Drosophila (Dobzhansky 1970), and the great tit, Parus major (Bulmer 1973), are thought to have about two lethal equivalents per individual, and the Japanese quail, Coturnix coturnix japonica, is thought to have about 3.4 (Sittmann, Abplanalp & Fraser 1986). Our estimates for captive carnivores, although based on only three populations, were quite low. More carnivore populations should be studied to determine if this is characteristic of the order or unique to the data sets we examined.

May (1979), assuming the number of lethal equivalents in humans was 2.2, estimated the cost of breeding in humans at F = 0.25 to be .42. However, his equation for calculating the inbreeding cost contained an error. The correct cost, based on formula (4), is .24. This es-

C = Founders captive-born.

M = Founders were a mix of wild-caught and captive-born.

U = Source of founders unknown. ^bB (slope) significantly different than zero at the 0.05 level.

Predicted inbred survival: e^{-(A+.25B)} Cost of inbreeding for F = 0.25: = 1 -(Predicted non = inbred survival; e



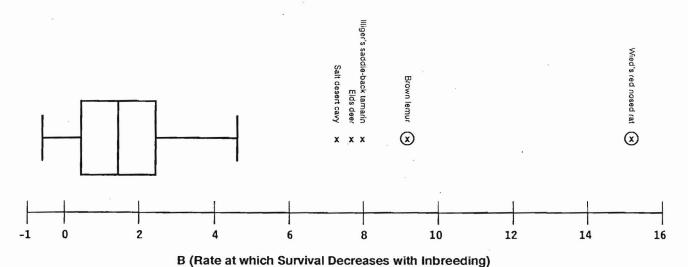


Figure 1. Box plots of B, a measure of the rate at which survival decreases with increasing inbreeding, for 40 mammalian populations. The median (middle vertical line in box), upper and lower quartiles (left and right ends of box), upper and lower inner fences (vertical lines), outlying values (x), and values beyond the outer fences (x) are shown (Hoaglin, Mosteller, & Tukey 1983).

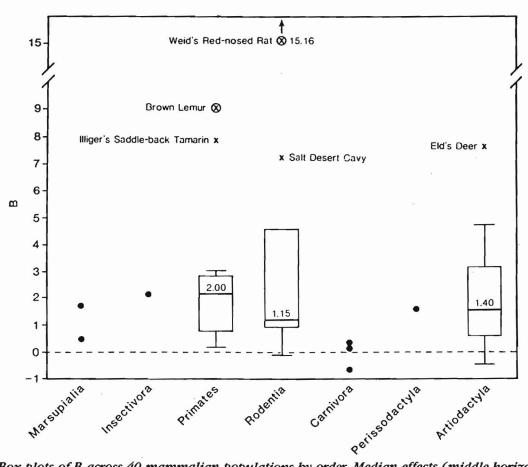


Figure 2. Box plots of B across 40 mammalian populations by order. Median effects (middle borizontal line in box), upper and lower quartiles (upper and lower ends of boxes), upper and lower inner fences (borizontal lines), outlying values (x), and values beyond the outer fences (x) are shown for the distribution of B in primates, rodents, and artiodactyls. Results for individual populations in other orders are shown by solid dots.

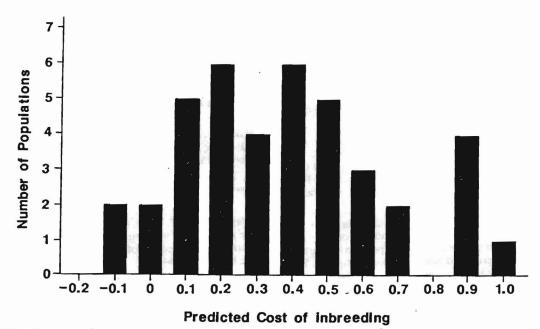


Figure 3. Distribution of the predicted cost of inbreeding in matings resulting in young with an inbreeding coefficient of 0.25 (i.e., matings between parents and offspring or full siblings) for 40 mammal populations.

timate is slightly lower than the average .33 cost of inbreeding found in our mammal populations.

The total costs of inbreeding in natural populations are probably considerably higher than our estimates. First, our estimate of the cost based on only one component of fitness (survival of young) is probably low. We were unable to count early embryonic deaths, exclude individuals with inbred ancestors, and follow individuals until the age of reproductive maturity. Furthermore, mortality rates of inbred young may be higher in natural populations, because many weak young that might die in the wild survive in captivity with the assistance of veterinary care. Second, there are likely to be additional costs of inbreeding in other components of fitness, such as litter size in species that normally bear multiple young and a reduction in fecundity of the inbred young that do survive to reproductive age (Wright 1977). (The reported higher recruitment rate of inbred young in the great tit (van Noordwijk & Scharloo 1981) is not supported by the data (Greenwood & Harvey 1982).) Third, inbred individuals with low levels of heterozygosity may be highly susceptible to viral epidemics (O'Brien et al. 1985).

Considering only the cost of inbreeding relative to the gain in inclusive fitness due to inbreeding, theory suggests that females should not mate with their fathers or sons unless the cost of inbreeding is less than .33 (Smith 1979). Although this is a highly oversimplified model, our data suggest that the cost of inbreeding in mammals is usually high enough (mean = .33) that females should not mate with their closest relatives. The limited data on the frequency of such matings in natural

populations of mammals agree with this prediction. Estimates based on observations of identifiable individuals during long-term field studies range from zero to 2% in 9 of 14 well-studied mammalian populations, and the highest documented frequency is 5.5% (Ralls, Harvey & Lyles 1986).

Estimates of the cost of inbreeding also have important applications to conservation biology. The effects of the accelerated rate of inbreeding in small populations, in both captivity and the wild, can potentially drive a population towards extinction (Gilpin & Soulé 1986). The susceptibility of most small populations of conservation interest to elevated levels of inbreeding is unknown, and predicting the degree to which mortality may be increased as a result of inbreeding is impossible. The results presented here provide estimates of the general relationship between the rates of inbreeding and juvenile mortality in a large variety of captive mammal populations and will be useful in developing conservation management programs for small populations (Ballou, in press). Unfortunately, however, our estimates of the cost of inbreeding for individual populations varied greatly and were not clustered near the mean value. Thus, the severity of inbreeding effects in any unstudied mammalian population is quite likely to differ from that predicted by models based on average values.

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Breeding Plans for Small Populations, Based on the Dynamics of Quantitative Genetic Variance

Russell Lande

Department of Ecology and Evolution

University of Chicago

Chicago, Illinois 60637 USA

Address for editorial correspondence:

Russell Lande
Dept. of Ecology and Evolution
University of Chicago
915 East 57th Street
Chicago, IL 60637

Habitat destruction and fragmentation will often make it necessary to protect small populations in nature preserves or to establish captive breeding programs to prevent their extinction. In most wild populations, ecological factors are likely to be more important than genetic factors in determining the probability of persistence into the forseeable future. This is because a wild population that can avoid extinction from Allee effects, edge effects, demographic and environmental stochasticity, and local extinction and colonization is also likely to be large enough to prevent appreciable inbreeding depression or loss of genetic variability from random genetic drift (Lande 1988). However, in wild populations artificially reduced to a small size, genetic factors, and their interactions with ecological factors, become increasingly important.

In the captive environment, demographic fluctuations caused by predation, diseases, weather and food supply can be at least partially controlled. If the goal of the captive breeding program is captive release into the wild at a later date, the breeding structure and size of the population can be managed to maintain a high proportion of the original genetic variability present in the wild population from which it was established. This is likely to increase its chance of survival upon reintroduction to the wild, since additive genetic variance is necessary for adaptation to a changing environment. Genetic considerations should therefore play a dominant role in breeding plans for captive populations with this goal. However, even in a carefully controlled environment, demographic factors such as population growth rate, age distribution and sex ratio should not be ignored (Foose 1980).

Soulé et al. (1986) proposed for captive populations the management goal of maintaining 90% of the genetic variability present in the original (base) population for a period of 200 years. Using a model of an ideal population with discrete, nonoverlapping generations and a Poisson distribution of progeny numbers, they computed by numerical methods the final or equilibrium population size that would be necessary to achieve the goal with a certain initial number of founders for a species with a given population growth rate

and generation time, assuming geometric growth of the population up to the final size. Their model accounted for the loss of genetic variability (i.e., heterozygosity or purely additive genetic variance in quantitative traits) caused by random genetic drift in a finite population. Already this or similar goals, and the breeding plans recommended by Soulé et al. (1986) to meet them, have been adopted in management plans for captive populations of several endangered species (e.g., for the gorilla, cheetah, addax, Asian wild horse, scimitar-horned oryx, greater one-horned Asian rhinoceros, and Florida panther [plans available from AAZPA Conservation Director]).

Most morphological, behavioral and physiological measurements are genetically complex (polygenic) quantitative traits, which are generally thought to be of critical importance in adaptation to natural environments (Franklin 1980; Lande and Barrowclough 1987). Here we investigate the influence of additional factors affecting the maintenance of additive genetic variance in quantitative characters, i.e. mutation, immigration from the wild, selection in the captive environment, and population subdivision. It is shown that these factors permit smaller final population sizes and founder numbers necessary to achieve the goal of preserving a certain fraction of the original genetic variability for a particular period of time. By using a continuous time model, which is probably more accurate than the discrete generation model for most real populations with overlapping generations, it is possible to derive general analytical solutions that allow breeding plans to be specified for management goals involving the maintainance of any fraction of the original genetic variability for any time period. The text develops the general models and provides explicit evaluations in graphical form for the particular management goal suggested by Soulé et al. (1986). Analytical formulas are presented in the Appendix.

Dynamics of additive genetic variance in quantitative traits

In the captive environment natural selection on most traits is likely to be greatly reduced or absent, so that random genetic drift and mutation are the most important factors affecting genetic variation in a population closed to immigration. Nevertheless, there may be substantial selection on some characters for adaptation to captivity, and evolutionary changes resembling domestication are likely to occur in captive populations, e.g. selection for docility and high reproduction (Arnold, this vol.). We first analyze random genetic drift and mutation in a population founded from a given initial number of individuals which grows to a constant final number. Immigration, selection, and subdivision in a population of constant size are then analyzed.

Random genetic drift and mutation

Let V_g be the (purely) additive genetic variance in a quantitative character. The input of additive genetic variance from mutation each generation, V_m , is assumed to be a constant independent of the amount of genetic variance already in the population. This can be justified by a detailed model of mutation in which at each locus there is a wide range of possible allelic effects with each allele mutating at the same rate with the same distribution of mutational changes in effect, although these parameters may differ between loci (Kimura 1965; Lande 1975). In a diploid randomly mating population, the expected rate of loss of heterozygosity, or additive genetic variance in a quantitative trait, due to random genetic drift in the absence of selection is $1/(2N_e)$ per generation, where N_e is the effective population size (Wright 1931, 1951; Latter and Novitski 1969). Measuring time, t, in generations, the dynamics of the expected value of the additive genetic variance, $\overline{V_g}$, under random genetic drift and mutation obey

$$\frac{\mathrm{d}\overline{V_g}}{\mathrm{d}t} = -\frac{\overline{V_g}}{2N_e} + V_m \tag{1}$$

(Clayton and Robertson 1955; Lande 1979).

The effective population size may change with time. Here we assume that it is always a constant multiple of the actual population size (N/N = constant) and, starting from an

effective number of founders, $N_e(0)$, the population grows exponentially at the rate r per generation until reaching the final effective size, K_e . Thus the time in generations to reach the final size is $\tau = r^{-1} \ln(K_e/N_e(0))$ and the effective population size follows

$$N_e(t) = \begin{cases} N_e(0)e^{rt} & \text{for } t < \tau \\ K_e & \text{for } t \ge \tau \end{cases}$$
 (2)

To account for the age distribution of the founders, $N_e(0)$ can be approximated using standard (discrete generation) formulas involving sex-ratio and distributions of progeny numbers (Crow and Kimura 1970; Lande and Barrowclough 1987), starting with the initial total reproductive values of males and females (Fisher 1958; Pollard 1973) instead of the actual numbers of each sex.

For a population with overlapping generations, the generation time, T, is defined as the average age of mothers and fathers of newborn individuals in a population with a stable age distribution (assuming that the sex ratio of offspring is independent of parental age) (Leslie 1966; Hill 1979). With a constant life history (age-specific mortality and fecundity rates independent of time), T depends on the growth rate of the population, being smaller for populations that are more rapidly increasing (Leslie 1966). Because the change in generation time within species is likely to be small in comparison to the range in generation times among species managed by a single institution, and to simplify the analysis and facilitate comparison of the general results with those obtained by Soulé et al. (1986) we assume that T is approximately constant and ignore other complications caused by changes in age structure.

Fig. 1 displays results accounting for random genetic drift, but ignoring mutation (assuming $V_m = 0$). The upper right panel with r = 0.5 is nearly identical to Fig. 1 of Soulé et al. (1986) except that the axes have been reversed to emphasize that we wish to determine the final effective population size, K_p , necessary to preserve 90% of the

original additive genetic variance in the base population after 200 years, given T, $N_e(0)$ and r. An important feature of Fig. 1 is that when mutation is neglected the final effective population sizes needed to achieve this goal are extremely large for species with generation times of a few years or less. Note that when r = 0.2 and $N_e(0) = 20$ the management goal can not be attained for species with generation times less than 21.6 years.

[Fig.1 here]

Fig. 2 shows analogous results incorporating a typical level of mutation that has been observed in quantitative characters in a variety of organisms, $V_m = 10^{-3} V_e$ where V_e is the environmental variance in the character that would be expressed in a genetically uniform population (Lande 1975; Hill 1982; Lynch 1988a). We assume that the typical quantitative character in the base population has a heritability $h^2 = V_g(0)/[V_g(0) + V_e] = 0.5$ so that $V_g(0) = V_e$. Franklin (1980) apparently chose these same values for mutability and heritability when he suggested that in the absence of selection a population with $N_e = 500$ would maintain typical levels of additive genetic variance (Lande and Barrowclough 1987). It should therefore come as no surprise that, even for species with very short generation times, the value of K_e needed to achieve the management goal never exceeds 450 (or 90% of Franklin's number).

Comparison of Figs. 1 and 2 reveals that accounting for mutation allows the management goal to be met with a smaller number of founders. In the discrete generation model, Soulé et al. point out that $N_e(0)$ must be greater than 5 to preserve 90% of the genetic variability in the base population, since if $N_e(0) = 5$ then $1/(2N_e(0)) = 0.1$ of the genetic variability will be lost in the first generation. The accumulation of genetic variance by mutation over several generations can compensate for a loss of this magnitude, so that founder numbers smaller than previously proposed may be acceptable.

[Fig.2 here]

Immigration from the wild

Loss of genetic variance in a small captive population can be offset by immigration

from the wild, assuming that the wild population remains large enough to maintain its original genetic variability. For a given effective population size, immigration from the wild also has the effect of retarding random genetic drift in the mean phenotype of the captive population away from that in the wild population. In an equilibrium analysis of the "island model" Wright (1931, 1951) showed that immigration of a few individuals per generation will prevent substantial loss of genetic variability or differentiation by random genetic drift. Here we analyze a relatively simple model of the dynamics of additive genetic variance and random genetic drift in the mean phenotype of a small captive population subject to immigration from a large wild population.

The immigration rate from the wild to the captive population is defined as m, such that a proportion m of the captive population is replaced by wild individuals matched for sex and age. Let the wild population have additive genetic variance $V_g(0)$ in a quantitative character with mean phenotype $\overline{z}(0)$, which are assumed to remain constant. The variance in the probability distribution of the mean phenotype in the captive population caused by random genetic drift is denoted as $V_{\overline{z}} = E[(\overline{z}(t) - \overline{z}(0))^2]$. In this definition it is assumed that the mean phenotype is measured on a hypothetical large number of progeny; measurement of the actual population with effective size N_e would increase the expected variance in $\overline{z}(t)$ by an amount $(\overline{V_g} + V_e)/N_e$. The dynamics of the expected additive genetic variance within the captive population and the expected random genetic drift in its mean phenotype follow the coupled pair of equations

$$\frac{\mathrm{d}\overline{V_g}}{\mathrm{d}t} = -\frac{\overline{V_g}}{2N_p} + V_m + m \left[V_g(0) - \overline{V_g} \right] + \frac{m(1-m)}{2} V_{\overline{z}}$$
 (3)

$$\frac{\mathrm{d}V_{\overline{z}}}{\mathrm{d}t} = -2mV_{\overline{z}} + \frac{\overline{V_g}}{N_{\rho}} \qquad \text{assuming } m << 1.0$$
 (4)

(Lande 1979; Lynch 1988b). The last two terms in equation (3) correspond respectively to

the genetic variance carried by the immigrants and the genetic variance that is produced by hybridization between populations. For simplicity we assume that N_e is constant and equal to the size of of the founder population. We also assume that immigration occurs at a small constant rate, $m \ll 1.0$.

Fig. 3 (left) shows that with typical levels of mutation even one effective migrant every few generations ($N_e m = 1/4$, 1/2, or 1) substantially reduces the effective population size necessary to achieve the management goal. The actual number of immigrants, Nm, differs from the effective number of immigrants. $N_e m$ can be estimated from the expected reproductive value of the immigrants times $N_e N$ for the captive population.

Fig. 3 (right) depicts the amount of random genetic drift in the mean phenotype for populations managed to maintain 90% of the original genetic variance after 200 years (as shown in Fig. 3 left). The mean phenotype in the population is expected to drift less than one phenotypic standard deviation in 200 years, except for populations with generation times less than 0.5 year in the absence of immigration. When $N_e m$ is in the range of 1/4 to 1, more phenotypic differentiation is expected to occur than in the absence of immigration, unless the generation time is less than 1 or 2 years. This result, which at first seems counterintuitive, occurs because these immigration rates allow the management goal to be met with smaller effective population sizes, which increases the rate of random genetic drift in the mean phenotype. With $N_e m > 2$, there is expected to be less phenotypic differentiation than in the absence of immigration because the stabilizing influence of immigration on the mean phenotype is stronger than the random genetic drift caused by reduced N_e .

[Fig. 3 here]

Selection in the captive environment

Newly established captive populations often experience substantial selection to adapt to the captive environment. This includes novel physical conditions such as confinement, and new social and biotic factors such as isolation or crowding, and exposure to an altered set of pathogens. There may be additional artificial selection by the managers (consciously or unconsciously) for docility and high reproductive rate, especially during the early history of the population. In addition, relaxation of natural selection may result in the gradual deterioration of some characters subject to directional mutation, and maintained by mutation-selection balance in wild populations, especially traits most closely related to fitness in the wild, e.g. sensory acuity, agility and cognitive function. Higher animal species may also experience a loss of culturally transmitted information during a period of a generation or more in captivity.

The effect of selection in the captive environment on the additive genetic variance of a particular trait can be modelled crudely by the loss of a constant proportion s per generation, so that equation (1) is modified to

$$\frac{d\overline{V_g}}{dt} = -\left(\frac{1}{2N_e} + s\right)\overline{V_g} + V_m \quad . \tag{5}$$

Fig. 4 (*left*) reveals that with typical rates of mutation, if s is as small as 1%, even an infinitely large population will not maintain 90% of the original genetic variance for 200 years, unless the generation time of the species is rather long. It may therefore be impossible to meet the management goal for characters under appreciable selection in captivity. Instead of causing dispair, this conclusion can be turned around, in the manner of Fig. 4 (*right*). For species with short generation times, populations with a moderate effective size will maintain nearly as much genetic variance in selected characters as an infinitely large population.

Deleterious or undesirable evolution in captive populations, caused by adaptation to captivity or by mutation and random genetic drift, can be counteracted by immigration from the wild, or by artificial selection imposed by managers. To have much effect in this context, the rate of immigration would have to be comparable to the strength of selection

 $(m \ge s)$. The imposition of artificial selection to counteract natural selection in captivity would help to prevent change in the mean phenotype, but may also increase the rate of loss of additive genetic variance. Another way of reducing evolutionary changes in a captive population is by increasing generation time and equalizing progeny numbers. Any required artificial selection should be exerted within progeny groups, with readjustment to equal size after selection (Lande and Barrowclough 1987).

[Fig. 4 here]

Population subdivision

Subdivision of a population and random genetic drift within the subpopulations converts the original genetic variation within the base population into genetic variation between subpopulations. Population subdivision also allows genetic variation between populations to accumulate by random genetic drift and fixation of new mutations. Once alternative alleles at a locus are fixed in different subpopulations, this component of genetic variability is permanently maintained and can not be lost as long as the subpopulations persist. Splitting a population into separate subpopulations with no gene flow or migration among them is therefore a powerful way of maintaining genetic variability, even though the total population size may be small.

Consider a panmictic population with an effective population size N_e that is divided at time 0 into n separate subpopulations, each with constant effective size N_e/n . The additive genetic variance maintained by this population structure after t generations can be measured by the amount that would exist if the all subpopulations were randomly mated and allowed to attain linkage equilibrium (e.g. after several generations at large population size). Since purely additive genetic variance within populations is expected to double when converted by random genetic drift to variation among populations (Wright 1951) the total additive genetic variance in the population after panmixia, V_{oP} , is expected to be

$$\overline{V_{gP}}(t) = \overline{V_{g}}(t) + \frac{1}{2}(1 - 1/n)V_{\overline{z}}(t)$$
 (6)

where $\overline{V_g}(t)$ and $V_{\overline{z}}(t)$ are respectively the expected genetic variance within subpopulations and the expected differentiation among subpopulations, as defined above eqns. (3) and (4).

The preservation of heterozygosity or additive genetic variance in a subdivided population is most easily illustrated when there is no mutation, migration or selection. Although smaller subpopulations lose genetic variance faster, Fig. 5 shows that splitting a population of a given total size into more subpopulations is expected to result in the preservation of more genetic variance. After a few times N_e/n generations, the amount of additive genetic variance preserved among n subpopulations approaches $(1 - 1/n)V_g(0)$.

[Fig. 5 here]

With mutation, but no migration or selection, the subpopulations will continue to differentiate, and, after many generations have elapsed, the total genetic variance as measured by eqn. (6) will actually exceed that originally contained in the base population. Fig. 6 (left) gives the total population size, N_e , needed to maintain 90% of the initial genetic variance in a typical quantitative character after 200 years, with various numbers of subpopulations. The curves for $n \ge 2$ are truncated because species with generation times less than a few years are always expected to maintain *more* than 90% of the original genetic variance, regardless of the total population size, because of the accumulation of new mutations among populations.

Subdivision can also help to counteract the erosion of genetic variability by selection in the captive environment, if subpopulations are small enough so that random genetic drift and fixation of alternate alleles in different subpopulations occurs faster than selection. For example, Fig. 6 (right) depicts the simple case where directional selection operates with the same intensity on all subpopulations, regardless of their mean phenotype (e.g. due to unconscious artificial selection for tameness). It can be seen that for species with intermediate generation times, splitting the population into many very small subpopulations makes the management goal attainable, and with feasible total population sizes. Stabilizing

selection toward the same phenotype in all subpopulations would retard their differentiation and reduce the impact of subdivision, whereas diversifying selection toward different phenotypes in different subpopulations would accelerate their differentiation and enhance the influence of subdivision in comparison to that shown in Fig. 6 (right).

[Fig. 6 here]

Summary and Discussion

Breeding plans for captive populations should be designed to meet a specific goal. Possible goals range from the establishment of a permanent captive population for public display in zoos or arboreta, to captive breeding for later release into the wild (Frankham et al. 1986; Foose et al. 1986). The present paper concerns captive breeding for later release into the wild. For many species, especially large mammals and birds, or species with specialized habitat requirements, continued habitat alteration (directly or indirectly by human exploitation) will cause extinction or near extinction in the wild, necessitating a period of captive propagation to produce stock for later release into natural or restored areas. Soulé et al. (1986) suggested the management goal of maintaining 90% of the initial heterozygosity for 200 years. We derived an analytical framework for the development of breeding plans designed to meet this goal for additive genetic variance in typical quantitative characters. Results are presented in the figures. General analytical formulas in the Appendix allow construction of breeding plans to meet other goals, such as maintanence of 75% of the original genetic variability for 100 years.

Building on the model of Soulé et al. (1986) which includes the number of founders, exponential growth of the population to its final size, and random genetic drift, the present results demonstrate that the management goal can be achieved with smaller population sizes if account is taken of mutation in typical quantitative traits. This is especially important for species with short generation times, as can be seen from comparison of Figs. 1 and 2.

Immigration from the wild of one effective individual every few generations would also permit substantial reduction in the size of the managed population necessary to meet the goal (Fig. 3), but this option is not possible if the wild population is extinct, and it may not be desirable if the wild population has been severly reduced in size for several generations so that it is highly inbred and depauperate of genetic variability.

These models analyze the dynamics of genetic variability, assuming that in the captive environment there is no selection on most characters. However, for some traits, such as tameness, and fecundity, natural or artificial selection for adaptation to captivity may occur. With appreciable selection in the captive environment, the management goal can not be met using a single panmictic population, except for species with rather long generation times. In this situation, a population with an effective size of a few hundred individual can maintain nearly as much genetic variability as an indefinitely large population, as shown in Fig. 4.

Breeding plans for closely managed populations often have a single (nearly) panmictic population with an effective size large enough to avoid severe inbreeding depression and to maintain substantial amounts of selectively neutral heterozygosity or additive genetic variance in quantitative traits for long periods of time (Franklin 1980; Foose et al. 1986; Soulé et al. 1986). Random exchange of one effective immigrant every few generations between subdivisions of a population renders it nearly panmictic with respect to selectively neutral variation (Wright 1951; Foose et al. 1986). Most of the deleterious effects of inbreeding depression can be avoided if the subpopulations have effective size greater than a few dozen individuals (Lande and Barrowclough 1987). This degree of subdivision also has the advantage of reducing the chance of catastrophic extinction (e.g. by epidemics) and regionalizing logistical problems including transportation costs (Foose et al. 1986).

Complete subdivision of a population acts to permanently maintain genetic variability between subpopulations rather than within them. Subdivision of a population into noninterbreeding units may be appropriate if the management goal can not be met with a single randomly mating population because of space limitations (Figs. 5 and 6 left). Extreme subdivision into numerous very small subpopulations may be the only method of maintaining a high proportion of the original genetic variation for characters that are under appreciable selection for adaptation to captivity. However, the subpopulations should not be so small that they experience severe inbreeding depression. Choice of the degree of subdivision (e.g., Fig. 6 right) should be based on consideration of the intensity of selection and the magnitude of inbreeding depression. Stronger selection requires more subdivision, but larger subpopulation size allows selection to more efficiently counteract inbreeding depression by eliminating deleterious recessive mutations when they become homozygous.

In addition to the goal of maintaining genetic variability, breeding plans should also limit evolution of mean phenotype in the captive population by random genetic drift or selection in the captive environment. The Appendix and Fig. 3 show that for the breeding plans described above, random genetic drift in the mean phenotype is not expected to be substantial, unless the generation time of the species is much less than one year (i.e., on the order of one month). Aside from reducing the intensity of selection (by equalizing family sizes, maximizing generation time, and eliminating conscious selection) or continually introducing immigrants from the wild, extreme population subdivision may be the most powerful method of reducing the influence of selection in the captive environment. To counteract deleterious mutations or undesirable evolutionary changes in quantitative traits, Lande and Barrowclough (1987) recommend artificial selection within families, maintaining equal family sizes after selection.

When a captive population is released into a natural or restored area, the initial founders must reproduce sufficiently fast for the population to grow and become established at a size large enough to avoid extinction from ecological and genetic factors. The number of individuals released should be sufficiently large to prevent substantial inbreeding and loss of genetic variability, and to overcome Allee effects such as the difficulty of finding a mate

in a sparse population. The period of captive propagation should encompass as few generations as possible, to minimize loss of genetic variation, cultural information and domestication effects. The environment of release should be similar to the original natural habitat to reduce the difficulty of adaptation. In many cases, multiple releases at various localities will be necessary for successful establishment in the wild (Griffith et al. 1989).

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Appendix

Random genetic drift and mutation. Eqn. (1) is first-order and linear, with nonconstant coefficient $1/(2N_e(t))$ given by eqn. (2). It can be solved using an integrating factor. From the solution, given $V_g(0)$, $N_e(0)$, r and T, we wish to derive the value of K_e that will satisfy the management goal. Thus we require that the final effective population size has been reached, $t \ge \tau$, and that after t = 200/T generations an expected proportion p (here p = 0.9) of the initial additive genetic variance is maintained, $\overline{V_g}(200/T) = pV_g(0)$. The solution of eqn. (1) at $t = \tau$ is

$$\overline{V_g}(\tau) = I(\tau) \left[V_g(0) + V_m \int_0^{\tau} [I(u)]^{-1} du \right]$$
(A1)

where the integrating factor is

$$I(\tau) = \exp\left\{-\frac{1 - e^{-r\tau}}{2N_{\rho}(0)r}\right\}$$
 (A2)

and $\tau = r^{-1} \ln(K_e/N_e(0))$. For $t \ge \tau$, the solution is

$$\overline{V_g}(t) = 2K_e V_m + \left[\overline{V_g}(\tau) - 2K_e V_m\right] \exp\left\{-\frac{t - \tau}{2K_e}\right\}$$
 (A3)

Although it is not possible to obtain an explicit expression for K_e from these formulas, t can be expressed in terms of K_e as

$$t = \tau + 2K_e \ln \left\{ \frac{\overline{V_g}(\tau) - 2K_e V_m}{pV_g(0) - 2K_e V_m} \right\}$$
 (A4)

in which $\overline{V_g}(\tau)$ is given by (A1). Generation times are then obtained from T = 200/t.

In the absence of mutation $(V_m = 0)$ the term in brackets in the denominator of (A4) becomes simply $I(\tau)/p$ as was used to construct Fig. 1. With mutation it is convenient to divide numerator and denominator in the bracketed term by $V_g(0)$, setting $V_m/V_g(0) = V_g(0)$

 $(V_m/V_e)(1-h^2)/h^2$ in which h^2 is the heritability of the character in the base population (see text). To construct Fig. 2, the integral in (A1) was evaluated by substituting $y = \alpha e^{-ru}$ with $\alpha = [2N_e(0)r]^{-1}$,

$$\int_{0}^{\tau} [I(u)]^{-1} du = r^{-1} e^{\alpha} [E_{1}(\alpha e^{-r\tau}) - E_{1}(\alpha)]$$
(A5)

where $E_1(x) = \int_x^\infty y^{-1} e^{-y} dy$ is the exponential integral. In the range $0 \le x \le 1$ (if r > 0 this requires that $2N_e(0)r \ge 1$), the exponential integral can be approximated with an error less than 2×10^{-7} by the function (Abramowitz and Stegun 1972)

$$E_1(x) = \ln x + a_0 + a_1 x + a_2 x^2 + a_3 x^3 + a_4 x^4 + a_5 x^5$$
 (A6)

with
$$a_0 = -0.57721566$$
 $a_3 = 0.05519968$ $a_1 = 0.99999193$ $a_4 = -0.00976004$ $a_2 = -0.24994055$ $a_5 = 0.00107857$

Immigration from the wild. Eqns. (3) and (4) constitute a coupled pair with constant coefficients, which can be solved by finding the eigenvalues and eigenvectors of the system. Since we have assumed that $m \ll 1$, the last coefficient in eqn. (3) can be approximated as $m(1-m)/2 \cong m/2$. We must analyze separately the cases of positive migration rate and no migration since the solution changes discontinuously as m approaches 0.

For m > 0, the equilibrium values of the variables are

$$\overline{V_g}(\infty) = 4N_e [V_m + mV_g(0)]/(4N_e m + 1)$$
 (A7)

$$V_{\overline{q}}(\infty) = \overline{V_{q}}(\infty)/(2N_{e}m) . \tag{A8}$$

Defining $\delta(t) = \overline{V_g}(t) - \overline{V_g}(\infty)$ and $\varepsilon(t) = V_{\overline{z}}(t) - V_{\overline{z}}(\infty)$ eqns. (3) and (4) become

$$\frac{\mathrm{d}}{\mathrm{d}t} \begin{pmatrix} \delta \\ \varepsilon \end{pmatrix} = \begin{pmatrix} -m - 1/(2N_e) & m/2 \\ 1/N_e & -2m \end{pmatrix} \begin{pmatrix} \delta \\ \varepsilon \end{pmatrix} \tag{A9}$$

The eigenvalues of the matrix in (A8) are -m and $\lambda = -1/(2N_e) - 2m$, with corresponding eigenvectors in transposed form $(N_\rho m, 1)$ and (-1/2, 1). Then

$$\overline{V_g}(t) = \overline{V_g}(\infty) + c_1 N_e m e^{-mt} - (c_2/2)e^{\lambda t}$$
(A10)

$$V_{\overline{z}}(t) = V_{\overline{z}}(\infty) + c_1 e^{-mt} + c_2 e^{\lambda t}$$
 (A11)

where, using $V_{\overline{2}}(0) = 0$ and (A8),

$$c_1 = [\overline{V_g}(\infty) - 2\overline{V_g}(0)]/(2N_e m + 1)$$

$$c_2 = 2[\overline{V_g}(0) - (1 + 1/(4N_e m))\overline{V_g}(\infty)]/(2N_e m + 1) .$$

Setting $\overline{V_g}(t) = pV_g(0)$ in eqn. (A10), and dividing all genetic variances by $V_g(0)$ as after (A4), Newton's method of iteration was used to find numerical values of t for given values of N_e , $N_e m$, \tilde{V}_m/V_e and the initial heritability h^2 . Numerical values of t were converted to generation times using T = 200/t to plot the solid curves in Fig. 3a, and they were also substituted into (A11) to construct the solid curves in Fig. 3b.

For m = 0, the solutions of eqns. (3) and (4) are

$$\overline{V_g}(t) = 2N_e V_m + [V_g(0) - 2N_e V_m] e^{-t/(2N_e)}$$
(A12)

$$V_{\overline{z}}(t) = 2[V_g(0) - 2N_e V_m][1 - e^{-t/(2N_e)}] + 2tV_m.$$
 (A13)

(Lande 1980). These formulas were used to plot the dashed curves in Figs. 3a and 3b, proceeding as with (A10) and (A11), except that an analytical expression for t can be easily obtained from (A12).

Selection in captivity. Eqn. (5) is linear with constant coefficients. Setting $\lambda = 1/(2N_e) + s$ the solution is

$$\overline{V_g}(t) = \lambda^{-1} V_m + [V_g(0) - \lambda^{-1} V_m] e^{-\lambda t}$$
 (A14)

Setting $\overline{V_g}(t) = pV_g(0)$ and solving for t yields

$$t = \lambda^{-1} \ln \left\{ \frac{V_g(0) - V_m / \lambda}{p V_g(0) - V_m / \lambda} \right\}$$
 (A15)

Again T = 200/t and the variances in the bracketed term can expressed in units of $V_g(0)$ as after eqn. (A4). Eqns. (A15) and (A14) were used respectively to produce the left and right sides of Fig. 4.

Population subdivision. From eqn. (6), using (A12) and (A13) with N_e divided by n, we find that with no mutation, and no selection or migration

$$\overline{V_{gP}}(t) = V_{g}(0)[1 - (1 - e^{-nt/(2N_{e})})/n]$$
 (A16)

which was used to construct Fig. 5. With a constant intensity of directional selection on each subpopulation, regardless of its mean phenotype, eqn. (5) with N_e divided by n describes the dynamics of $\overline{V_g}$, and the expected differentiation among subpopulations is given by $dV_{\overline{Z}}/dt = n\overline{V_g}/N_e$. The expected total genetic variance after panmixia in generation t, with selection and mutation, but no migration, is then

$$\overline{V_{gP}}(t) = \left[V_g(0) - V_m \lambda\right] \left[c/\lambda + (1 - c/\lambda)e^{-\lambda t}\right] + (1 + ct)V_m \lambda$$
(A17)

where $\lambda = n/(2N_e) + s$ and $c = (n - 1)/(2N_e)$. Setting $\overline{V_g}_P(t)/V_g(0) = 0.9$, this equation was evaluated as above for a typical character with $h^2 = 0.5$ and $V_m/V_e = 0.001$. Newton's method was employed to obtain numerical solutions for t which were converted to generation times using T = 200/t for the construction of Fig. 6.

Random genetic drift in the mean phenotype. For completely additive genetic variance Wright (1951) showed that random drift in the mean phenotype of a single population is expected to cause a squared deviation between the initial and final mean phenotypes of $2V_g(0)$ based on fixation of the original genetic variation. Random genetic drift and fixation of new mutations are expected to add a quantity less than $2tV_m$, regardless of $N_e(t)$ (Lande 1980; eqn. A13). Defining $v_{\overline{z}}(t) = V_{\overline{z}}(t)/[V_g(0) + V_e]$, then

$$v_{\overline{z}}(t) < 2h^2 + 2t(V_m/V_e)(1 - h^2)$$
 (A18)

At t = 200/T, the mean phenotype of a typical character with heritability $h^2 = 0.5$ and $V_m/V_e = 0.001$ is not expected to drift more than one phenotypic standard deviation because of fixation of genetic variation in the base population, and less than an additional 1/(5T) phenotypic standard deviations based on new mutations. Thus unless T << 1, random genetic drift in the mean phenotype is not likely to be substantial in breeding plans for a single population carried out on a timescale of 200 years.

The same conclusion holds with population subdivision, regardless of the sizes of the subpopulations or the migration rates between them. Let the *i*th subpopulation have mean phenotype \overline{z}_i (measured in a large number of offspring), additive genetic variance V_{gi} and effective size N_{ei} . The ratio of actual to effective size is assumed to be the same in all subpopulations, so that the total effective size in the absence of subdivision would be $N_e = \sum N_{ei}$. The grand mean phenotype and the weighted average genetic variance within subpopulations are

$$\overline{z} = \sum N_{ei} \overline{z}_i / N_e \quad \text{and} \quad \overline{V}_g = \sum N_{ei} V_{gi} / N_e$$
 (A19)

The increased variance in the probability distribution of \bar{z} due to one generation of random genetic drift is

$$Var_{drift}[\overline{z}] = \sum (N_{ei}/N_e)^2 V_{gi}/N_{ei} = \overline{V_g}/N_e.$$
 (A20)

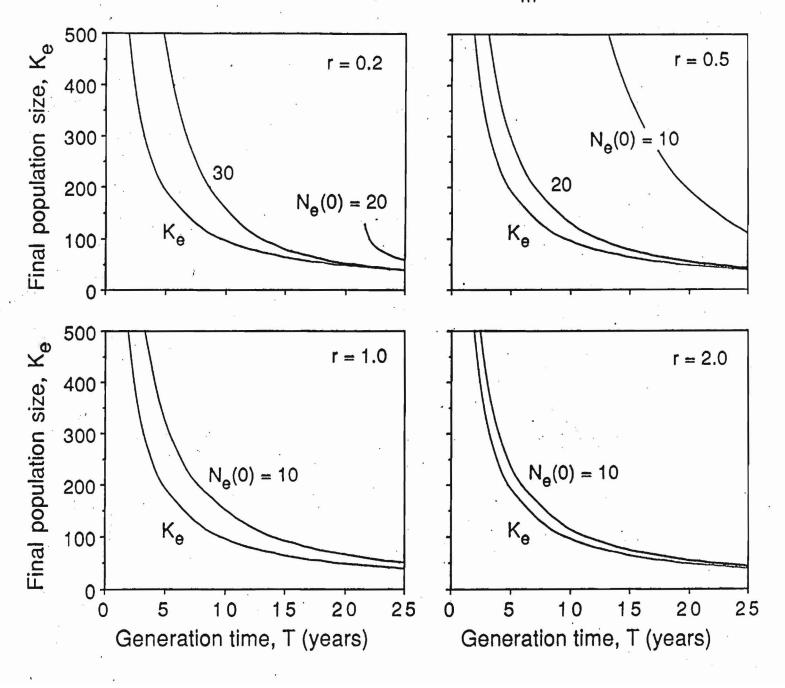
This result is not influenced by migration among subpopulations, provided that individuals do not incur reduced fitness during migration, because with purely additive genetic variance migration does not alter \bar{z} . Thus random genetic drift in \bar{z} occurs at the same rate as if the population were panmictic with additive genetic variance \bar{V}_g . Because population subdivision is expected to decrease the additive genetic variance within subpopulations (Wright 1951; Lynch 1988b), the rate of genetic drift in the grand mean phenotype of a subdivided population must be less than that for a single panmictic population with the same total effective size, analyzed in (A18).

Figure Captions

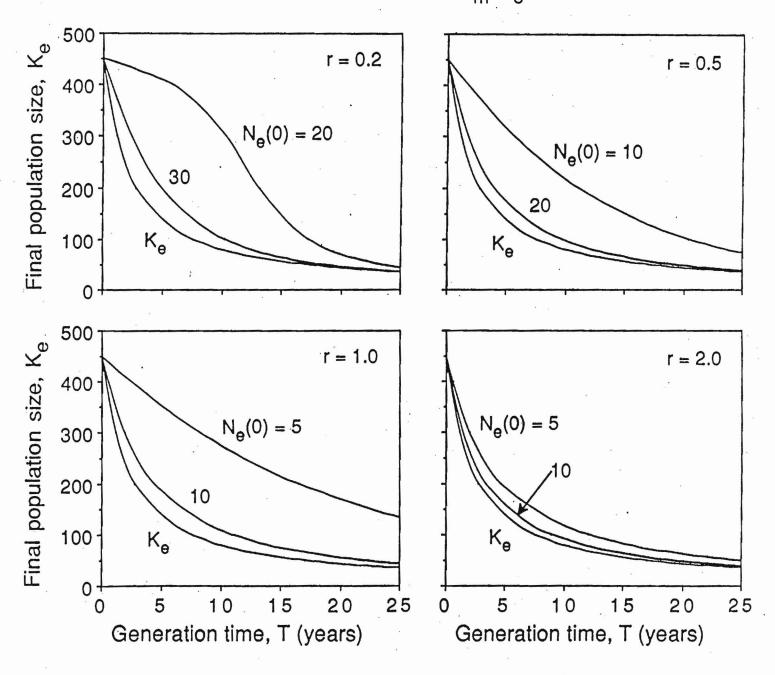
- Fig. 1. Final effective size of a captive population, K_e , necessary to expect 90% of the original heterozygosity, or additive genetic variance in quantitative characters, in the base (wild) population after 200 years, as a function of the generation time, for various values of the effective number of founders, $N_e(0)$, and population growth rate per generation, r. From eqns. (1) and (2), assuming no mutation.
- Fig. 2. The same as Fig. 1, but for a typical quantitative character with additive genetic variance created by mutation at the rate $V_m/V_e = 0.001$ per generation, and a heritability in the base (wild) population of $h^2 = 0.5$.
- Fig. 3. Left.-- Effective population size, N_e , needed to expect 90% of the original additive genetic variance after 200 years, as a function of the generation time, for various values of the effective number of immigrants per generation from the wild, $N_e m$, assuming $V_m/V_e = 0.001$ and $h^2 = 0.5$. Right.-- Expected amount of random genetic drift in the mean phenotype, in units of phenotypic standard deviations in the wild population, as a function of the generation time, when N_e is kept for 200 years at the size given in the left graph. From eqns. (3) and (4).
- Fig. 4. Left.-- Effective size of a captive population, N_e , necessary to expect 90% of the initial additive genetic variance after 200 years, as a function of the generation time, for various values of the rate of selective loss of genetic variance, s. Right.-- Expected proportion of additive genetic variance maintained after 200 years as a function of N_e , for various values of the generation time, assuming s = 0.01. From eqn. (5).

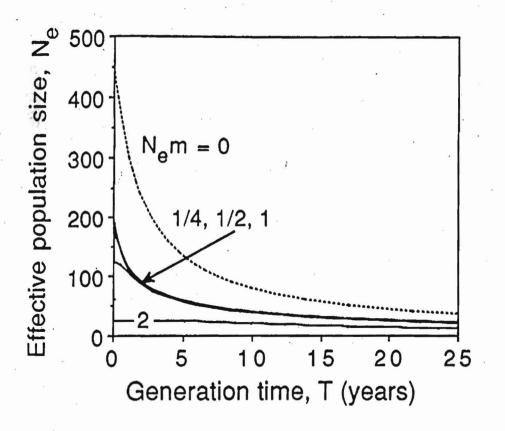
- Fig. 5. Expected proportion of original heterozygosity or additive genetic variance maintained as a function of time, for various numbers of subpopulations, n. Time is scaled in units of $2N_e$, where N_e is the total effective size if the population were panmictic. There is no mutation or selection, and no gene flow or migration among subpopulations. From eqn. (6).
- Fig. 6. Left.-- Total population size, N_e , needed to maintain 90% of the initial additive genetic variance after 200 years, as a function of the generation time, for various numbers of subpopulations, n. Evaluated for a character with $V_m/V_e = 0.001$ and $h^2 = 0.5$, but with no selection and no migration among subpopulations. Right.-- Same as the left side, but there is selection, s = 0.01 and no mutation, $V_m = 0$. From eqns. (5) and (6).

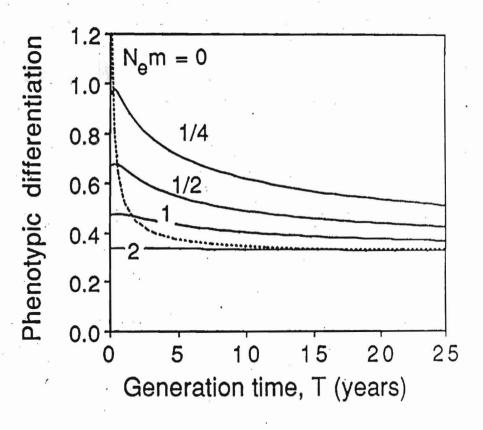
Random genetic drift: $V_m = 0$

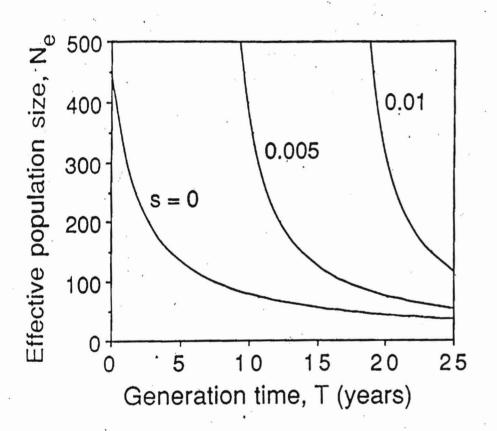


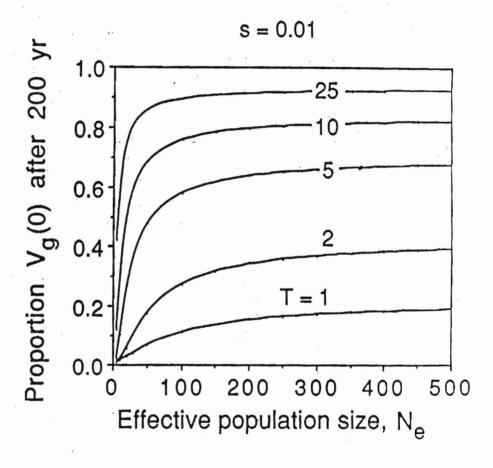
Drift and mutation: $V_m/V_e = 0.001$

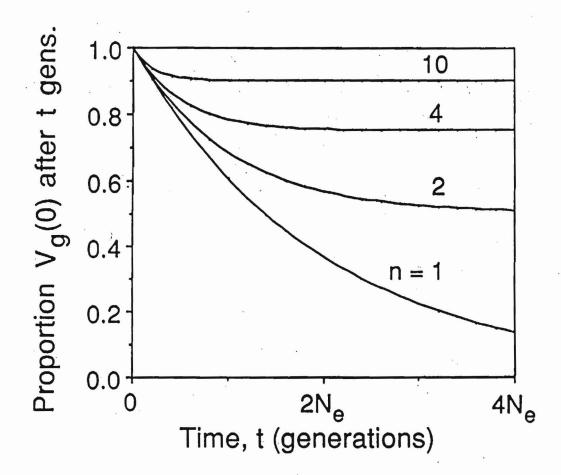


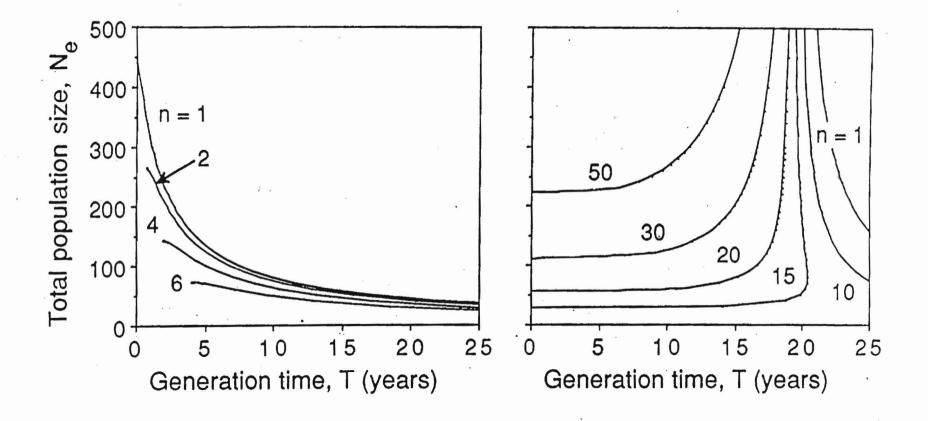












GENETIC MANAGEMENT CONSIDERATIONS

FOR THREATENED SPECIES

WITH A

DETAILED ANALYSIS OF THE FLORIDA PANTHER

(Felis concolor coryi).

A report by the participants in a genetic augmentation workshop sponsored by the U. S. Fish and Wildlife Service in cooperation with the Captive Breeding Specialist Group SSC/IUCN.

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Introduction And General Position Statement

Biodiversity is maintained and enhanced by natural, geographic structure in the environment. To take a large scale example, different continents contain distinctive floras and faunas such that overall global species diversity is much higher than would otherwise be expected. Human-mediated introductions of exotic animals and plants have resulted in reduced global species diversity and are increasingly recognized as highly undesirable in terms of ecological effects on recipient biotas. Numerous examples exist in which extinction of native species was attributable to the introduction of exotic taxa. Recent experience in North America with exotics such as the zebra mussel and grass carp exemplify additional and sometimes disastrous ecological problems that can attend species introductions.

Perhaps less well appreciated is that geographic translocation of conspecifics within the range of a species can also have strong negative consequences. In the last two decades, the evidence from molecular genetics has confirmed and extended earlier suspicions based on morphological comparisons that geographic populations within many species are genetically differentiated to varying but often substantial degrees. Geographic differentiation within a species may have both historical and adaptive components. The following are some of the likely consequences of ill-conceived translocations of individuals and genetic material from one population to another:

- 1. Homogenization of the genetic composition of populations through decay of between-population differences;
- 2. Blurring or irretrievable loss of genetic information on the intraspecific evolutionary histories of populations;
- 3. Placement in jeopardy or outright destruction of local adaptations, through introduction of foreign genetic material, breakup of coadapted gene complexes, or genetic swamping;
- 4. Creation of reproductive difficulties when transplanted individuals differ from recipients in karyotype or other genetic characteristics that may decrease fitness of intercross progeny or their descendants;
- 5. Disruption, in some species, of the social structure and population stability of the recipient population;
- 6. Subsequent spread of introduced forms into unintended areas;

- 7. Unintentional introduction or spread of parasites or disease vectors;
- 8. Creation of a false sense of management accomplishment (and a masking of underlying environmental difficulties) in situations where repeated translocations from a demographically strong source population are absorbed lost in a recipient population that is not self-sustaining and represents a demographic sink.

Human-mediated translocation of plants and animals is fraught with dangers and should be strongly discouraged as stated in the IUCN Policy on Translocation (IUCN, Gland, 1990). However, in some special circumstances, translocation (managed gene flow and population augmentation) may be warranted and desirable to maintain small populations that are isolated because of human-induced fragmentation of the environment. The burden of proof in any proposed translocation program should rest squarely on the advocates rather than on the opponents of this management option. The purpose of this document is to outline the necessary procedure for considering or initiating a translocation program.

Exceptions To The General Position On Translocation Of Plants And Animals:

Identifying Candidate Species for Genetic Management and Population Augmentation.

Translocation (managed gene flow and population augmentation) may be necessary when a population is small and artificially isolated due to human-induced habitat fragmentation. The guidelines outlined here apply to the augmentation and genetic management of existing populations. They do not apply to introduction of exotic species for game, food or amusement, reintroductions of species into formerly occupied areas, introductions for biological control or environmental remediation (e.g. release of natural or genetically engineered organisms to metabolize or sequester pollutants).

Two types of threats to continued existence of a population could lead to categorizing it as a candidate for population augmentation:

- 1. Demographic threats. Current or past rates of population decline, current or anticipated achievement of a critical small size, and skewed sex ratios or age structure that would threaten the existence of a population.
- 2. Genetic threats. Current or anticipated loss of genetic variability that is currently or potentially adaptive, and inbreeding depression.

Demographic Threats

Current trends in population size should be assessed in the context of historical demographic

information. Data on the life history and age structure, the temporal and spatial structure of the population, and its behavioral/social system including territoriality and cultural transmission are especially important.

The possibility of a critical threshold size or density of a population necessary to its survival should be investigated. Such a threshold could result from the difficulty of finding a mate in a sparsely distributed population, cooperative hunting or group defense behavior, dispersal from limited areas of suitable habitat into unsuitable habitat, or the dynamics of local extinction and colonization in a fragmented habitat (Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.).

The first course of action in response to a perceived demographic threat should be to remove the cause of the threat, and to allow the population to increase by itself. If the demographic threat cannot be removed in time to allow natural recovery, then temporary augmentation of the population from the same or closely similar genetic stock should be considered. Use of a genetically differentiated stock for purposes of demographic augmentation should be avoided if possible. In the absence of genetic threats, local amplification of the population, e.g. by captive breeding, is preferred.

Genetic Threats

The main criteria for genetic threats are small population size and (geographic) isolation caused by human action, e.g habitat destruction. Often, if not usually, genetic threats will be manifested only after demographic threats are apparent; that is, genetic threats become important at smaller population sizes. Loss of genetic variability in all types of characters becomes a significant concern for populations below an effective size of a few hundred individuals. However, some characters such as disease resistance may be based on genetic variants that are usually rare and found only in very large populations. It is conceivable that a specific genetic threat, such as lack of resistance to a particular disease, could be met by introduction of a specific resistant allele or genotype into a population, rather than random gene flow.

Desirability of preserving a population in a given area can be based on a number of considerations, including the degree of genetic differentiation from other populations of the same species as indicated by morphological, molecular and reproductive traits. The risks from demographic and genetic factors have to be weighted against the risk of diluting or swamping local genetic differences or adaptations by artificial gene flow or introduction of genetic incompatibilities such as major chromosomal rearrangements. A level of gene flow much less than the local selective advantage of a character is unlikely to result in swamping of that character by gene flow, although other less adaptive characters may be significantly diluted or swamped. The adaptive value of a character can be inferred from behavioral or ecological observations. However, its adaptive value can be directly demonstrated in terms of fitness effects only by measurements of natural selection in the natural environment. This requires studying

individual variation within a population or transplantation experiments among populations in different environments, which may not be feasible in many species.

Different manifestations of inbreeding depression should be distinguished, along with the types of evidence for their occurrence. Within a population, decrease of the mean of a character such as body size upon inbreeding can be estimated from pedigree data or breeding experiments. Fitness components including reproductive rates and offspring viability are often subject to substantial inbreeding depression upon matings between close relatives in historically large outcrossing populations. Inbreeding depression affecting an entire population, e.g. due to the fixation of a deleterious recessive gene, can be documented by transplantation experiments among populations (which again may be impractical for many species), or implicated by extensive comparative data among populations.

Inbreeding depression usually is manifested only upon matings between close relatives, or continued random mating in small population of effective size at or below a few dozen individuals.

Before augmenting a population to reduce current or future inbreeding depression, ideally it should be verified by experimental intercrossing, e.g., in a captive stock initiated as part of an augmentation program, that inbreeding depression does indeed exist and can be ameliorated by artificial gene flow. Augmentation should be based on the most similar genetic stock available, even another, small, isolated population that may be suffering from genetic problems provided that these are not identical in detail to those of the target population (i.e. the source population could show inbreeding depression in morphological traits different from those in the target population). Augmentation through a captive population to a wild population allows control of the rate and amount of genetic material to be introduced.

Time scales for action should be evaluated by balancing the relative risks of extinction or genetic damage to the population versus the risks associated with artificial gene flow.

Levels of Gene Flow

The level of artificial augmentation should be commensurate with the demographic or genetic risks faced by the population. Demographic augmentation should counteract (artificial) causes of population decline (including interaction with exotic introduced species), until these can be ameliorated or removed.

Current genetic problems, especially inbreeding depression, require enough gene flow to solve the problem. This may initially be greater than the level of original gene flow to prevent anticipated genetic risks from small population size and geographic isolation caused by human action. However, the cumulative genetic augmentation necessary to mitigate current inbreeding depression generally should not require addition (or substitution) of more than several percent

(2-5%) of the total genetic material in the target population.

After currently existing genetic problems have been solved by genetic augmentation, if the only apparent genetic risk is in the future, the management goal should be to achieve a natural level (that which occurred before isolation of the population) of gene flow. This can be assessed from historical and current observations of dispersal and geographic distribution, and/or (with caution) from molecular genetic studies (e.g. estimates of number of migrants per generation among population subdivisions [Slatkin, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics 16:393-430; Slatkin, M. and N.H. Barton. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43:1349-1368.). The level of artificial gene flow should be lower than the estimated natural level if the only remaining source is more genetically differentiated than the historical source(s).

Procedural Overview For Population Augmentation Program

- I. Overall Procedural Issues Advanced Planning & External Review of Plan.
 - A. The decision trees and sequence of steps below should be documented in advance and sent out for external peer review.
 - B. Suitable reviewers, in addition to other agencies and academic reviewers, should include 3 Specialist Groups of the IUCN World Conservation Union (who offer expertise based in part on assembly of experience and mistakes made by others worldwide):
 - 1. Reintroduction Specialist Group
 - 2. Captive Breeding Specialist Group
 - 3. Relevant Taxon Specialist Group (e.g., Cat Specialist Group)

II. Source of Stock

- A. <u>Demographic</u> supplementation of an existing local population should generally be accomplished with stocks known to be very similar genetically, and evaluated in advance for risk of disease transmission.
 - 1. Stock from another historically nearby (i.e. contiguous) population which formerly exchanged significant numbers of dispersing individuals with the

threatened population and is genetically very similar, is suitable.

- 2. Stock withdrawn directly from the population at risk and amplified by captive breeding or other means, is suitable.
- When a population has been completely <u>extirpated</u>, the preferred source of stock for re-establishment may be a more complex issue which warrants further analysis.
- B. Genetic supplementation of an existing local population should generally be accomplished with stocks known to be very similar but not identical genetically, and evaluated in advance for risk of genetic incompatibilities and disease transmission. See the following section of this document, where this issue is developed in more detail.
- III. Method of Introduction the emphasis here is on practical means of lowest disease risk which can be monitored for success and effect see Follow-up section.
 - A. Introduction of early life stage material offers the advantage of natural integration and cultural transmission. Possibilities include:
 - 1. Artificial insemination where techniques exist.
 - 2. Embryo transfer where techniques exist.
 - 3. Egg-swapping
 - 4. Youngster swapping
 - B. Introduction of adults with relevant wild experience
 - C. Introduction of captive-bred individuals trained for release.

IV. Follow-up

- A. Sound follow-up study design (in advance) is critical:
 - 1. Managers need to know outcomes.
 - 2. Techniques can only be improved if their success and failure is measurable.

- 3. Success must be recognizable so the effort can stop when success has been assured or if it becomes apparent that the chosen strategy will not succeed.
- 4. Poor follow-up has made many release programs a wasted effort from which little is learned.
- B. Follow-up is part of the necessary ongoing monitoring and evaluation needed for a population at risk. This should consist of at least:
 - 1. Creation of studbook data sets for the wild population and any existing captive populations.
 - 2. Analytical evaluation of age- and sex-specific fecundities, mortalities, age structure, and population growth or decline rates.
 - 3. Before/after evaluation of genetic composition of population, changes in fitness traits.
 - 4. Public reactions before, during, and after the translocation.
 - 5. Evaluation (of a surviving population) should begin with a 3-5 year baseline study prior to treatment (concurrently with capture studies) and continue for 3-5 years following treatment. Reevaluation of the program should occur at least every 3-5 years.

Criteria For Assessing Appropriateness Of Population Augmentation Program

The following steps should be examined prior to any genetic augmentation of a natural population. The urgency of preventing imminent extinction might necessitate action based on an assessment of partial information before each step can be addressed fully, but adequate attention to the concerns below should not be needlessly postponed until a crisis demands sudden action on behalf of a population. Translocation of organisms involves considerable risks not only to that population, but to all components of the natural communities affected (see introductory section). Concern for the natural environment and biodiversity demands that artificial intercrossing (see definitions) be undertaken only after careful deliberation, after all reasonable precautions have been taken, and after alternatives have been examined. Possible benefits of augmentation must be weighed against costs and risks of artificial translocations, and lack of knowledge concerning any points below must be viewed as contributing substantially to the risks.

Verify that the problems facing the population include genetic loss.

Possible indicators of genetic loss include (temporal trends or traits relative to other populations): (1) Projection of a high rate of genetic loss in the past and/or in the future based on population size and/or structure; (2) Low genetic variation observed in the population; (3) High rate of observed close inbreeding; (4) High prevalence of morphological abnormalities; (5) Health problems; (6) Compromised reproductive status (e.g., poor sperm count or viability, lack of regular cycling of females); (7) Low reproductive output; (8) Poor survival. For the last four possible indicators of genetic problems, attempts should be made to assess whether nongenetic causes (e.g., poor nutrition, social stress, shrinking habitat, or disease) might be responsible for poor performance.

Confirm that genetic problems can be ameliorated by intercrossing.

Experimentally verify potential reversal of genetic problems by intercrossing. This would likely be in a captive setting, in which non-genetic factors could be controlled and data easily collected while not placing the wild population at risk. Such studies could be concurrent with the genetic and demographic studies of the wild population.

Evaluate habitat availability, occupancy, quality, and trends to demonstrate the existence of sufficient habitat to allow the population to benefit from the introduction of additional genes.

There is rarely value in augmenting a population in already saturated habitat, or if continued habitat deterioration is likely to preclude population recovery. Restocking should not be used to continually replenish areas that are functionally population "sinks", and it would commonly be difficult for translocated animals to become established in a resident population that fully occupies available habitat. However, there may be situations in which genetic problems could be remedied while steps are taken to recover habitat quality or to prepare alternative habitat. The purpose would not be to bolster numbers of animals (genetic augmentation might take the form of demographic exchange rather than addition), but rather to improve the genetic health of a population in order to increase resiliency to perturbations and to allow for population expansion when habitat becomes available or to increase viability within existing habitat with lessening of human related pressures.

Demonstrate lack of negative effects of intercrossing (before gene pools are irreversibly mixed).

Serious problems are much less likely to arise if the source and recipient populations had exchanged migrants prior to human-caused habitat or population fragmentation. Notwithstanding the perceived similarity of the populations, it would be prudent to test experimentally, or otherwise under controlled circumstances, the viability, fecundity, and morphological continuity of first and second generation intercrosses.

Confirm availability and appropriateness of potential source population(s).

To minimize negative impacts (foreseen and otherwise) while achieving desired goals of restoring genetic and demographic viability to a small, isolated population, the following ranked list of criteria is suggested for choosing source population(s):

- 1. Use source population(s) historically in closest geographic proximity, preferably one(s) formerly in contact with the remnant (recipient) population and not formerly separated by geographic barriers to natural dispersal. The goal of the translocation is to restore, to the extent possible, processes that augmented genetic variation prior to human disruption of natural gene flow.
- 2. Use source population(s) demonstrated to be genetically similar to the recipient population. Karyotypic differences between populations are often indicative of difficulties in intercrossing (often not apparent until the second generation), and information on karyotypic similarity can often be obtained relatively quickly. The diversity of molecular (allozyme, immunological, DNA) techniques available allow quantification of the degree of genetic divergence over a very wide range, from relationships among higher order taxa down to familial relationships within a local pedigree. Study of genetically based morphological variation can be important in revealing adaptive divergence among populations.
- 3. Use source population(s) from similar habitats. The goal is to allow restoration of potentially adaptive genetic variants into a population that is so small as to be subjected to considerable non-adaptive drift (loss of alleles adapted to components of the habitat and fixation of deleterious alleles).

Establish ability (and plan) to monitor impacts of translocations for intercrossing.

Expected outcomes should be specified. Potential dangers must be identified. Methods need to be designed for determining if anticipated benefits are achieved without serious negative impacts. Contingency plans should be made for changing, halting or, if possible, reversing a management plan that fails to meet pre-defined acceptable levels of performance. Data collection throughout is essential to evaluate success and to help guide future efforts at recovery of endangered populations.

The evidence from each of the above considerations must be evaluated relative to each other and to the perceived urgency of action. The required level of assurance of benefit and minimization of risk could be less if the population is unlikely to persist for long in the absence of action. If risks are judged to be low (e.g., source and recipient populations are known to have regularly exchanged migrants until recently), modest benefits (e.g., sustenance of historic levels

of variation) may lead to a decision to proceed with intercrossing. Higher risks should be accepted only if benefits are large and highly likely to be obtained and if the cost of not taking the action is judged to outweigh the risks.

Definitions

1. Problems With The Word "Hybrid": Mixing Species, Subspecies, And Populations

Words such as "hybrid", "intergrade", "mongrel", and "interbreed" tend to carry strong but varying connotations to most people. For example, many taxonomists confine the use of "hybrid" to the products of crosses between distinct species, whereas geneticists commonly use the word in reference to products of crosses between any organisms that carry different genetic markers. "Intergrade" usually refers to progeny from crosses between "subspecies", but definitions and criteria for identification of subspecies vary. Furthermore, many traditionally-recognized named subspecies (i.e., populations within a species assigned a Latin trinomial) are often highly suspect as guides to the major evolutionary or genetic partitions within species, having originally been described from very limited assessments of morphological or other attributes with unknown genetic basis (See next section on Subspecies).

To provide a general and neutral word to be used in initial discussion regarding progeny resulting from parents of different sources, we suggest "intercross". This word should be used in a generic sense to encompass what is normally meant by more conceptually loaded terms such as hybrid or intergrade. Additional refinement of what is meant by the term in particular instances must be achieved by reference to additional sources of information, such as the magnitude and pattern of genetic divergence and reproductive relationships of the populations or taxa involved. A schematic representation of the term is as follows:

INTERCROSS

"Hybrid" "Intergrade" "cross",interbreed" (Species level) (subspecies level) (geographic populations)

(requiring additional knowledge on such factors as magnitude of genetic differentiation, reproductive relationships, geographic partition, etc).

2. Problems of Using Named Subspecies As Units For Conservation, Management, And Recovery Decisions

The use of named subspecies as units in conservation, management, and recovery decisions is plagued with a series of problems. These problems are highlighted by the history of using subspecies nomenclature in systematics. For several decades the prevailing practice among systematists has been to avoid naming subspecies. The move away from naming subspecies was spurred by the observation that different traits often show different patterns of geographic variation within a species (discordant geographic variation (Wilson, E.O. and W.L. Brown. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2:97-111.). In this common situation, the naming of subspecies depends on which traits or characters are being considered. Because of this arbitrary aspect of subspecies designation, most systematists stopped naming subspecies in the 1960's or earlier. Nevertheless, subspecies names persist in the literature.

Increasing application of molecular techniques in the past 30 years has further weakened the case for using named subspecies as units for conservation. The molecular techniques now enable us to estimate the phylogenetic relationships of populations within a species (Avise, J.C. and R. Martin. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surveys in Evolutionary Biology). Sometimes the new molecular results show geographic or phylogenetic patterns that coincide with the old subspecies names. Frequently, however, the new results conflict with the old nomenclature. The conflicts may reflect: (a) discordance between molecular and phenotypic patterns of geographic variation, (b) molecular resolution of units not represented by named subspecies (e.g., units within subspecies), (c) failure of named subspecies to reflect phylogenetic relationships. Thus, valid units commonly exist within species, but often these are not reflected by the named subspecies.

Valid units within a species could be diagnosed by searching for geographic concordance between different sets of traits. The issue in making a conservation decision is whether new molecular information shows geographic concordance with older subspecies names based on analysis of phenotypic traits or geographic separation. Taking analysis a step further, one can ask whether the phylogenetic relationships of populations are concordant across traits (Ball, R.M. and J.E. Nigel, J.C. Avise. 1990. Gene genealogies within the organismal pedigrees of random mating populations. Evolution in press.). Using this more detailed analysis requires data on multiple, genetically-based traits. For example, when multiple genetic differences concordantly distinguish populations, those populations might be considered a candidate unit for conservation, regardless of whether they reside in the same or different named subspecies.

Application Of Decision Criteria To Florida Panther Genetic Management:

Augmenting The Florida Panther Population By Intercrossing With FELIS CONCOLOR From Other Populations

1. Does the Florida panther meet requirements to be a candidate as an exception to the general guideline that proscribes augmentation with genetically divergent stock?

The Florida panther was formerly widespread throughout the southeastern United States and was contiguous with other populations (subspecies) of Felis concolor. Due to human destruction of habitat and direct persecution of animals, the subspecies has been reduced over the past few centuries to a remnant population existing only in south Florida. The south Florida population is very small, numbering no more than 30-50 adult panthers. The number of breeding animals may be no more than 20-30. Extensive surveys of possible habitat and investigations of reported sightings has demonstrated that the only remaining viable, breeding population of Felis concolor coryi is the south Florida population under intensive study and management. Isolated animals elsewhere, if they exist, could not be part of the breeding population. The remnant population of Florida panther is well-separated from the next closest population of F. concolor, in western Texas, and the two cannot exchange migrants.

Thus, the Florida panther population meets the criteria of being very small and totally isolated from all conspecifics, due to human-induced fragmentation and destruction of habitat and animals.

2. Is the Florida panther population at substantial risk of extinction?

The Population Viability Analysis conducted on the Florida panther projects, under existing demographic and genetic conditions, the extinction of the population within 25-40 years. The population size is well below criteria that have been suggested for numbers needed to assure viability (see above; O.H. Frankel and M.E. Soule. 1981. Conservation and Evolution. Cambridge University press; Franklin, I.R. 1980. Evolutionary change in small populations. In: Soule, M.E. and R.A. Wilcox (eds.). Conservation Biology. Sunderland, MA, Sinauer. Pp. 135-150.). The habitat available to the south Florida population is not sufficient to allow for expansion of the population to a size that would assure self-sustaining capabilities. Recovery of the population, whether or not it includes genetic augmentation, will require habitat preservation and management, and the identification and/or development of additional suitable habitat within the historic range of the subspecies.

3. Do the problems facing the Florida panther include genetic loss with adverse effects?

The Florida panther PVA projected a loss of 3% to 7% of genetic diversity (heterozygosity) per generation under current conditions of population size and structure. This loss is expected to accelerate unless aggressive management reverses habitat contraction and population decline. During the past decade (1981-1991), mortality of founder animals (those containing genes not known to be contained elsewhere among the living panthers) has been 49% per 24 months (M. Roelke, pers. comm., FL GFWFC). Of the 5 populations of Felis concolor that have been investigated by molecular genetic methods, the Florida population has genetic variation (7.5% polymorphic loci, 0.028 mean heterozygosity). Much of the genetic variation that does exist in the Florida panther population is contained in those animals believed to be intergrades between F. concolor coryi and as yet unidentified subspecies from Central or South America. Assuming that the ancestral population of Florida panthers contained as much genetic variation as do other populations of the species, approximately 50% of the genetic variation that once characterized the subspecies has already been lost.

The pedigree available information demonstrate that close inbreeding (matings between parents and offspring) has been documented in at least 3 breeding events. Second generation inbreeding is probable but undocumented.

There are a number of indicators that inbreeding and losses of genetic diversity are having damaging effects on the population. Male Florida panthers average more than 93% abnormal sperm, more than any of 5 other felid species examined to date. Of male panthers examined since 1985, 44% are cryptorchid (having only one descended testicle), and the rate of cryptorchidism has been increasing markedly since then. As of 1991, 90% of living male Florida panthers are cryptorchid (M. Roelke, FL GFWFC). Vaginal fibropapillomas were observed in at least six female panthers. These papillomas are thought perhaps to impede penile penetration during copulation and or impede transport of sperm through the female tract. Two of the females did not breed during 6.5 years of observation even though they were in regular contact with breeding males (1990 FP Report, FL GFWFC).

Recently, heart murmurs have been detected in Florida panther young adults and kittens. It is not known whether this condition is genetic in cause or whether it will change with age. However, 2 panthers have died since 1988 due to complications associated with congenital atrial septal defects.

Several unusual morphological traits that have traditionally been used to help characterize the subspecies are likely non-adaptive genetic traits that have become common in the small population by chance. Prior to 1990, all panthers thought to be historic *F. c. coryi* have a kink in the end of the tail, while this abnormality is rare among those panthers with some South American ancestry. Likewise, the majority of the historic *F. c. coryi* have a cowlick on the back. The cowlick shows up in museum specimens, and may have been common in the Florida

panther population for at least 100 years. Differences in skull morphology distinguishing Florida panthers from other subspecies are probably indicative of genetic divergence among subspecies, perhaps representing adaptive differentiation. These differences would not be taken as indications of deleterious effects of inbreeding.

Inbreeding is known to cause increased juvenile mortality and decreased reproduction in many populations (Falconer, D.S. 1990. Introduction to Quantitative Genetics. 3rd Ed. Longman, New York; Ralls, K. and J. Ballou. 1983. Extinction: lessons from zoos. Pages 164-184 in C.H. Schonewald-Cox, S.M. Chambers, B. MacBryde, L. Thomas eds. Genetics and Conservation. Menlo Park, CA: Benjamin/Cummings; Ralls, K., J.D. Ballou, and A.R. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology 2:185-193; Wildt, D.E., M. Bush, K.L. Goodrowe, C. Packer, A.E. Pusey, J.L. Brown, P. Joslin, and S.J. O'Brien. 1987. Reproductive and genetic consequences of founding isolated lion populations. Nature 329:328-331.). Juvenile mortality has not been noted to be elevated in Florida panthers but it has not yet been well-quantified. Similarly, there is not yet evidence of poor reproductive performance by those panthers that have been breeding. Of those female panthers that have not been breeding, non-genetic causes (e.g., poor nutrition, lack of available males) have been implicated.

The above observations together strongly indicate that loss of genetic variation has been and continues to be substantial in the Florida panther population and that inbreeding and genetic loss has increasing impacts on the panthers. The lack of demonstrated loss of fitness (survival and reproduction) attributable to inbreeding may suggest that genetic losses have not so damaged the population as to preclude recovery of the population as it exists genetically at this time.

4. Are the perceived genetic problems correctable via intercrossing?

It is possible that managed translocation of animals already within the south Florida population could ameliorate immediate effects of close inbreeding. (Known pedigrees are not sufficiently deep to provide detailed knowledge of the genealogical relationships between animals in the ENP and in the Big Cypress subpopulations.) The PVA for the Florida panther and the consequent management decisions outline courses of action designed to manage the existing gene pool to recover the population. If the existing genetic variation can be captured and the founder base expanded rapidly, it is hoped that the population can be recovered without intercrossing to other subspecies. If deleterious genetical traits persist in spite of aggressive management of the existing gene pool, it may be possible and desirable, and perhaps necessary for population survival, to augment the genetic variability of the Florida panther with genetic material from other subspecies. The history of intercrossing of Florida panthers in captivity and in the Everglades National Park suggest that the reproduction and health concerns identified above may be reversible. Neither the ENP sub-population nor the Piper captive stock (both thought to be composed of mixtures between Florida panthers and South American panthers) show

cryptorchidism and kinked tails occur only rarely.

The histories of neither the Piper stock nor the ENP animals (thought to be partly derived from the Piper stock) are well documented. Controlled, experimental crosses among populations would be needed to confirm that deleterious traits could be prevented by genetic augmentation via intercrossing. Animals produced by experimental inter-populational crosses could be examined for sperm quality, presence or absence of health problems (e.g., heart murmur, vaginal fibropapillomas), and morphological traits (e.g., cryptorchidism, kinked tails).

5. Would there be negative effects of intercrossing?

The amount of genetic divergence between the Florida panther and other F. concolor subspecies appears to be slight (O'Brien data, 1990 FL GFWFC Report), indicating a recent and shallow evolutionary separation of populations that formerly would have been connected by gene flow. The weak inter-populational differentiation is consistent with observations that pumas are capable of long-distance dispersal. Based on the success of crossing between much more divergence populations of other carnivores, and the apparent success in crossing between Florida panthers and a South American stock (among the populations most genetically divergent from the Florida panther) likely during the creation of the Piper stock and the intergradation into the ENP population, it seems very unlikely that crosses between Florida panthers and similar subspecies from elsewhere in North America would display any negative effects in the first or later generations. The crossing experiments proposed above to verify the benefits of intercrossing also would provide an opportunity to confirm the lack of deleterious effects of intercrossing. Any evidence of "hybrid breakdown" in health, viability, or reproduction should be examined carefully in experimental crosses through at least 2 generations.

6. Are appropriate source populations available for intercrossing with Florida panthers?

The closest extant geographic population to the Florida panther is in south and west Texas. Animals from this source have already been used for experimental releases in northern Florida, and those animals appeared to adapt well to that habitat. Molecular evidence indicates that this population is genetically similar to the Florida panther, although not necessarily the most similar of the extant subspecies. Given the apparent close genetic relationships among all the North American populations, any other population could probably be used to augment the Florida panther population.

. Further genetic research should be done to quantify more precisely the relationship of the Florida panther to other populations. Although the Texas population seems suitable for intercrossing experiments, other candidate populations may be found to show much closer genetic

affinities, more genetic variation, or more similar habitat use. In particular, nothing is yet known of the relationships of Central American populations of F. concolor to Florida, other North American, or South American populations. Central American populations inhabiting approximately comparable environments may be found to have close genetic affinities to the Florida panther. Another group of animals of interest and deserving of more extensive genetic analysis, is the Piper stock. Although it is inbred and exhibits hip problems, this captive stock has some Florida panther ancestry, and may contain Florida panther genes no longer present in the wild.

It should be noted that an option to utilize the most genetically divergent population of F. concolor available for intercrossing was considered. Such a strategy could maximize the input of new genetic material into the Florida panther population. If the desire were to replace the Florida panther with a healthy population of the species (but not necessarily most closely related to the animal that formerly inhabited the SE US and that still inhabits south Florida), then use of a source population or a mixture of multiple source populations to maximize genetic variation could be appropriate. At this time, however, it is still hoped that the Florida panther can be saved from extinction with as little genetic alteration as possible. The attempt should be to preserve and restore a population that resembles the ancestral populations of the subspecies as closely as possible, augmenting the gene pool of the population as much as is necessary to assure continued viability of the population.

7. Strategy for incorporating intercrossing into the recovery of the Florida panther

As stated in the Recovery Plan, in the Population Viability Analysis, and above, it is believed that the Florida panther can be recovered to viable populations with aggressive management of the existing animals. Recovery will require management and restoration of habitat combined with measures to increase productivity and survival in the wild and in a captive population. The survival and continued adaptive evolution of the Florida panther is far from assured, however, and many uncertainties in our data on the current demographic and genetic status of the population, concerning the future changes in the environment, and in our understanding of basic population processes are recognized in the various recovery documents. The extent of genetic deterioration of the Florida panther and the impact that past and ongoing genetic losses will have on the viability of individual animals and the population remains one of the areas of greatest uncertainty and concern.

The recovery of the Florida panther should proceed through three levels of increasingly interventive management. First, ongoing attempts to secure and enhance the wild population must continue. Second, the newly established captive population has been identified as an important demographic and genetic back-up for the existing wild population and as the probable only source of sufficient Florida panthers for translocation to re-establish populations in other parts of the former range. Third, having identified (above) the evidence that genetic problems

are likely contributing to the vulnerability of the Florida panther, and that opportunity probably exists to utilize other populations of the species to genetically augment the Florida panther population, it would be recommended that panther management and recovery should include intercrossing experiments. Given the urgency of action to protect the panther (PVA projects extinction in 25-40 years if current genetic and demographic trends continue), and the necessarily long development time to implement captive propagation and intercrossing wisely, it is important that the three components of panther management proceed simultaneously. Sequential implementation of the three phases, rather than overlapping implementation, would leave the population highly vulnerable to extinction between phases if one were found to be insufficient and then next phase became the primary focus of recovery efforts. Time exists now to cautiously and wisely investigate options while not jeopardizing complementary components of an overall program and while animals exist with which to undertake such actions.

The PVA projects the captive breeding program to be implemented over a 20 period. During that time, concurrent experiments on intercrossing Florida panthers with other populations can proceed. Given the potential for serious deleterious consequences of unwise and poorly planned intercrossing of populations (see opening section), and the necessity for producing two generations of intergrades to confirm the presumed benefits and the lack of dangers in intercrossing, it would be prudent to begin investigations of intercrossing as soon as is possible. It is fortunate that experimental verification of the assumptions of a program of intercrossing can be done before such a program becomes the only and last hope for preserving Florida panthers. By crossing male F. c. coryi to females from other populations (perhaps by artificial insemination), investigations of intercrossing could proceed without harm to the wild population in Florida nor to the captive breeding program designed to propagate Florida panthers. Panthers from Texas or elsewhere could be used immediately. Knowledge gained from such crosses would be valuable even if future genetic investigations reveal better source populations for augmentation of the Florida panther. If intercrossed panthers are never needed because efforts to protect the Florida panther with its existing gene pool are successful, any such animals produced would be good subjects for planned trial releases into candidate reintroduction sites. If it becomes desirable or necessary to augment the Florida panther population by intercrossing, the animals produced experimentally could be used as the initial stock for such augmentation.

For the purpose of restoring genetic health to the Florida panther population it should not be necessary to introduce many animals from (an)other population(s). Demographic recovery and stability of the Florida panther population (and considerable genetic stability) can be afforded by the captive breeding program with Florida panthers bred solely from the genetic stock already existing in south Florida. However, intercrossing would be necessary to accelerate improvement of the genetic health and variation of the existing population and with relatively few animals should be sufficient to restore genetic variation, should that course be determined to become necessary. In that case, further analyses will be needed to determine the optimal amount and rate of genetic augmentation.

Any efforts to genetically augment Florida panthers by intercrossing must be closely monitored. Releases of panthers produced in captivity, especially if by intercrossing, should be made in areas where the resident population (if any) is well monitored and, consequently, social interactions between resident and translocated animals can be documented. The social structure of the recipient population should be evaluated and prepared for the introduction of individuals from captivity to reduce the likelihood of social disruption and death of important individuals in the population. All released or translocated panthers should be monitored by radio-collars, in order to track dispersal, habitat use, and social interactions with other panthers, and to indicate quickly death or serious injury. If possible, unique genetic markers for each translocated panther should be identified, permitting later verification of which animals successfully enter the breeding population in the wild. The ongoing data collection that serves now to provide understanding of the population status and structure will become the baseline data for comparison to similar data taken following translocations or other manipulations of the population.

PARTICIPANTS

Steven J. Arnold Dept. Ecology & Evolution 940 E. 57th Street University of Chicago Chicago, IL 60637 PH: 312-702-3402 FX: 312-702-9740

John C. Avise Dept. of Genetics University of Georgia Athens, GA 30602 PH: 404-542-6599 FX: 404-542-3910

Jonathan Ballou Dept. Zoological Research National Zoological Park Washington, DC 20008 PH: 202-673-4815 FX: 202-673-4686

Jan Eldridge
USFWS Region 3
Endangered Species Program
Ft. Snelling
Twin Cities, MN 55111
PH: 612-725-3276
FX:

David Flemming U.S. Fish & Wildlife Service 75 Spring Street, S.W. Atlanta, GA 30303 PH: 404-331-3580 FX: 404-730-3419

Nate Flesness ISIS 12101 Johnny Cake Ridge Road Apple Valley, MN 55124 PH: 612-431-9295 FX: 612-432-2757

Dennis B. Jordan USFWS/FL Panther Recovery Coordinator 117 Newins-Ziegler Hall, U of FL Gainesville, FL 32611-0307 PH: 904-392-1861

FX: 904-392-1707

Bob Lacy
Dept. of Conservation Biology
Brookfield Zoo
3300 Golf Road
Brookfield, IL 60513
PH: 708-485-0263
FX: 708-485-3532

Russell Lande Dept. of Biology University of Oregon Eugene, OR 97403-1210 PH: 503-346-2697 FX: 503-346-2364

Tom H. Logan
Bureau Chief Wildlife Research
FL Game & Fresh Water Fish Comm.
620 S. Meridian
Tallahassee, FL 32301
PH: 904-488-3831
FX: 904-488-6988

W.T. Olds, Jr.
U.S. Fish & Wildlife Service
75 Spring Street, S.W.
Suite 1276
Atlanta, GA 30303
PH: 404-331-6343
FX: 404-730-3419

Jack Pons FL D.N.R. 3900 Commonwealth Blvd. Tallahassee, FL 32399 PH: 904-487-0940 FX: 904-487-1469

Bruce Rodgers
National Park Service
Southeast Region
75 Spring Street, S.W.
Atlanta, GA 30303
PH: 404-331-4916
FX: 404-331-4943

Ulysses S. Seal CBSG 12101 Johnny Cake Ridge Road Apple Valley, MN 55124 PH: 612-431-9325 FX: 612-432-2757

Bob Wayne Dept. of Biology U.C. Los Angeles Los Angeles, CA 90024 PH: 213-825-9110 FX: 213-206-3987 Today, Sherlock Holmes would be a molecular biologist. For each of us, save identical twins, carries a unique genetic pattern in our DNA. It would be a case of "Elementary, my dear Watson!"

newscientist

GENETIC Number 52 FINGERPRINTING

Pauline Lowrie and Susan Wells

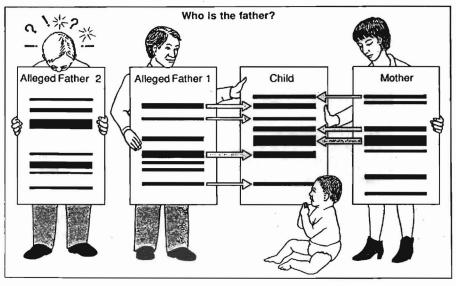
N July 1977, Monica Lemos de Lavalle, by then eight months' pregnant, was abducted by the security forces in the province of Buenos Aires, Argentina, with her husband and their 14-month-old daughter, Maria. Five days later, Maria was abandoned by her abductors near the house of her maternal grandmother. The fate of the young couple, and the baby Monica carried, remained unknown. Then a man just released from a secret concentration camp in Argentina told the grandmother that her daughter Monica had also been imprisoned there.

In 1985, authorities from the new democratic government questioned a former policewoman who had worked at the camp, and had a daughter she claimed as her own. Two years later, genetic tests carried out by the new government's Genetic Data Bank showed with a 99.98 per cent certainty that the girl was in fact the daughter of Monica Lemos de Lavalle. The child is now reunited with her sister and grandmother, although her parents are still missing, presumed dead.

These new genetic tests, known as genetic fingerprinting, are now helping to reunite with their grandparents many children who "disappeared" during the period of military rule in Argentina (1976-1983). Because the grandparents of the kidnapped children are aging, and many of the children are still missing, the Argentinian government agreed to establish a genetic data bank in May 1987. The bank stores blood samples from the relatives of missing children, and carries out

Sue Wells teaches biology at Frodsham High School, Cheshire, and Pauline Lowrie teaches biology at Sir John Deane's College, Northwich, Cheshire. They are the authors of Microorganisms, Biotechnology and Disease published by Cambridge University Press.

All diagrams are by Peter Gardiner



Pater pinpointed: DNA fingerprints can reveal a child's real father in paternity suits

the genetic fingerprinting tests that can identify their lost children.

Genetic fingerprinting was developed by Alec Jeffreys at the University of Leicester in 1984. He was studying the gene for myoglobin, a protein that stores oxygen in muscles. He found that part of the gene did not carry instructions for the manufacture of myoglobin. Instead, this bit of DNA consisted of an unusual sequence of bases, repeated several times. These repeated sequences, called minisatellites, seem to be useless but harmless bits of DNA. Yet Jeffreys realised they might prove useful to geneticists. He thought that these variable, short sequences, each about 10 to 15 basepairs long, could act as genetic markers for the myoglobin gene-helpful in tracking location on a particular down its chromosome.

To produce large quantities of the mark-

ers, Jeffreys isolated two minisatellites and introduced them into bacteria. He then extracted the multiplied markers from the bacteria and labelled them with radioactive chemicals. Now he had genetic probes that would bind to and so reveal the presence of minisatellites in any DNA sample.

But another surprise was in store. Jeffreys discovered that these minisatellite sequences were repeated many times in different parts of the DNA, not just in the myoglobin gene. Stranger still, the pattern of these repeats turned out to be different in each individual. Everyone has these repeated minisatellite regions in their DNA, but the number of repeats is unique to every individual. Moreover, each of us inherits these repeats from our parents, half of them from our mother and half from our father. Only identical twins end up with the same numbers of minisatellite sequences.

WO sorts of probes are used to produce most genetic fingerprints. One sort, the multi-locus probes, are a short length of radioactive doublestranded DNA. These probes bind onto the DNA in many places and produce a DNA fingerprint with many bands for comparison-especially important in paternity testing. In unrelated people, only one in four bands (0.25) match another person's DNA fingerprint. So if there are, say, 10 bands in a DNA fingerprint, the chance match of these is expected once in 0.210, or approximately once in a million individuals. When many bands are analysed, paternity is established with virtual certainty. Multi-locus probes are also favoured in forensic investigations when the sample is plentiful and in good condition.

Single-locus probes are copies of a single long length of DNA (often part of a chromosome) which bind to the DNA at only one point. This type of probe produces only two bands in any individual, one from the mother and one from the father. Less DNA is needed than when using multi-locus probes because the large single-locus probes give such a strong signal, and so are best when the sample is tiny. Even partially decomposed DNA often shows a clear profile pattern with single-locus probes. They also allow mixtures of biological samples to be analysed. Because each individual usually produces two bands, a vaginal swab from a rape victim yielding eight bands suggests that the victim was raped by three men.

Forensic investigations commonly use three or four different single-locus probes on a single sample to produce DNA prints consisting of six to eight bands. Using more than one single-locus probe improves the validity of the test.

DNA extracted from Fragments separated into stains or body fluids bands during electrophoresis Isolated DNA cut to give fragments Smaller mobile fragment migrate towards anode

A DNA probe (or genetic marker) is a synthetic length of DNA, made in the laboratory. The DNA fingerprinting process depends on DNA probes that are made up of repeated sequences of bases. Geneticists splice the extended repeats into the DNA of a circular piece of DNA known as a plasmid and introduce it into bacteria-a procedure known as cloning. The bacteria then treat the foreign plasmid as their own and make more copies of it as they reproduce. To make a batch of DNA probe, researchers grow the bacteria in the laboratory, isolate the plasmids and extract the repeated sequences of DNA. It is then easy to attach a radioactive label to the probes, by replacing phosphate molecules with a radioactive isotope of phosphate.

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Making a DNA fingerprint Patterns in the gel

TO MAKE a genetic fingerprint, you need a sample of any tissue that contains cellsblood, saliva, hair roots or semen will do. The cells contain DNA, housed in the chromosomes within a cell's nucleus. Biologists extract the DNA from the sample and cut it at specific points using so-called restriction enzymes. The fragments of DNA, placed on

an agarose gel, are separated by running an electric current through the gel, a process known as electrophoresis. The pieces of DNA have a negative charge, so when a positively charged electrode is placed at the other end of the gel, the charged fragments of DNA travel towards it through the gel. The shorter, lighter fragments travel more quickly through the gel, while the longer, heavier fragments move more slowly. So this tends to separate the fragments according to their size.

The pattern on the gel, invisible at this stage, is covered by a nylon membrane and a layer of paper towels. The towels draw the DNA fragments upwards into the nylon membrane by capillary action. Radioactive DNA probes are now applied to the membrane, and these bind to any complementary minisatellite sequences. Excess, unattached

probe is simply washed away.

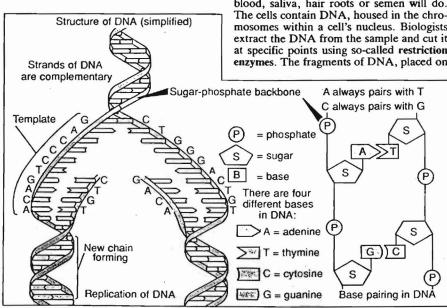
To make the pattern of bound minisatellite fragments visible, researchers now put an X-ray film next to the membrane. The places where the radioactive DNA probe has bound to the DNA fragments causes a visible fogging on the film. This creates a pattern of bands, or a DNA profile, commonly called a DNA fingerprint.

Bar codes for biologists

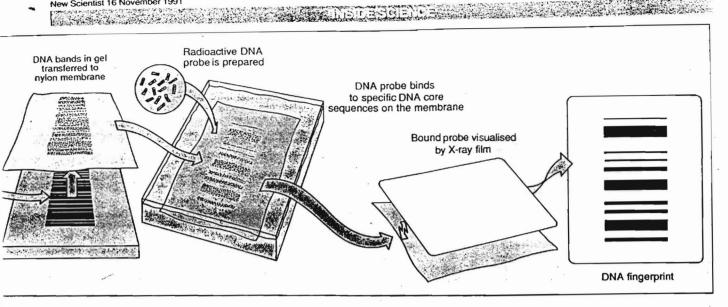
Contaminant problems

THE FINAL DNA fingerprint is a pattern on X-ray film of light and dark bandsdarker bands contain more DNA fragments. It looks a bit like the bar codes now found on retail goods. Researchers can describe the profile as a series of numbers, each referring to the length of the DNA fragment-calculated by measuring how far the fragment has travelled through the gel compared with marker bands of DNA of known length.

Although these techniques are now standard practice in molecular biology lab-oratories, great care must be taken in carrying out genetic fingerprinting tests. Forensic samples of DNA are rarely pure: typically, bloodstains on clothing or furnishing fabrics will be contaminated with all sorts of other material. In rape cases, the vaginal or anal swab used to obtain a sample of the



The genesis molecule: twisted into a double helix, sections of DNA form genes



attacker's semen also contains cells from the victim, so the victim's DNA must also be analysed alongside the sample from the alleged attacker. DNA from fungi and bacteria are also invariably present, and show up in the fingerprint. DNA decays rapidly, especially in warm or damp conditions. If the DNA has decayed, some of the DNA sites attacked by restriction enzyme may be lost, and thus result in too few or too many DNA fragments.

Any contaminants, such as dyes from blue denim jeans, can combine with the restriction enzymes, causing them to cut in the wrong places, so that there are too few or too many pieces of DNA. When contaminated fragments of DNA are sorted in the gel, they may be mixed with ions that affect their charge, so that they travel different distances through the gel and shift the bands to an

unpredictable extent. Proteins from the environment can have the same effect, by attaching to the DNA fragments and weighing them down.

If the DNA is contaminated, even DNA samples from the same person can give DNA fingerprints where the ends do not align, although their relative positions remain the same—a problem known as band shift. In the probing stage at the end of the process, probes can bind to the contaminating DNA rather than the human sample, causing spurious bands, or the contaminant may

interfere with the probe, so it does not bind

as expected, leading to missing bands.

Assumptions and doubts **Problems with relatives**

GENETIC fingerprinting also relies on the assumption that people within a country marry and have children at random and therefore that the bands present in a genetic fingerprint are distributed randomly in a population. Some studies in the US cast doubt on this assumption. In most Western countries, there are many smaller ethnic and religious groups where certain genetic characteristics may be more common.

Members of such groups are likely to marry within their community, and so tend to be somewhat more closely related genetically than the population as a whole. This modest "inbreeding" increases the chances that a child will inherit the same repeated sequence from both parents-and so be homozygous for that sequence. Homozygotes carry one, rather than two, bands for a given probe because they have received the same DNA sequence from each parent. Their genetic fingerprint will show one dark band rather than two lighter ones. This can bias calculations based on the assumption that everyone will have two bands.

Despite these problems, genetic fingerprinting has been widely used in the British courts to secure convictions. But responses to the technique in the US courts have been more guarded. In some cases courts have rejected DNA evidence. The difficulty is to ensure that rigorous standards are always upheld. "Blind" trials have been carried out Steps to a genetic signature: chop up the DNA, then sort and probe the fragments

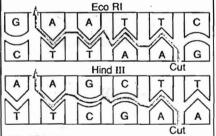
in the US, with different commercial laboratories running DNA tests on the same samples. In these trials, some laboratories failed to identify mixed DNA as coming from two individuals, or found false positives (declaring a match between samples which in fact came from different individuals). European forensic laboratories are now trying to agree on standard techniques for producing genetic fingerprints, in an attempt to overcome some of the criticisms raised against the technique in the US. Standardising the technique means agreeing on which restriction enzymes and probes to use, as well as running a known set of controls for comparison and checking that probes are uncontaminated. Most experts agree that the technique still shows as much promise as ever, provided that proper precautions are taken to obtain uncontaminated samples and avoid sloppy laboratory practices.

DNA forensics Identification of rapists

A VAGINAL swab taken from the victim can be used to obtain a DNA fingerprint. The swab holds DNA from both the victim and the rapist. The complex fingerprint that results must then be compared with the victim's DNA fingerprint, made from a sample of the victim's blood cells. Any bands derived from the vaginal swab DNA not present in the victim's blood cell sample must have come from the rapist. This technique means that not only can the rapist be identified with a high degree of certainty, but also wrongly-accused suspects can be proven innocent.

Other criminals, such as murderers and burglars, can also be identified provided that a biological specimen, such as a minute drop of blood or a few hair roots, has been left at the scene of the crime. A genetic fingerprint can be produced from as little as 50 microlitres of blood, 5 microlitres of semen or 10 hair roots. Mouth swabs, fetal material and muscle tissue from dead bodies are also suitable sources of DNA.

Restriction enzymes How restriction enzymes cut DNA



ANY bacteria make restriction enzymes to protect themselves from invading foreign DNA molecules, such as viruses. The restriction enzymes attack the invading DNA by chopping it up. Each kind of enzyme (there are hundreds) recognises a particular, and different, sequence of between four and six bases and cuts the DNA there. Many restriction enzymes have been purified from various species of bacteria, and more than 100 are commercially available. For example, Eco RI comes from Escherichia coli and Hind III from Haemophilus influenzae.

The polymerase chain reaction

CIENTISTS at the Cetus Corporation in the US in 1985 invented the polymerase chain reaction (PCR). It is an ingenious technique for copying minute amounts of DNA many times over and has already revolutionised genetic testing. The procedure can "amplify", or make more copies of, a tiny bit of DNA—so that there is enough for tests such as genetic fingerprinting even if you start out with only the tiny amount of DNA contained in a single cell.

The technique works by exploiting the ability of an enzyme, DNA polymerase, to make copies of DNA. First, researchers heat the DNA, so that the double helix unwinds. Short sequences of DNA, called primers, are then attached to each end of each single strand of the target piece of DNA. These primers tell the enzyme where to start making copies. Next, researchers add the enzyme DNA

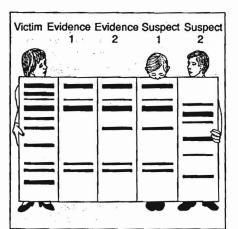
polymerase, together with a mixture of free bases. The enzyme directs the manufacture of a complementary sequence of DNA, making two complete double strands of DNA, both identical to the original piece of DNA. This cycle is repeated many times over, each doubling the amount of DNA in the sample.

This technique has not yet been widely used forensically, partly because PCR is particularly sensitive to contamination and partly because it involves "manufactured" DNA which is not readily accepted as evidence in court. But it is a useful technique in all sorts of research. Even archaeologists have exploited it. For instance, Erika Hagelberg at the John Radcliffe Hospital in Oxford, working with colleagues from the University of Oxford's archaeology unit, has extracted mitochondrial DNA from bones of English Civil War skeletons, and amplified it using

PCR—giving clues to our genetic history.

One interesting forensic application of PCR arose when the remains of a body wrapped in a carpet were discovered at a house in Cardiff in 1989. Facial reconstruction led the police to guess that the body was that of Karen Price, a teenager who had disappeared in 1981, but no one could be sure. Erika Hagelberg extracted a tiny amount of DNA from one of the bones, and sent it for analysis to Alec Jeffreys at Leicester.

The sample was heavily contaminated with microbial DNA and decayed, but by using PCR the researchers amplified six minisatellite regions. By comparing these sequences with DNA from Karen Price's parents, the evidence was strong that the body was indeed that of Karen Price. In February 1991 this was accepted by Cardiff Crown Court, the first time PCR has been accepted as evidence in a British court.



Clues to a crime: DNA fingerprints from forensic evidence implicate suspect 1

DNA fingerprinting can also help forensic scientists to identify corpses that are decomposed, or unidentifiable because only part of a body, such as an arm, has been found. Comparison of the DNA fingerprint from the body with those of living relatives, such as parents, brothers and sisters, can lead to a positive identification. Jeffreys has extracted DNA from bones supposed to be those of Joseph Mengele, the Nazi war criminal, and is now trying to obtain blood samples from living relatives to determine whether the remains really are Mengele's.

Because a child inherits half its DNA from its mother and half from its father, DNA fingerprints can be used in disputes about who the father is. The bands in a child's DNA fingerprint that do not match its mother's must come from the child's father. This has proved invaluable in immigration disputes. A Home Office-sponsored pilot study commissioned from Cellmark Diagnostics and Jeffreys in 1985 examined 36 families wishing to enter Britain to join their rel-

atives. The study found that nearly 90 per cent of the cases were genuine—although half of the applications had previously been rejected due to lack of sufficient evidence to convince the immigration authorities that the people really were related.

Researchers find DNA fingerprinting useful in studies of wild animals too. Only about 20 Californian condors remain in the US, split between San Diego Zoo and Los Angeles Zoo. The condors have now been "fingerprinted" so that zookeepers can establish relatively unrelated breeding pairs to encourage variation in the offspring. San Diego Zoo has a similar programme with its Galapagos tortoises.

Our ultimate identity card In sickness and in health

THE TECHNIQUE can also help doctors to monitor bone marrow transplants. Leukaemia is a cancer of the bone marrow and the diseased marrow must be removed. But bone marrow makes new blood cells, so the sufferer will die without a transplant of healthy marrow. Doctors can quickly tell whether the transplant has succeeded by taking DNA fingerprints. If the transplant has worked, a fingerprint from the patient's blood shows the donor's bands. But if the cancerous bone marrow has not been properly destroyed, then the cancerous cells multiply rapidly and the patient's own bands predominate.

Geneticists have also used the technique of genetic fingerprinting to identify identical twins. If twins are truly identical, formed by the division of a single fertilised egg, they have identical genetic fingerprints. The technique can confirm that twins who have been separated since early childhood and brought up in different environments really are genetically identical. This information is important because the study of twins can shed

light on many diseases that have both a genetic and environmental component, such as cancer, depression, diabetes, Alzheimer's disease and schizophrenia.

Geneticists studying inherited diseases such as cystic fibrosis are now using genetic fingerprinting to analyse blood samples taken from members of a family with an affected child. Such studies can help researchers to track down the gene responsible, and discover where it is located on a particular chromosome. Probes that bind to DNA in many places can act as genetic markers to locate a region inherited in the same way as the disease. This shows that this DNA region is physically very close on the chromosome to the particular disease gene. Ellen Solomon and her team of researchers at the Imperial Cancer Research Fund have used the technique to pinpoint the gene for familial polyposis coli, a type of colon cancer that affects people in their early 20s, and which is now known to be located on chromosome 5.

Many more applications for DNA fingerprinting will no doubt be developed. Indeed, one day hospitals may take DNA fingerprints of all newborn babies and store the information on computer, turning each person's genetic material into long identity card.

FURTHER READING

"The oldest DNA in the world", Julie, Johnson, New Scientist, 11 May 1991. "Is DNA fingerprinting ready for, the courts?", William C. Thompson and Simon Ford, New Scientist, 31 March 1990.

The next Inside Science will be published on 8 February 1992 and will look at immunisation and vaccination.

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"In press", 1990 - Orford Surveys in Evol. Biol.

PRINCIPLES OF GENEALOGICAL CONCORDANCE IN SPECIES CONCEPTS AND BIOLOGICAL TAXONOMY

John C. Avise and R. Martin Ball, Jr.

Department of Genetics
University of Georgia
Athens, GA., 30602, USA

Running title: Genealogical concordance

ABSTRACT

We suggest a conceptual and methodological approach to lower-level taxonomy that emphasizes principles of genealogical concordance, and that combines elements of the biological and the phylogenetic species concepts (BSC and PSC, respectively). Under the proposed concordance principles, biotic units warranting formal recognition are identified by concordant phylogenetic partitions at multiple, independent, hereditary characters. Such concordant patterns among the genealogical histories of independentlytransmitted traits are likely to appear within an organismal pedigree only under evolutionary conditions where intrinsic or extrinsic reproductive barriers (RB's) have been present. When the barriers are intrinsic (genetically based), we suggest that species recognition is warranted (as under the BSC), since the cladogenetic process is likely irreversible. When the barriers leading to genealogical concordance are purely extrinsic (geographic), we suggest that subspecific status is indicated. In addition, long-term geographic barriers to gene flow may be reflected in geographically-concordant subdivisions in the phylogenies of genes across a number of taxa; two such examples from the fauna of the southeastern U.S. are presented. By applying principles of genealogical concordance to the recognition of subspecies and species, a historical, phylogenetic perspective that is lacking in the BSC is combined with a focus on the modes and consequences of reproductive isolation that is neglected under the PSC.

INTRODUCTION

For more than half a century, the biological species concept (hereafter BSC) has been a major theoretical framework orienting research on the origins of evolutionary diversity (Dobzhansky, 1937). Under the BSC, species are "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1970, p. 12). Numerous authors have expressed sentiments on the BSC similar to those of Ayala (1976, p. 18): "among cladogenetic processes, the most decisive one is speciation-- the process by which one species splits into two or more..... Species are, therefore, independent evolutionary units. Adaptive changes occurring in an individual or population may be extended to all members of the species by natural selection; they cannot, however, be passed on to different species." Thus under the BSC, species are perceived as biological and evolutionary entities that are more meaningful and less arbitrary than other taxonomic categories such as subspecies or genera (Dobzhansky, 1970). The BSC has served to focus attention on questions concerning the evolution of intrinsic reproductive barriers (RB's), including: what genetic changes produce RB's, and hence new species?; what morphological, developmental, or behavioral traits are involved?; and, what ecological, demographic, or evolutionary conditions favor RB evolution?

As judged by its continued widespread employment in textbooks and as a guide to research strategy (e.g., Coyne and Orr, 1989), the BSC appears to have survived a variety of criticisms (both philosophical and operational) leveled against it over the last 30 years (Ehrlich, 1961; Ehrlich and Raven, 1969; Levin, 1979; Raven, 1976; Sokal and Crovello, 1970; Sokal, 1973; Wiley, 1978). Recently, another serious challenge has come from some

systematically-oriented evolutionists who argue that the BSC lacks a sufficient phylogenetic perspective, and hence provides an inappropriate guide to the origins and products of evolutionary diversification (Cracraft, 1983; de Queiroz and Donoghue, 1988; Donoghue, 1985; Eldredge and Cracraft, 1980; McKitrick and Zink, 1988; Mishler and Donoghue, 1982; Nelson and Platnick, 1981; Rosen, 1979). Many of these critics of the BSC argue that "reproductive isolation should not be a part of species concepts" (McKitrick and Zink, 1988, p. 3). This has led to another call for abandonment of the BSC, and its replacement by the *phylogenetic species concept* (hereafter PSC).

We believe there is much of value in the PSC, but that some of its proponents go too far in suggesting a total abandonment of the BSC. The purpose of this paper is to introduce another conceptual approach for taxonomic and species recognition based on principles of genealogical concordance defined below. These principles derive from most easily from theories and observations in molecular evolution, but can also be applied to hereditary morphological, behavioral and other phenotypic attributes traditionally studied by systematists. Concepts of genealogical concordance in taxonomic recognition combine what we perceive to be the better elements of the PSC and BSC.

SYNOPSIS AND CRITIQUE OF THE PHYLOGENETIC SPECIES CONCEPT

Under the PSC, a species has been defined as a monophyletic group composed of "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft, 1983, p. 170). Cracraft intentionally avoids explicit reference to reproductive disjunctions, and instead focuses directly on the distributions

of diagnostic, heritable trait(s). As emphasized by Cracraft (1983, p. 170), assemblages constituting a phylogenetic species "simply must be diagnosable from all other species." Each successful diagnosis is taken to indicate a phylogenetic separation-- the key concept underlying the phylogenetic species. The PSC has several suggested advantages over the BSC, including the following (Cracraft, 1983): (a) assemblages diagnosed under the PSC are phylogenetic units, and as such provide more informative subjects for evolutionary and ecological study; (b) the PSC eliminates the need for direct concern with reproductive compatibilities (that in nature are often difficult to observe directly, and normally cannot be assessed among allopatric forms); and (c) attention is focused on the geographical and genealogical histories of populations.

We are sympathetic to the general goal of the PSC of calling for greater attention to historical relationships of populations (Avise, 1989a; Avise et al., 1987a). However, current formulations of the PSC (e.g., Cracraft, 1983; McKitrick and Zink, 1988) have limitations as a replacement for the BSC:

(a) The number of species recognized under the PSC depends on the resolving power of the analytical tools available: The first clause of the PSC definition, "the smallest diagnosable cluster of individual organisms," indicates that any diagnostic trait uniting an array of individuals to the exclusion of others is sufficient to define a phylogenetic species (provided also that the trait is inherited and monophyletic). Some authors (e.g., Cracraft, 1983) suggest that the diagnostic trait may be either primitive or derived, while others (McKitrick and Zink, 1988) restrict consideration to derived traits only. However, there is considerable sentiment that a single diagnostic trait, no matter how "trivial," is sufficient for clade definition

(Wiley, 1981), and hence for species recognition under the PSC. For example, McKitrick and Zink (1988, pp. 9-10) contemplate the prospect of finding a group of birds with one extra hooklet on the barb of the seventh primary feather, and conclude "There is no theory to suggest that a trait must be of a certain quality or magnitude to provide historical information or to delimit species.... Thus, no character is potentially more or less useful as a tool to reconstruct patterns of speciation (sensu the PSC)."

What would be the consequences of recognizing a distinct species for each diagnostic trait? Cracraft (1983, p. 173) suspects that within ornithology "the phylogenetic species concept should not increase the number of taxa already recognized" (although many subspecies would be elevated to species status). McKitrick and Zink (1988, p. 9) suspect that closer scrutiny of biochemical, morphological and other characters on a microgeographic scale will likely reveal the existence of many more phylogenetic avian taxa, but that "The notion that there should be an upper limit to the number of species described does not appear to have any value, heuristic or otherwise."

We believe that such statements concerning the PSC overlook the huge size and extreme variability of eukaryotic genomes. Evidence from molecular biology demonstrates enormous genetic polymorphism within most taxa. For example, nucleotide diversity (a measure of heterozygosity at the nucleotide level) ranges from about 0.002 to 0.019 for various loci (Nei, 1987, p. 267). Since a typical gene consists of several thousand nucleotide pairs, randomly-drawn haplotypes from conspecific individuals will normally differ in nucleotide sequence. Even cursory assays of restriction-fragment-length-polymorphisms (RFLP's) of particular genes

such as mitochondrial DNA (mtDNA) or minisatellite nuclear DNA have revealed extensive intraspecific genetic heterogeneity. Most recognized biological species are already divisible into large numbers of diagnosable subunits [often geographically subdivided (Avise et al., 1987a)]; and in some taxa nearly every organism can be distinguished with the limited genetic information already at hand (Avise et al., 1989; Burke, 1989). The data from direct nucleotide sequencing, and from multiple loci, will make such levels of genetic distinction commonplace (e.g., Jeffreys et al., 1985; Kocher et al., 1989; Lander, 1989). If each individual organism is genetically unique at a high level of resolution, then the grouping of individuals requires that we ignore distinctions that occur below some arbitrary threshold. The evolutionary significance of any such threshold must surely be questionable.

(b) Unless persistent extrinsic (geographic) or intrinsic RB'S are present, different gene genealogies will usually disagree in the boundaries for "species" under the PSC. A strict application of the PSC definition is also difficult to apply given the vast numbers of gene genealogies and their expected idiosyncratic distributions within and among population pedigrees. The nuclear genome of most birds and mammals, for example, consists of about 2-3 billion nucleotide pairs. Under a conventional mutation rate of $\mu = 10^{-9}$ per nucleotide site per generation (Nei, 1987), a typical individual is likely to carry 2-3 newly arisen mutations, and a species composed of even a few million animals would be expected to carry several million new mutations every generation. Under a reasonable population demography (Poisson distribution of surviving progeny with mean 2 per family), nearly two-thirds of new neutral mutants are expected to survive for at least one generation, and nearly two percent will likely survive beyond 100

generations (Spiess, 1977, pp. 376-377). Each new mutation that survives (a derived trait) will have its own particular geographic and population distribution, depending on such factors as its place of origin and age, the fitness conferred on its bearers, and the historical gene flow regime of the species (Fig. 1). Except in the special evolutionary circumstances discussed beyond (which involve intrinsic or extrinsic RB's), little or no concordance should exist among the assemblages of individuals diagnosable with independent derived mutations or their derivatives: non-overlaps, partial overlaps, or nested arrangements in group membership should typically characterize various organismal assemblages diagnosed by independent genetic traits (Fig. 1). Due to inherently stochastic aspects of the hereditary process-- mutational origins, allelic segregation during meiosis, and the vagaries of population demography-- alleles at each genetic locus that have "trickled" through an organismal pedigree will exhibit a unique phylogenetic tracing (Ball et al., 1990).

(c) Shared ancestry in sexually-reproducing organisms implies historical membership in a reproductive community. The PSC could clearly be applied to the identification of "species" in asexually-reproducing organisms.

However, the second clause of Cracraft's (1983) PSC definition-- "parental pattern of ancestry and descent"-- was intended to extend the PSC to sexually-reproducing organisms. Species then constitute a phylogenetic "lineage" within which matings and successful reproduction have taken place (McKitrick and Zink, 1988). Thus when the PSC is applied to sexually-reproducing forms, historical reproductive communication and continuity implicitly accounts for shared possessions of heritable diagnostic traits. In other words, "species" under the PSC are recognizable precisely because

their members derive from reproductive communities of individuals (a general philosophy that the BSC has always emphasized).

Thus overall, if a broader framework of the PSC is to contribute to a significant advance in systematic practice (and we believe it can), a shift from issues of diagnosability to those of magnitudes and patterns of phylogenetic differentiation (and of the historical and reproductive reasons for such patterns) will be required. A powerful approach to these issues should involve reference to the following principles of genealogical concordance.

GENEALOGICAL CONCORDANCE

The extant haplotypes (DNA sequences) present in any "species" represent the gene lineages that have survived through an organismal pedigree. Within any pedigree, such lineage tracings (gene phylogenies) can differ greatly from locus to locus (Ball et al., 1990), due to the vagaries of meiotic segregation, mating pattern, and the reproductive success of individuals through which the alleles were transmitted. Such differences among gene phylogenies within an organismal pedigree arise inevitably, even when all loci experience nucleotide substitutions at the same rate, and when complicating factors such as recombination, gene conversion, and "sampling error" due to the idiosyncratic origins of the particular mutations assayed are neglected. A clear distinction must therefore be drawn between gene phylogenies and organism phylogenies (Avise, 1989a; Nei, 1987; Takahata, 1989; Wilson et al., 1985), and hence, between phylogenetic diagnoses based on single genetic traits versus those based on broader trends in the information content from multiple loci.

Suppose, as shown in Fig. 2, that an ancestral, random mating population

is sundered into two daughter populations, through either a geographic or genetic barrier to gene flow. Immediately following this separation, at any locus some haplotypes in daughter population 1 will likely be genealogically closer to some haplotypes in daughter population 2 than they are to other haplotypes in 1 (and vice versa). Phylogenetic partitions based on traits encoded by a single gene would therefore be discordant with the population subdivision. The status of particular gene phylogenies in these daughter populations changes through time due to demographically-based processes of lineage sorting, until eventually all remaining haplotypes in population 1 are genealogically closer to others in 1 than to any haplotypes in 2, and vice versa (Neigel and Avise, 1986; Pamilo and Nei, 1988; Tajima, 1983). The rate of the process is demography-dependent, but commonly takes about $2N_{\theta}$ - $4N_{\theta}$ generations, where N_{θ} is the effective size of the daughter populations. In other words, in terms of any gene phylogeny, two isolated daughter populations are expected to evolve from conditions of initial polyphyly, through paraphyly, and eventually to a state of reciprocal monophyly (Neigel and Avise, 1986), at which point the major phylogenetic subdivisions in the gene genealogy become coincident with the major population-level subdivisions (as defined by the intrinsic or extrinsic barriers to reproduction). Secondary admixture and introgressive hybridization between the two populations could of course blur the evidence for this historical separation.

Thus in taxonomic recognition, the operational challenge involves assessment of when the arrays of individuals grouped by particular genetic trait(s) coincide with the historical, organismal-level partitions that are seldom observable directly. Under what biological or evolutionary

conditions should the biotic partitions registered by various genetic traits faithfully mirror the phylogenetic separations of the taxa that we might wish to recognize formally?

Gene-gene phylogenetic concordances

One important consideration must be whether many independent gene phylogenies (those from unlinked and non-epistatic loci) provide *concordant* support for the organismal assemblages identified. As shown below, such concordances are likely to arise only when populations have been reproductively separated from one another (either by intrinsic or extrinsic RB's) for reasonably long periods of time. The following examples from computer simulations are intended to provide a heuristic introduction to concepts of genealogical concordance. They represent a preliminary extension of prior single-gene treatments (Neigel and Avise, 1986; Ball et al, 1990) to multiple loci considered together.

The current programs are slight modifications of those described in Ball et al. (1990), which should be consulted for assumptions, demographic conditions, and other details. The original programs were designed to: (a) produce a random-mating population pedigree; (b) choose for analysis haplotypes at particular loci that in effect have "trickled" through the organismal pedigree under Mendelian rules of segregation; and (c) find the times to the most recent common ancestor for randomly drawn pairs of haplotypes from those loci. In the present application and extension of these simulations, we considered again random mating ancestral populations (in this case, each composed of $N \equiv 100$ individuals) that become split into two daughter populations (each $N \equiv 50$) by a geographic or genetic barrier to successful reproduction.

Ten simulated populations were created and allowed to run for 1000 generations with no barriers to gene flow. At the end of the 1000th generation, 100 gene genealogies were chosen from each population and a barrier to gene flow was erected. The ten pairs of daughter populations were allowed to continue for another 500 generations with 100 additional gene genealogies being chosen for analysis for each pair of populations every ten generations. The 51,000 gene genealogies so created (100 genes X 10 simulated populations X 51 time points) were then analyzed by picking one of the daughter populations at random and determining the size of the largest monophyletic group containing only individuals from that daughter population. By this process, we hoped to show the development of concordant gene patterns through time. The results are shown in Fig. 3.

The results from these preliminary simulations support our intuitive expectations that populations isolated from one another for increasing lengths of time should be genealogically differentiable by increasing numbers of loci. Thus if the phylogenetic histories of many independent genes in an empirical survey were to separate individuals into concordant arrays, such a finding would be consistent with long-term reproductive separation of those arrays. Furthermore, concordance among the gene arrays is highly unlikely if there were no reproductive barrier. Therefore, we suggest that such population subdivisions concordantly identified by multiple independent genetic traits should constitute the population units worthy of recognition as phylogenetic taxa (see beyond).

Our simulations involve monitoring actual times to common ancestry in the pedigree (and thus ignore stochastic errors in the gene tree arising from the mutational process). In reality, many loci will evolve too slowly to provide markers for identifying recently separated populations, and in addition the sensitivities of assay methods employed may be inadequate to detect all genetic differences that exist. Thus in practice, it is unrealistic to suppose that most or all loci should contribute to the concordance distinguishing historically-separated population units. Nonetheless, unless multiple genetic traits distinguish arrays of organisms, those arrays cannot necessarily be assumed to reflect significant phylogenetic population subdivisions.

It might be argued that the requirement of multiple gene concordance for taxonomic recognition is overly restrictive. After all, genealogical concordance will not develop until some time after reproductive isolation has occurred, and in the interim, the isolated groups are not acknowledged. The problem is based on more that the simple failure to diagnose reproductively isolated groups. It revolves rather on the problem of determining what a significant period of reproductive isolation is. There must be innumerable instances of temporary population isolation within any "species" exhibiting limited dispersal capabilities. Most of these instances will be of such short duration that the populations cannot develop independent evolutionary histories. It is only when reproductive separations among such populations extends to longer periods of time that genetic differences accumulate, and genealogical concordances appear.

In theory, the times to reciprocal monophyly in the gene genealogies distinguishing two isolated populations are also directly related to effective population size (Neigel and Avise, 1986): small populations reach a state of reciprocal monophyly more rapidly than large populations. However,

the probability of detecting distinguishing characters over short timescales is also lower. Thus local populations will seldom exhibit high degrees of concordance among gene genealogies (or prove to be distinguished by large genetic distances), particularly if they are periodically connected to other such populations through gene flow, and/or are evolutionarily ephemeral (Avise, 1989a).

We suspect that the number of phylogenetic population units within most currently recognized "biological species," as identified by genealogical concordance, will be relatively low (certainly far less that the number of "local populations" or family units, though often greater that one-- see beyond). Such phylogenetic units, supported by concordant distributions of multiple, independent traits (which can be biochemical, morphological, behavioral, etc., provided they have independent genetic bases), should represent the population assemblages that have been isolated from one another by long-term impediments to interbreeding.

A distinction should also be made between the use of multiple genes (or characters) in a discriminatory versus a concordance sense. For example, discriminant function analysis (Sneath and Sokal, 1973) is a multivariate statistical approach designed to maximally separate populations based on the accumulated information from many characters, each of which may overlap in distribution between the populations. Although concordance principles are similar in that they also apply to multiple characters, the concern is not whether the populations can be distinguished, but rather with the level of concordant support for such distinctions.

Gene-geography concordances among taxa

The branches in the phylogenetic trees for particular loci often show

strong geographic clustering (Fig. 1; Avise et al., 1987a). While we have argued that justification for the recognition of the major subdivisions in an organismal phylogeny may ultimately necessitate concordant support from the phylogenetic partitions of multiple genes, such information may seldom be available. Are there any conditions under which concordances between geography and the subdivisions in single-gene genealogies (such as those provided by mtDNA) yield compelling evidence for longstanding, phylogenetic population subdivisions?

We propose that if major phylogenetic distinctions in particular gene trees were geographically concordant across populations of a number of independent taxa, separations in the organismal pedigrees due to historical isolation would be strongly implicated. In a similar fashion, vicariance biogeographers have long emphasized that patterns of geographic congruence in the phylogenies of multiple, unrelated taxa should reflect the historical patterns of disjunctions in environments occupied by those organisms (e.g., Platnick and Nelson, 1978; Rosen, 1978).

Work in our laboratory over the past decade provides two applications of such comparative methods as applied to the "intraspecific" gene trees registered in mtDNA. First, within each of five recognized species of freshwater fishes, the earliest branching point observed in the mtDNA phylogenies readily distinguished populations in the eastern versus western portions of the species' ranges in the southeastern U.S. (Fig. 4; Bermingham and Avise, 1986). These concordant patterns in the mtDNA gene trees therefore suggest two major areas of endemism for southeastern fish populations, a result further supported by a conventional biogeographic reconstruction involving concentrations of species' distributional limits in

the region (Swift et al., 1985). For one of the assayed species (*Lepomis macrochirus*), allozyme data were also available, and they provided strong, independent genetic support (gene-gene concordance) for the phylogenetic units identified by mtDNA (Fig. 4; Avise et al., 1984).

A second example of geographic concordance in mtDNA phylogenies across a number of taxa involves coastal marine species in the southeastern U.S. (Avise et al., 1987b; Bowen and Avise, unpublished; Lamb and Avise, unpublished; Reeb and Avise, 1990; Saunders et al., 1986). Within each of six taxonomically-recognized species or species groups, ranging from oysters (Crassostrea virginica) and horseshoe crabs (Limulus polyphemus) to toadfishes (Opsanus beta and O. tau), diamondback terrapins (Malaclemys terrapin), and seaside sparrows (Ammodramus maritimus), the earliest (and most strongly supported) separations in the reconstructed mtDNA phylogenies involved distinction of most Atlantic coast populations from those in the Gulf of Mexico and southeastern Florida (Fig. 5). These assayed species are confined to coastal margins, and are typically associated with salt marsh and estuarine conditions. Reeb and Avise (1990) discuss the paleo-climatic and geologic evidence for Pliocene/Pleistocene disjunctions in suitable habitat that likely initiated the phylogenetic population separations, as well as the ecologic and hydrologic limits to gene flow in south Florida that today may help to maintain these historical patterns of population subdivision.

SUGGESTIONS FOR TAXONOMIC PRACTICE

Concordances among the genealogical histories of independent loci are likely to arise only under conditions where intrinsic or extrinsic RB's have severed genetic exchange between populations for periods of time

considerably longer than the evolutionary effective sizes of those populations. If the RB's are genetically-based (intrinsic), the populations exhibiting gene-gene phylogenetic concordances may be either sympatric or allopatric, but in either event would constitute valid species under the conventional BSC. If the RB's are exclusively extrinsic (based solely on longstanding geographic barriers to gene flow), phylogenetic concordances may also be exhibited, either among independent loci within a taxon, or at a given locus among several unrelated taxa that had been concomitantly subdivided by the geographic barrier.

However, there remains a fundamental distinction between concordances in gene genealogies that have arisen from intrinsic versus purely extrinsic isolating barriers. The former are likely to be irreversible evolutionarily, while the latter can be ephemeral due to breakdowns of geographic barriers. If intrinsic RB's had not yet evolved in allopatry, secondary population contacts could lead to introgressive hybridization, and disintegrations of genealogical concordance (decay of gametic-phase disequilibrium). For this reason, species deemed distinct under the BSC (isolated by intrinsic RB's) will tend to evolve independently and will accumulate genetic differences through time, while the genetic differences between allopatric populations separated solely by extrinsic gene-flow barriers would remain in jeopardy [unless the barriers remained intact for very long periods, in which case intrinsic RB's (and hence biological species) would likely arise as a byproduct of overall genetic divergence].

Species descriptions-- retention of the BSC

Therefore, we suggest that the biological and taxonomic category "species" continue to refer to groups of actually or potentially interbreeding

populations isolated by *intrinsic* RB's from other such groups. In other words, we favor a retention of the philosophical framework of the BSC. However, the *evidence* for evolutionarily significant RB's (whether intrinsic or extrinsic) will normally be indirect, and will involve concordant genetic differences among the populations involved. We recognize (as have many others) that there are operational difficulties with a strict application of this BSC, particularly as applied to allopatric forms, due to: (1) elements of uncertainty and subjectivity in applying the definition to certain disjunct populations, where the issue of reproductive compatibility in nature is difficult to assess; and (2) the occurrence of intermediate situations where limited hybridization and introgression occur in localized areas. In spite of these problems, by objectively examining organisms from the perspective of the gene-gene and gene-geography concordances described in this paper, assessments of the degree and pattern of phylogenetic separation will be facilitated.

Subspecies descriptions-- application of a modified PSC

The growing literature of molecular biology has demonstrated that many species (as defined by the BSC) are further subdivided into genetically distinct sets of geographic populations exhibiting considerable historical, phylogenetic separation from one another (e.g., Avise et al., 1987; Wilson et al., 1985). While such populations may not qualify as distinct species under the BSC (i.e., they are not isolated by intrinsic RB's), their longstanding separations have resulted in the accumulation of considerable genetic differences that in principle and practice are reflected in geographically congruent patterns of divergence at multiple loci.

To illustrate, the bluegill sunfish (Lepomis macrochirus) in the

southeastern U.S. consists of two genetically distinct forms distributed east versus west of the Apalachicola River drainage separating Alabama from Georgia (Fig. 4). The two forms differ in nucleotide sequence divergence by ≈ 8.5% in mtDNA (Avise et al., 1984), exhibit two nearly fixed allozyme differences at assayed nuclear genes (and an overall genetic distance of D ≈ 0.15-- Avise and Smith, 1974), and evidence additional differences in morphological and physiological traits (Hubbs and Allen, 1944; Hubbs and Lagler, 1958). Yet the two forms hybridize extensively in a secondary contact zone in parts of Georgia and the Carolinas. Within particular hybrid populations, alleles at nuclear loci are in gametic phase equilibrium with one another, as well as with the distinct mtDNA genotypes (Avise and Smith, 1974; Asmussen et al., 1987), thus providing strong evidence for near random-mating. In these freshwater fish, barriers to gene flow between populations in eastern and western river drainages are purely But the barriers have been of sufficiently longstanding duration extrinsic. that these populations are now distinguished by many genetic characteristics. We propose that such sets of populations, concordantly recognizable by many independent genetic differences, reflect the major phylogenetic partitions within a biological species that are worthy of formal subspecies recognition. [The two bluegill forms had indeed been assigned the Latin trinomials L.m. macrochirus and L.m. purpurescens.]

We therefore suggest the following definitional guidelines for the taxonomic category "subspecies" in sexually-reproducing organisms: subspecies are groups of actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction

must normally come from the concordant distributions of multiple, independent, genetically-based traits.

Since the populations constituting distinct subspecies are reproductively compatible, subspecies will normally be allopatric (though some of their populations may meet in secondary hybrid zones), and any significant phylogenetic partitions will be registered by multiple loci exhibiting congruent geographic distributions. The longer the geographic isolation, the greater the opportunity for genetic divergence and also for the accumulation of concordant phylogenetic distinctions at multiple loci. It remains to be seen how often genealogical concordance will be observed among geographic populations within biological species, such that subspecies designations are warranted, but we suspect that many biological species (such as the bluegill sunfish) will prove to have rather fundamental phylogenetic subdivisions resulting from historical population separations.

ADVANTAGES AND DIFFICULTIES OF CONCORDANCE PRINCIPLES IN TAXONOMY

Advantages of concordance principles

(a) The category "subspecies" will rest on a firmer empirical foundation. Conventionally, subspecies descriptions have been based on one or a few traits (such as pelage color or size) that allowed distinction of a high percentage of individuals in a geographic region from those in other areas (e.g., Mayr, 1969). As noted and criticized by Wilson and Brown (1953, p. 104), "The tendency in this method has been to delimit races on the basis of one or several of the most obvious characters...; the remainder of the geographically variable characters are then ignored, or if they are considered at all, they are analyzed only in terms of the subspecific units

previously defined." We agree with Wilson and Brown's (1953, p. 110) contention that "geographical variation should be analyzed first in terms of genetically independent characters, which would then be employed synthetically to search for possible racial groupings."

- (b) Major phylogenetic units within biological species will be afforded formal taxonomic recognition. Sets of long-isolated populations, reflecting historical disjunctions in suitable habitat, probably occur within the boundaries of many biological species (as delimited by intrinsic RB's). Such populations would be afforded subspecies status under concordance principles. The resulting taxonomies can be of great use in reconstructing historical biogeography (Avise et al., 1987), as well as in summarizing the apportionment of intraspecific genetic diversity which should aid the management and preservation efforts of conservation biology (Avise, 1989b). With the partitions in intraspecific phylogeny properly recognized (by concordance principles), the interpretation of characters at variance with the primary pattern should also be facilitated. For example, characters likely to be under intense selection pressures related to ecological circumstance (such as pelage color or body size) may often be geographically discordant with the phylogenetic subdivisions. Thus under concordance principles (as under the PSC, but not the BSC), explicit attention is focused on phylogenetic histories of populations.
- (c) The category "species" will remain similar to that currently employed, and intrinsic RB's retain primacy as a conceptual guide to species distinctions. Unlike the PSC, which would require a drastic revision of taxonomic designations at the species level, application of concordance principles should have little effect on current species-level taxonomies.

The conventional procedure for distinguishing biological species already rests implicitly on concordance principles— intrinsic reproductive barriers are deduced from the indirect evidence of differences (sometimes requiring close scrutiny) in numerous morphological, behavioral, and other assayable traits. Since reproductive assessments seldom can be made directly (see Sokal and Crovello, 1970), such character-state surrogates of reproductive unions and disjunctions are likely to remain of prime utility in species descriptions.

To the extent that genetically-based RB's are irreversible evolutionarily, they constitute irrevocable partitions of biotic diversity. The genes directly responsible for RB's, by cementing biotic subdivisions, will have a correlated effect on the phylogenetic partitions of many other loci in the genome (in the presence of RB's, all neutral loci will eventually evolve to a status of concordant reciprocal monophyly). Thus under concordance principles (as under the BSC, but not the PSC), intrinsic RBS properly occupy a position of fundamental evolutionary significance.

Potential difficulties of concordance principles

(a) Some species may be overlooked. Occasionally, populations may have evolved intrinsic barriers to reproduction so recently that phylogenetic separation and concordance are not yet evident in genes other than those directly responsible for the RB's themselves. While it seems unlikely that RB-producing genetic traits alone would normally distinguish species (except perhaps in very young polyploid assemblages, or in other situations where chromosomal or other genetic changes rapidly and recently precipitated intrinsic reproductive isolation), some "good" biological species could be missed under concordance principles (they would likely be

overlooked under the PSC and BSC also, unless the critical genetic trait conferring reproductive isolation were examined).

Some events that give species under the BSC may not be immediately recognizable under an implementation of concordance principles. In the special case where a single character change results in intrinsic reproductive isolation of two groups, there will be no immediate concordance between that character and others, although such concordance will inevitably develop through time. Overlooking valid biological species that were recently isolated is of special concern because such taxa should afford the chance to study the initial stages of speciation. Thus intrinsic RB's should retain primary as a conceptual basis for species recognition (as under the BSC).

- (b) Subjective taxonomic judgements may be required for intermediate levels of genetic congruence and divergence. Admittedly, there are several gray areas in this heuristic construct for taxonomic recognition under concordance principles. For example, how many gene phylogenies must support the subspecies distinctions?; and how much concordance must characterize the geographic distributions of the gene phylogenies? In principle, levels of genealogical concordance can vary along a continuum (see Fig. 3), so any specific suggestions for implementing concordance methods will necessarily involve an element of arbitrariness. However, all taxonomic schemes that divide the elements of the continuous pattern of evolutionary differentiation into discrete categories (such as subspecies and species) face similar difficulties with intermediate situations.
- (c) Obtaining phylogenies for independent genes may be difficult.

 Ideally, complete information on the histories of allelic relationships at

each of many loci would be most desirable in the search for genealogical concordance. However, apart from the large number of mtDNA phylogenies presented in recent years (Avise et al., 1987a; Wilson et al., 1985), very few gene trees have as yet been generated for any taxa at the microevolutionary scale (Aquadro et al., 1986; Avise 1989a; Langley et al., 1988), despite the increased availability of laboratory methods for restriction site mapping and nucleotide sequencing. In the assay of nuclear genomes, one technical complication involves isolation and assay of haplotypes from diploid organisms; but a more serious problem involves the likelihood that intragenic recombination or gene conversion will have shuffled nucleotide sequences at a locus, thus confounding reconstruction of gene genealogies (Aguade et al., 1989; Hudson and Kaplan, 1988; Stephens, 1985; Templeton et al., 1987). It remains to be seen whether significant disequilibria involving intragenic restriction sites or nucleotide sequences (of use to phylogenetic reconstruction) will commonly be found among geographically separated populations.

Since complete gene genealogies may remain difficult to obtain for most nuclear loci, frequencies of phylogenetically-unordered alleles (such as those provided by allozyme methods, or restriction-fragment-length polymorphism (RFLP) analyses-- Avise, 1989a) will continue to provide an important source of molecular character states normally used in the search for geographically concordant population subdivisions. Differences in morphological, behavioral, and other phenotypic attributes, provided they are genetically-based and independent, will of course continue to be important characters for survey in the search for patterns of geographic and genetic concordance.

SUMMARY

One important root of the PSC probably traces to Simpson's (1951) paleontological perspective on taxa, summarized in his definition of an evolutionary species (Simpson, 1961, p. 153) as "a lineage (ancestraldescendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies". Current versions of the PSC, apparently motivated by a perceived lack within the BSC of an adequate emphasis on history and phylogeny, have led some PSC proponents to reject the BSC's emphasis on reproductive isolation. Principles of genealogical concordance provide a compromise or composite stance between the BSC and PSC. Concepts of concordance are far from new in systematics (see, e.g., Wilson and Brown, 1953) and numerous statements can be found in support of the desirability of concordant information prior to taxonomic recognition. For example, Mayr (1969, p. 192) notes that "geographic variation in the salamander Plethodon jordani is too discordant to justify the recognition of formal subspecies, even though the variation of each individual character shows a definite geographic trend." Yet such sentiments too seldom have been followed, and many taxa continue to be recognized on the basis of one or a few diagnostic traits. The new generation of systematists may avoid a repeat of such errors by requiring concordance among several independent characters before advocating formal taxonomic recognition of putative population disjunctions. By focusing on the phylogenetic consequences of intrinsic RB's, and by emphasizing that important historical partitions can also be present within biological species because of extrinsic RB's, concordance principles should provide a useful set of philosophical and operational guidelines for the recognition of biotic and

taxonomic diversity.

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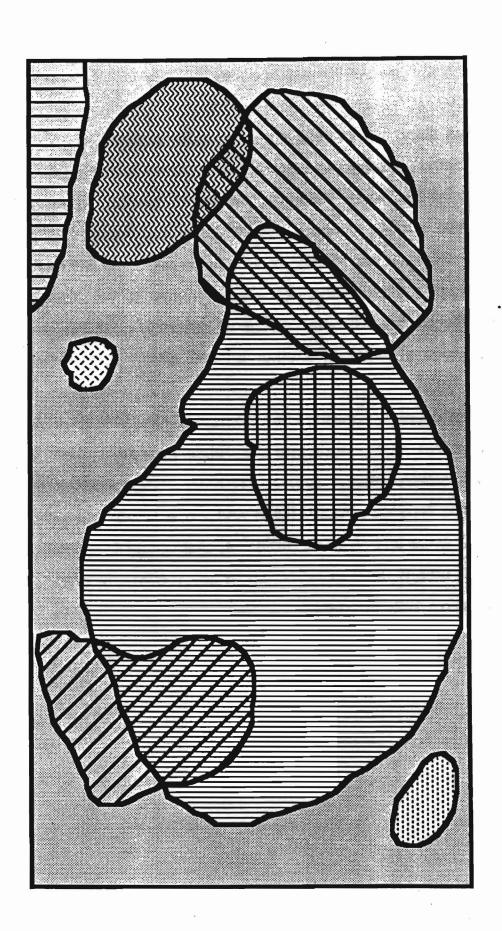
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FIGURE LEGENDS

- Figure 1. Examples of possible geographic distributions of various derived mutations in a continuously-distributed species with limited dispersal capability (compared to the geographic range occupied).
- Figure 2. Schematic presentation of the distribution of haplotype lineages (at a single gene) through an ancestral population subdivided (at time A) by a geographic or other barrier to reproduction. With respect to this particular gene genealogy, between levels A and B the daughter populations 1 and 2 are polyphyletic [that is, at any point in that time interval, some individuals in population 1 are genealogically closer to some individuals in population 2 than to other individuals in population 1, and vice versa (see nodes a, b, c and d)]; between levels B and C, the populations exhibit a paraphyletic relationship in the gene tree (that is, at any point in that time interval, all individuals in population 1 form a monophyletic subset (tracing to node e) within the more ancient gene tree of population 2, some of whose extant members diverged at nodes c and d; below time level C, populations 1 and 2 are reciprocally monophyletic in the gene tree, tracing to nodes at f and g, respectively.
- Figure 3. The time-course of the approach to monophyly in the gene genealogies of daughter populations separated by an absolute barrier to reproduction at time zero. In computer simulations, for each of 10 independent pedigrees, genealogies of 100 genes were monitored per pedigree every tenth generation. The vertical axis is the proportion of outcomes (±0.5 S.D.) in which at least 75% (upper curve) (or 100%, lower curve) of the individuals were part of the largest monophyletic

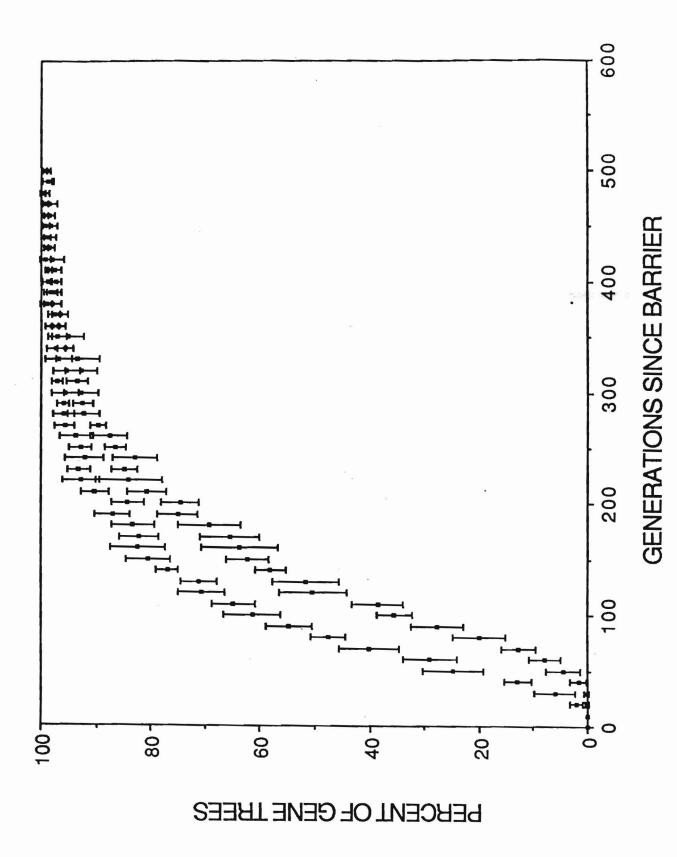
- group (in a gene tree) in the daughter population. See text for additional details.
- Figure 4. Pie diagrams showing the geographic distributions of the two major mtDNA phylogenetic branches observed within each of five species of freshwater fishes [1, warmouth sunfish, 2, redear sunfish, 3, spotted sunfish, 4 bowfin (Bermingham and Avise, 1986); 5, bluegill sunfish (Avise et al., 1984)]. Also shown (panel 6) are frequencies in the bluegill sunfish of the two electromorphs at the allozyme locus Got-2 [which are also very similar to observed geographic distributions at alleles at another nuclear gene, Es-3 (Avise and Smith, 1974)].
- Figure 5. Pie diagrams showing the geographic distributions of the two major mtDNA phylogenetic branches observed within each of six coastal-restricted marine species [1, horseshoe crab, Saunders et al. (1986); 2, American oyster, Reeb and Avise (1990); 3, seaside sparrow, Avise and Nelson (1989); 4, diamondback terrapin, Lamb and Avise (in prep.); 5, toadfish, Avise et al. (1987b); 6, black sea bass, Bowen and Avise (in prep.)].

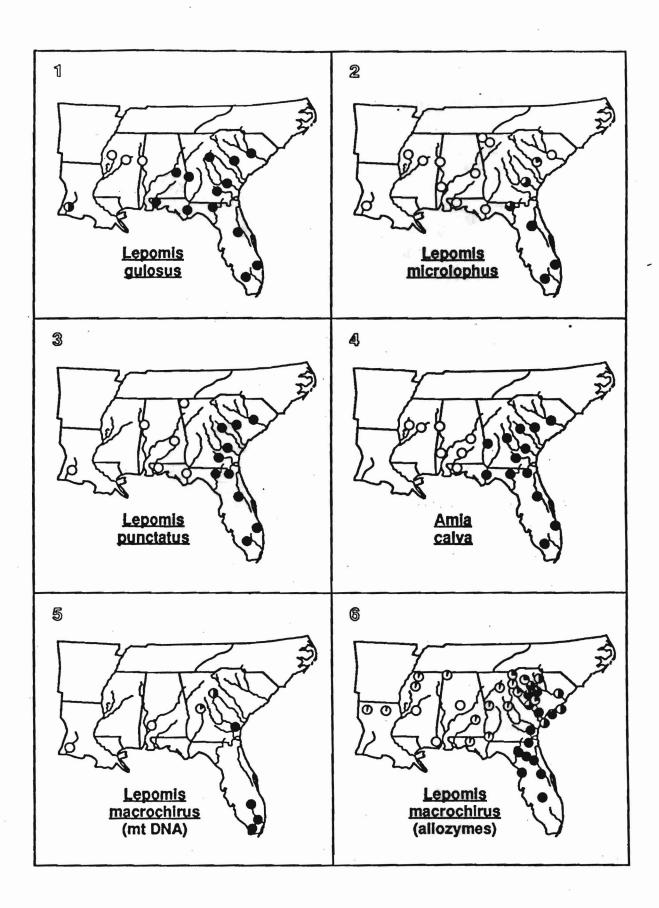


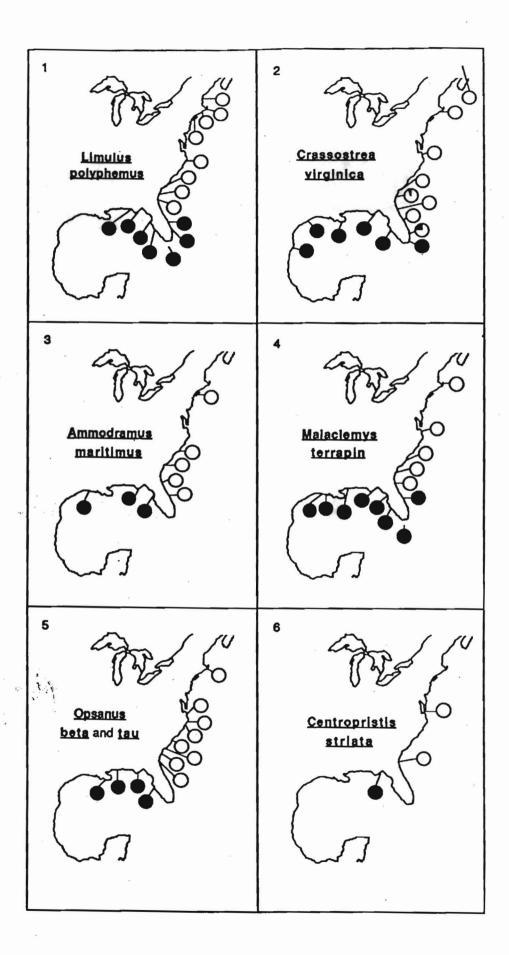
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POPULATION 1

POPULATION 2







KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 10
MACE-LANDE THREAT CATEGORIES

Assessing Extinction Threats: Toward a Reevaluation of IUCN Threatened Species Categories

GEORGINA M. MACE

Institute of Zoology Zoological Society of London Regent's Park, London NW1 4RY, U.K.

RUSSELL LANDE

Department of Ecology and Evolution University of Chicago Chicago, Illinois 60637, U.S.A.

Abstract: IUCN categories of threat (Endangered, Vulnerable, Rare, Indeterminate, and others) are widely used in 'Red lists' of endangered species and have become an important tool in conservation action at international, national, regional, and thematic levels. The existing definitions are largely subjective, and as a result, categorizations made by different authorities differ and may not accurately reflect actual extinction risks. We present proposals to redefine categories in terms of the probability of extinction within a specific time period, based on the theory of extinction times for single populations and on meaningful time scales for conservation action. Three categories are proposed (CRITI-CAL, ENDANGERED, VULNERABLE) with decreasing levels of threat over increasing time scales for species estimated to bave at least a 10% probability of extinction within 100 years. The process of assigning species to categories may need to vary among different taxonomic groups, but we present some simple qualitative criteria based on population biology theory, which we suggest are appropriate at least for most large vertebrates. The process of assessing threat is clearly distinguished from that of setting priorities for conservation action, and only the former is discussed here.

Resumen: La categorización de la Unión Internacional para la Conservación de la Naturaleza (UICN) de las especies amenazadas (en peligro, vulnerables, raras, indeterminadas y otras) son ampliamente utilizadas en las Listas Rojas de especies en peligro y se ban convertido en una berramienta importante para las acciones de conservación al nivel internacional, nacional, regional y temático. Las definiciones de las categorías existentes son muy subjetivas y, como resultado, las categorizaciones bechas por diferentes autores difieren y quizás no reflejen con certeza el riesgo real de extinción. Presentamos propuestas para re-definir las categorías en términos de la probabilidad de extinción dentro de un período de tiempo específico. Las propuestas están basadas en la teoría del tiempo de extinción para poblaciones individuales y en escalas de tiempo que tengan significado para las acciones de conservación. Se proponen tres categorias (CRITICA, EN PELIGRO, VULNERABLE) con niveles decrecientes de amenaza sobre escalas de tiempo en aumento para especies que se estima tengan cuando ménos un 10% de probabilidad de extinción en 100 años. El proceso de asignar especies a categorías puede que necesite variar dentro de los diferentes grupos taxonómicos pero nosotros presentamos algunos criterios cualitativos simples basados en la teoría de la biología de las poblaciones, las cuales sugerimos son apropiadas para cuando ménos la mayoría de los grandes vertebrados. El proceso de evaluar la amenaza se distingue claramente del de definir las prioridades para las acciones de conservación, sólamente el primero se discute aquí.

Introduction

Background

The Steering Committee of the Species Survival Commission (SSC) of the IUCN has initiated a review of the overall functioning of the Red Data Books. The review will cover three elements: (1) the form, format, content, and publication of Red Data Books; (2) the categories of threat used in Red Data Books and the IUCN Red List (Extinct, Endangered, Vulnerable, Rare, and Indeterminate); and (3) the system for assigning species to categories. This paper is concerned with the second element and includes proposals to improve the objectivity and scientific basis for the threatened species categories currently used in Red Data Books (see IUCN 1988 for current definitions).

There are at least three reasons why a review of the categorization system is now appropriate: (1) the existing system is somewhat circular in nature and excessively subjective. When practiced by a few people who are experienced with its use in a variety of contexts it can be a robust and workable system, but increasingly, different groups with particular regional or taxonomic interests are using the Red Data Book format to develop local or specific publications. Although this is generally of great benefit, the interpretation and use of the present threatened species categories are now diverging widely. This leads to disputes and uncertainties over particular species that are not easily resolved and that ultimately may negatively affect species conservation. (2) Increasingly, the categories of threat are being used in setting priorities for action, for example, through specialist group action plans (e.g., Oates 1986; Eudey 1988; East 1988, 1989; Schreiber et al. 1989). If the categories are to be used for planning then it is essential that the system used to establish the level of threat be consistent and clearly understood, which at present it does not seem to be. (3) A variety of recent developments in the study of population viability have resulted in techniques that can be helpful in assessing extinction risks.

Assessing Threats Versus Setting Priorities

In the first place it is important to distinguish systems for assessing threats of extinction from systems designed to help set priorities for action. The categories of threat should simply provide an assessment of the likelihood that if current circumstances prevail the species will go extinct within a given period of time. This should be a scientific assessment, which ideally should be completely objective. In contrast, a system for setting priorities for action will include the likelihood of extinction, but will also embrace numerous other factors, such as the likelihood that restorative action will be successful; economic, political, and logistical considerations; and perhaps the taxonomic distinctiveness of the

species under review. Various categorization systems used in the past, and proposed more recently, have confounded these two processes (see Fitter & Fitter 1987; Munton 1987). To devise a general system for setting priorities is not useful because different concerns predominate within different taxonomic, ecological, geographical, and political units. The process of setting priorities is therefore best left to specific plans developed by specialist bodies such as the national and international agencies, the specialist groups, and other regional bodies that can devise priority assessments in the appropriate regional or taxonomic context. An objective assessment of extinction risk may also then contribute to the decisions taken by governments on which among a variety of recommendations to implement. The present paper is therefore confined to a discussion of assessing threats.

Aims of the System of Categorization

For Whom?

Holt (1987) identifies three different groups whose needs from Red Data Books (and therefore categories of threat) may not be mutually compatible: the lay public, national and international legislators, and conservation professionals. In each case the purpose is to highlight taxa with a high extinction risk, but there are differences in the quality and quantity of information needed to support the assessment. Scott et al. (1987) make the point that in many cases simple inclusion in a Red Data Book has had as much effect on raising awareness as any of the supporting data (see also Fitter 1974). Legislators need a simple, but objective and soundly based system because this is most easily incorporated into legislation (Bean 1987). Legislators frequently require some statement about status for every case they consider, however weak the available information might be. Inevitably, therefore, there is a conflict between expediency and the desire for scientific credibility and objectivity. Conservationists generally require more precision, particularly if they are involved in planning conservation programs that aim to make maximal use of limited resources.

Characteristics of an Ideal System

With this multiplicity of purposes in mind it is appropriate to consider various characteristics of an ideal system:

(1) The system should be essentially simple, providing easily assimilated data on the risk of extinction. In terms of assessing risk, there seems to be little virtue in developing numerous categories, or in categorizing risk on the basis of a range of different parameters (e.g., abundance, nature of threat, likelihood of persistence of threat, etc.). The categories should be few in number,

existing models (e.g., grizzly bear: Shaffer 1983; spotted owl: Gutiérrez & Carey 1985; Florida panther: CBSG 1989), and there is much potential for further development.

Although different extinction factors may be critical for different species, other, noncritical factors cannot be ignored. For example, it seems likely that for many species, habitat loss constitutes the most immediate threat. However, simply preserving habitats may not be sufficient to permit long term persistence if surviving populations are small and subdivided and therefore have a high probability of extinction from demographic or genetic causes. Extinction factors may also have cumulative or synergistic effects; for example, the hunting of a species may not have been a problem before the population was fragmented by habitat loss. In every case, therefore, all the various extinction factors and their interactions need to be considered. To this end more attention needs to be directed toward development of models that reflect the random influences that are significant to most populations, that incorporate the effects of many different factors, and that relate to the many plant, invertebrate, and lower vertebrate species whose population biology has only rarely been considered so far by these methods.

Viability analysis should suggest the appropriate kind of data for assigning extinction risks to species, though much additional effort will be needed to develop appropriate models and collect appropriate field data.

Proposal

Three Categories and Their Justification

We propose the recognition of three categories of threat (plus EXTINCT), defined as follows:

CRITICAL: 50% probability of extinction

within 5 years or 2 generations,

whichever is longer.

ENDANGERED: 20% probability of extinction

within 20 years or 10 genera-

tions, whichever is longer.

VULNERABLE: 10% probability of extinction

within 100 years.

These definitions are based on a consideration of the theory of extinction times for single populations as well as on meaningful time scales for conservation action. If biological diversity is to be maintained for the foreseeable future at anywhere near recent levels occurring in natural ecosystems, fairly stringent criteria must be adopted for the lowest level of extinction risk, which we call VULNERABLE. A 10% probability of extinction within 100 years has been suggested as the highest level of risk that is biologically acceptable (Shaffer 1981) and seems appropriate for this category. Furthermore,

events more than about 100 years in the future are hard to foresee, and this may be the longest duration that legislative systems are capable of dealing with effectively.

It seems desirable to establish a CRITICAL category to emphasize that some species or populations have a very high risk of extinction in the immediate future. We propose that this category include species or populations with a 50% chance of extinction within 5 years or two generations, and which are clearly at very high risk.

An intermediate category, ENDANGERED, seems desirable to focus attention on species or populations that are in substantial danger of extinction within our lifetimes. A 20% chance of extinction within 20 years or 10 generations seems to be appropriate in this context.

For increasing levels of risk represented by the categories VULNERABLE, ENDANGERED, and CRITICAL, it is necessary to increase the probability of extinction or to decrease the time scale, or both. We have chosen to do both for the following reasons. First, as already mentioned, decreasing the time scale emphasizes the immediacy of the situation. Ideally, the time scale should be expressed in natural biological units of generation time of the species or population (Leslie 1966), but there is also a natural time scale for human activities such as conservation efforts, so we have given time scales in years and in generations for the CRITICAL and ENDANGERED categories.

Second, the uncertainty of estimates of extinction probabilities decreases with increasing risk levels. In population models incorporating fluctuating environments and catastrophes, the probability distribution of extinction times is approximately exponential (Nobile et al. 1985; Goodman 1987). In a fluctuating environment where a population can become extinct only through a series of unfavorable events, there is an initial, relatively brief period in which the chance of extinction is near zero, as in the inverse Gaussian distribution of extinction times for density-independent fluctuations (Ginzburg et al. 1982; Lande & Orzack 1988). If catastrophes that can extinguish the population occur with probability p per unit time, and are much more important than normal environmental fluctuations, the probability distribution of extinction times is approximately exponential, pe^{-pt} , and the cumulative probability of extinction up to time t is approximately $1 - e^{-pt}$. Thus, typical probability distributions of extinction times look like the curves in Figures 1A and 1B, and the cumulative probabilities of extinction up to any given time look like the curves in Figures 1C and 1D. Dashed curves represent different distributions of extinction times and cumulative extinction probabilities obtained by changing the model parameters in a formal population viability analysis (e.g., different amounts of environmental variation in demographic parameters). The uncertainty in an

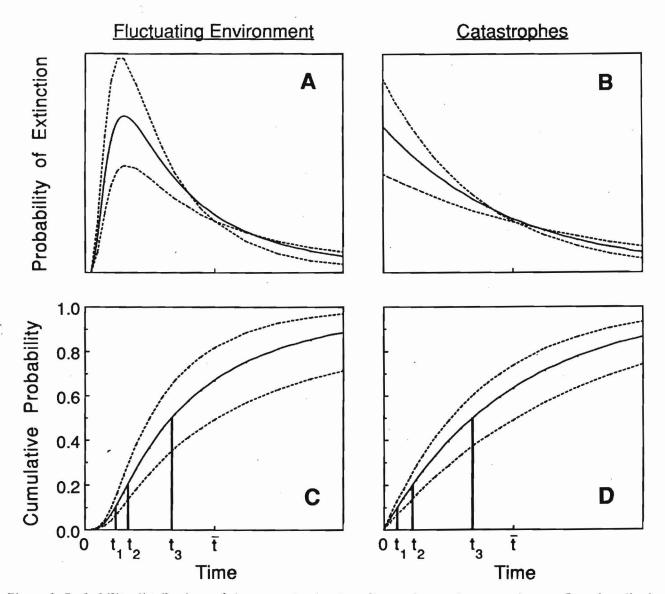


Figure 1. Probability distributions of time to extinction in a fluctuating environment, inverse Gaussian distributions (A), or with catastrophes, exponential distributions (B). Corresponding cumulative extinction probabilities of extinction up to any given time are shown below (C and D). Solid curves represent the best estimates from available data and dashed curves represent different estimates based upon the likely range of variation in the parameters. t_1 , t_2 and t_3 are times at which the best estimates of cumulative extinction probabilities are 10%, 20%, and 50%. \overline{t} is the expected time to extinction in the solid curves.

ENDANGERED:

20% probability of extinction within 20 years or 10 generations, whichever is longer, or

- (1) Any two of the following or any one criterion under CRITICAL
 - (a) Total population $N_e < 500$ (corresponding to actual N < 2,500).
 - (b) Population fragmented:(i) ≤5 subpopulations with N_e >

- $100 \, (N > 500)$ with immigration rates <1 per generation, or (ii) ≤ 2 subpopulations with $N_e > 250 \, (N > 1,250)$ with immigration rates <1 per generation.
- (c) Census data of >5% annual decline in numbers over past 5 years, or >10% decline per generation over past 2 generations, or equivalent projected declines based on demographic data after

variability and catastrophes, substantial differences may arise in the results from analyses of equal validity performed by different parties. In such cases, we recommend that the criteria for categorizing a species or population should revert to the more qualitative ones outlined above.

Reporting Categories of Threat

To objectively compare categorizations made by different investigators and at different times, we recommend that any published categorization also cite the method used, the source of the data, a date when the data were accurate, and the name of the investigator who made the categorization. If the method was by a formal viability model, then the name and version of the model used should also be included.

Conclusion

Any system of categorizing degrees of threat of extinction inevitably contains arbitrary elements. No single system can adequately cover every possibility for all species. The system we describe here has the advantage of being based on general principles from population biology and can be used to categorize species for which either very little or a great deal of information is available. Although this system may be improved in the future, we feel that its use will help to promote a more uniform recognition of species and populations at risk of premature extinction, and should thereby aid in setting priorities for conservation efforts.

Summary

- Threatened species categories should highlight species vulnerable to extinction and focus appropriate reaction. They should therefore aim to provide objective, scientifically based assessments of extinction risks.
- The audience for Red Data Books is diverse. Positive steps to raise public awareness and implement national and international legislation benefit from simple but soundly based categorization systems. More precise information is needed for planning by conservation bodies.
- An ideal system needs to be simple but flexible in terms of data required. The category definitions should be based on a probabilistic assessment of extinction risk over a specified time interval, including an estimate of error.
- Definitions of categories are appropriately based on extinction probabilities such as those arising from population viability analysis methods.
- 5. We recommend three categories, CRITICAL, EN-

- DANGERED, and VULNERABLE, with decreasing probabilities of extinction risk over increasing time periods.
- 6. For most cases, we recommend development of more qualitative criteria for allocation to categories based on basic principles of population biology. We present some criteria that we believe to be appropriate for many taxa, but are appropriate at least for higher vertebrates.

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KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 11 CONSERVATION STRATEGIES - GENERAL

Conservation: Tactics for a Constant Crisis

MICHAEL E. SOULÉ

s wildlife conservation failing? In the United States, species diversity appears to be declining at an accelerating rate (1). Even the Endangered Species Act of 1973 (ESA) has not significantly slowed the deterioration of the nation's biological estate, although this is largely the result of lack of support from the federal administration. Currently there are over 4000 species and subspecies recognized as candidates for endangered species status, but the listing process administered by the U.S. Fish and Wildlife Service is bogged down because of lack of funding. There are no recovery plans for nearly half of the 600 or so species in the United States that have been officially listed as threatened or endangered, and the score or so of recovering species is balanced by an equal number that may be extinct (2).

The situation is generally much worse in other nations. Biologists with extensive experience in developing countries are saying that by almost any quantitative standard conservation is failing, and that current approaches to conservation, such as traditional parks and reserves, are unlikely to succeed (3, 4). Worldwide, only about 3% of the land is set aside in 5000 nature reserves or protected areas (5), but many of these reserves are deteriorating (6). Because the moist tropics are far richer in species diversity than other biogeographic regions, and because deforestation will probably eliminate almost all of the tropical forests outside of protected areas by 2100 (7), biogeographers estimate that from 25 to 50% or more of tropical species will vanish in the next century or sooner (Fig. 1) (8). Even if humanity were to depart the earth, recovery of biotic diversity by evolutionary mechanisms would require millions of years, depending on how deep, taxonomically, the extinction crisis cuts (9).

Such dire predictions are now leading to a reappraisal of conservation's goals and tactics. In this article, I conclude that this reappraisal would be more fruitful if there were a deeper appreciation of the biological and social contexts of conservation actions, particularly how both biogeography and political geography dictate different conservation tactics in different situations. I also argue for an actuarial approach to the viability of protected areas—one that considers the social factors determining the half-life of nature reserves.

The Biospatial Hierarchy

Effective conservation is impossible without some knowledge of biotic (biological) diversity (biodiversity). For most scientific purposes, "life" is classified taxonomically, based on similarity and presumed evolutionary relationship. For purposes of protection, however, the living components of nature are usually classified in a "biospatial" hierarchy of nested sets. In practice, there are about five levels to this hierarchy: (i) whole systems at the landscape or ecosystems levels, (ii) assemblages (associations and communities), (iii)

species, (iv) populations, and (v) genes (10). Place, not evolutionary relationship, is the basis for the biospatial hierarchy, because most conservation strategies are geographically anchored (11, 12).

The targets at the top of the biospatial hierarchy are ecosystems (or landscapes and seascapes making up interacting ecosystems), including such topographic features as entire drainages. A frequently cited example is the Yellowstone National Park region, including the adjacent Grand Teton National Park and other federally managed lands. Ideally, ecosystem conservation protects the contained biotic communities: habitats, species, populations, and genes, not to mention all ecological interactions, processes, and some of the traditional, human cultural practices that have been historically associated with the ecosystem.

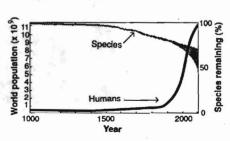
At the second level, an arbitrary number of biotic assemblages can be defined within ecosystems, although the species themselves show little correlation in their distributions when climate changes (13). Nevertheless, state, federal, and international conservation programs often base their conservation strategies on the completion of the network of biotic community types—the so-called coarse-filter approach. The discovery of "gaps" in the network of assemblages is most often based on systems of biogeographic classification (12, 14).

The third biospatial level, species, is defined as groups of populations that routinely exchange genes or are phenotypically similar (15). The selection of protected areas is frequently based on the presence of one or more endangered species, often large-bodied or attractive ones. In addition, regions with high species diversity, such as tropical forests, coral reefs, or regions with large proportions of local endemic species, such as isolated mountain ranges or oceanic islands, are frequently identified as targets of conservation. Another reason for focusing on species is that the management of protected areas is often facilitated by attending to a relatively small number of so-called keystone or indicator species; these species may not be endangered themselves, but they are used to monitor the status of a much larger assemblage of species (16–18).

Next is populations: Populations, whether mobile or sedentary, are dynamic assemblages of individuals which maintain genetic and sometimes social information in lineages that may ramify and merge as individuals are born, reproduce, and die. Endangered populations, and those of species that mediate important ecological processes, are often targets of conservation, so that their viability is a major concern (18, 19). Theoretical treatments of population viability are influencing public policy, such as the debate over the spotted owl in the Pacific Northwest (20).

At the small end of the biospatial hierarchy of conservation targets are genes. Genes are sometimes conserved ex situ (21, 22) as seed collections, in tissue culture or germplasm collections, or as cryopreserved semen, ova, embryos, and tissues. The extraction of genes from nature annually produces multibillion dollar benefits for agriculture, biotechnology, and public health (23). In nature, genetic

Fig. 1. The expected inverse correlation between human population size and the survival of species worldwide. Extinction rates depend on the size of the habitat fragment and occur at a decreasing rate as habitat fragments age. Anthropogenic extinctions be-



fore A.D. 1000 are ignored. The shape and width of the extinction curve reflect the uncertainty of the predictions; the curve is based in part on the assumption that most of the extinct species will be small organisms with geographically limited distributions.

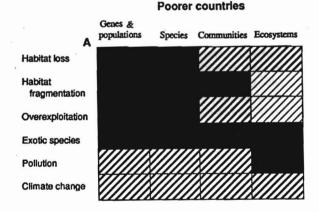
The author is professor of conservation biology, Board of Environmental Studies, University of California, Santa Cruz, Santa Cruz, CA 95064.

variation maintains the fitness and evolutionary flexibility of natural populations (16). Reserves in seminatural areas have been set aside to preserve the wild relatives of commercially important plants, especially to protect genes and gene combinations providing resistance to pests, drought, and other climatic factors (24).

The Six Classes of Interference and the North-South Distinction

The five levels of the biospatial hierarchy—are being undermined by six major classes of human interference (25), as shown in Fig. 2. These six factors are (i) the loss of habitat; (ii) the fragmentation of habitat-producing deleterious area, edge, demographic, and genetic effects; (iii) overexploitation; (iv) the spread of exotic (introduced and alien) species and diseases; (v) air, soil, and water pollution; and (vi) climate change. These factors have all been discussed in great detail (16, 19, 22, 26, 27). The intensities of shading in the two parts of Fig. 2 are subjective, but suggest that the present and future hazards posed by the six factors are not equal in strength or concordant in rank across the range of conservation targets, or from economically poorer to economically richer nations.

Clearly the impact of a given factor depends on the time, the place, and the circumstances. As indicated in Fig. 2, economics, culture, as well as the temperate-tropical disparity in species diversity and other biogeographic patterns, explain the differences in biotic vulnerability between tropical, poor countries, and temperate, wealthier ones. The vastly greater number of species in the tropical



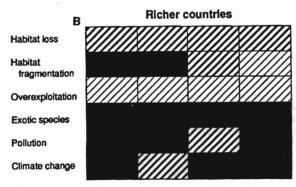


Fig. 2. Relative impacts of factors affecting terrestrial biotic diversity in (A) poor and (B) rich countries. Shading indicates intensity of impact: solid = highest; thick lines = intermediate; thin lines = lowest. Ecosystems refers to landscape level formations including, for example, mangrove habitats, coral reefs, riverine/riparian systems, forests, and savannas. The distribution of impacts on aquatic and marine systems differs somewhat from those shown here

nations, the much smaller geographic ranges of tropical species on average (28), in addition to the high rates of habitat destruction in most of these countries, means that species in the tropics are particularly vulnerable to habitat loss and fragmentation. Similarly, not all parts of the planet will be equally susceptible to the impacts of acid rain, ozone thinning, or greenhouse warming; for example, the effects of greenhouse warming will be much greater at high than low latitudes, except, perhaps, for marine systems (29). Other aspects of biogeography are relevant to geographic heterogeneity in biotic vulnerability; on oceanic islands, for example, introduced predators are typically more damaging than on continents (16, 25, 30), and introduced animals (goats, pigs, rats, mongooses, snakes, and predatory snails for instance) and plants may have catastrophic effects (31).

Although it is difficult to generalize, one can point to some rough principles about the global vulnerability of terrestrial biodiversity (32). Habitat loss, fragmentation, and the direct and indirect effects of exotic species are problems everywhere (Fig. 2A), but overharvesting of economically important species is now of greater concern in poorer countries. Pollution and climate pose major threats in the temperate zone nations (Fig. 2B). As discussed below, north-south differences in socioeconomic variables and biogeography mean that conservation tactics must be tailored to the location.

The Seven Sources of Biotic Degradation

The six classes of interference may constitute the most obvious proximal causes of biotic attrition, but the more fundamental causes are rooted in the contemporary human condition, especially as they are amplified by the explosive growth in human numbers in the last three centuries (Fig. 1). These more fundamental causes are listed in Table 1. The following brief descriptions of these factors are neither systematic nor exhaustive, but even this superficial treatment demonstrates why simple approaches (such as a network of protected areas alone) will fail.

Population growth. The continuous increase in human numbers exacerbates nearly every other environmental problem (33, 34). The population reached 1 billion about 1800, and appears to be headed toward 10 billion by 2046 and 12 billion by 2100, according to recent World Bank and United Nations projections. Ecologists argue that such numbers are incompatible with many ecological and evolutionary processes, including the persistence of large predators, the continuation of annual migrations of birds (35), speciation in large organisms (36), and the protection and maintenance of native biotas in the face of increasing pressure from human beings and

Table 1. Categories of fundamental human factors that contribute to the erosion of biological diversity.

Factor	Example of impact on conservation
Population growth	Population pressures
Poverty	Hunger, deforestation, trade in rare and endangered species, failure of grass roots support
Misperception	Desire for quick results and denial of long-term failures
Anthropocentrism	Lack of support for nonutilitarian causes
Cultural transitions	Unsustainable resource management during colonization and rapid social change
Economics	Failure of planning because of internationalization of markets and erratic pricing of commodities
Policy implementation	Civil disruption, wars, corruption, failure of law enforcement

A Constitution

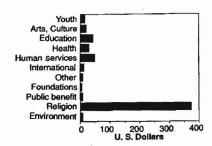


Fig. 3. Average charitable contributions per household in the United States. [Adapted from (67)]

introduced species. For nonhuman species, this "demographic winter" will last until human beings decide to reduce their numbers to levels compatible with the restoration of pre-explosion biotic processes (37). Human populations are already declining in many industrialized countries.

Poverty. The problem is not merely the shear magnitude of human numbers, however; it is compounded by poverty, the aspirations of people the world over for a better quality of life, and by social and political forces that impede the smooth transition to minimum (let alone "optimal") levels of prosperity, health, and justice (38). Disparities in income produce disparities of impacts. The per capita contribution to atmospheric pollution (and, hence, global climate change) is often orders of magnitude higher for citizens of the industrialized countries than for those in poorer nations (34), and economic pressures from the former contribute to unsustainable land use practices in the latter. Habitat destruction and extinction, however, will occur most rapidly in the tropics (Fig. 2A), where lack of economic opportunity, demographic momentum, and restrictions on reproductive choice are the engines that power the destruction of life.

It is probable that the price of raising human economic welfare to a standard similar to that in the wealthier countries will be biotic devastation in the tropics on a scale inconsistent with the persistence of wildlands except, perhaps, in remote, nonarable regions (39). Ehrlich and Wilson (40) point out that the magnitude of human aspirations, including demands on natural resources, if multiplied by the expected increases in human numbers, would require the human co-option of most remaining wildlands for grazing, farming, energy production, mining, transportation, and other uses. Therefore, the loss of most tropical wildlands in the next 50 years or so, an epochal catastrophe for earthly life, appears a virtual inevitability.

Misperception and time scale. Gradual environmental degradation goes almost unnoticed (41), whereas governments often overreact to sudden events of lesser overall impact. This short-term mentality is also reflected in current social mores and public policies favoring quick profits and results. The problem is that the benefits of conservation projects can only be measured on a scale of centuries. This difference in time scales between economic development projects and some conservation projects leads to conflicts because the business of conservation is keeping options open, whereas business as usual (economic development) often forecloses them.

Anthropocentrism. Many conservationists argue that current cultural values are antithetical to effective conservation policies, and that a new ethic or a revolutionary change in human consciousness is necessary before significant progress is possible (42). There are many calls for less human-centered, more biocentric economic policies. The anthropocentric orientation of most societies (43) however, augurs poorly for behavioral revolutions. If charitable donations reflect how Americans rank society's needs, it is evident that humanitarian concerns are dominant; money flows primarily to religious organizations and to medical, cultural, and social welfare causes. Figure 3 shows that only 1.5% of donated monies go to support environmental (nonhuman) groups and causes. This percentage is likely to increase, though, as donors learn about the

environmental foundations of physical and social welfare.

Mindful of biases favoring our own species, nearly every book, report, or "strategy" written to promote or guide the conservation of biodiversity presents a list of utilitarian justifications, including the free services and amenities provided by nature (for example, water purification and storage, habitat for fish and livestock, vistas), and the promise of life-extending pharmaceuticals and agro-industrial products that are yet undiscovered in the tissues of organisms (23). Unfortunately, the political effectiveness of narrowly utilitarian arguments for large protected areas in the tropics and elsewhere is weak, in part because the promise of long-term economic and health benefits to society as a whole appears abstract to individuals and corporations more concerned with survival and short-term economic gains.

Cultural transitions. The most destructive cultures, environmentally, appear to be those that are colonizing uninhabited territory and those that are in a stage of rapid cultural (often technological) transition (44). The cultural groups that appear to be the least? destructive to natural systems are those that have been occupying the same place for centuries or more (45). Overharvesting of wild animals, of aquatic and marine organisms, and of forests, is predictable, therefore, when human groups (i) have little or no experience in their current geographic setting or (ii) are undergoing integration into the world economy. Wealthy, well-educated, industrialized cultures may have the potential for minimizing environmental damage, but show little promise of this at present. Because most of the world's people are not only poor, but in a transitional phase between traditional agrarian self-sufficiency and a modern, highinput agricultural or industrial-urban society, relatively little value is placed on the protection of nature, and even where nature is highly valued, such valuation is often left out of economic calculus.

Economics. Environmental destruction and the erosion of biological diversity in the tropics and elsewhere is exacerbated by systems of commerce that create demands from the industrialized north for products, the production of which causes massive habitat destruction (46). The "cool chain" industry, for example, produces fresh produce such as fruit, vegetables, cut flowers, and mariculture produce (such as, shrimp) in the poorer countries and ships them in refrigerated carriers to the richer countries (47). This new industry contributes to the destruction of many habitats including lowland forests, mangrove, estuarine, and reef habitats. Better known are the coffee, sugar cane, banana, cacao, forest products, and cattle industries that account for the loss of a large proportion of tropical forests in developing countries (23, 48). In addition, a major contributor to forest and woodland destruction is the cutting of trees for the production of fuel wood and charcoal for domestic cooking and heating uses. Before the international price-fixing agreements among petroleum producers, most people in developing countries could afford to cook with kerosene. Now they must rely on wood, charcoal, and dung, contributing to the deterioration of forests and soils (49).

Notwithstanding the grave moral, social, and geopolitical implications of current economic disparities, the redress of such imbalances is unlikely to occur in time to save most seminatural biological systems from massive attrition. Few would question the goals of economic and social justice or their fashionable surrogate, sustainable development, but the premise that a new economic order would, alone, solve the biodiversity crisis (50) is suspect. The North American, let alone the Costa Rican experience (4), suggests that social justice and other progressive changes cannot protect biological diversity in the face of rapidly changing economic conditions including the internationalization of markets, increasing human numbers, the loss of cultural and ecological traditions, not to mention ethnic and religious conflicts. Even wealthy countries such as the United States and Canada justify the removal of the last

remnants of ancient forests on the grounds of economic necessity; attempts to save that remaining 15% of original forests in the Pacific Northwest have yet to prove successful (18). In addition, corruption and bureaucratic inefficiency appear to be virtually indelible.

Policy implementation. There are many reasons for the inability of modern states to enforce laws and implement conservation policies, especially policies that require short-term sacrifices for the sake of long-term benefits. For example, the setting aside and long-term protection of land from the national estate is improbable in societies with many poor or landless people, powerful oligarchies, or corruptible judges and bureaucrats.

In countries where adequate resources are lacking for the protection and management of protected areas, even relatively secure reserves are subject to the removal of trees and to the poaching of game. Most poor nations simply lack the resources to preserve biotic diversity in situ (51). Such attrition is frequent during "normal" times (52), but during periods of social unrest, the loss of biodiversity can be catastrophic (53).

Many conservation and development projects are destined to fail in a statistical sense, given their unstable social or political contexts. Wars and the breakdown of civil administration can undermine decades of successful policy implementation. In Africa, recent wars in Ethiopia, Sudan, Liberia, Libya, Morocco, Somalia, South Africa, Zimbabwe, Uganda, Chad, Angola, Mozambique, Rwanda, Burundi, and other countries have led to the partial or complete collapse of nature reserves, the destruction of habitat, and the local extinction of endangered species (53). The frequency of events such as wars should be built into the planning processes of responsible agencies and organizations. This is not to say that we should abandon reserves in regions where civil chaos is frequent. Rather, expectations and policies must be tuned to appropriate distributional parameters—for example, to the mean and variance of persistence times of protected areas in similar situations and to the kinds of damage that protected areas are likely to suffer, including the killing of most large animals. The lower the mean and the higher the warriance, the greater the emphasis there must be on redundancy, on alternative approaches, and on backup, ex situ projects. It would be prudent, in other words, to think of nature reserves as ephemeral islands, and to plan accordingly.

> The human condition is dynamic and unpredictable and will remain so for at least a century, if for no other reasons than the momentum of the population explosion and the unsatisfactory economic and social status for billions of people during the 21st

century. The "biotic condition," therefore, will also be tenuous during this interval. Fortunately, conservationists have an increasing number of tools with which to deal with the crisis.

Tactics and Conflicts

The eight paths to biotic survival. What tools are available to protect living nature from humanity? Table 2 presents a brief survey of eight conservation tactics or systems (5). The tactics are defined roughly in order of least to most artificial or intrusive.

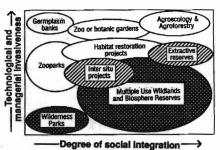
- 1) In situ refers to those conservation systems based on bounded wild areas with relatively little human disturbance; it includes most protected areas, from wilderness parks to the core areas of biosphere reserves (54). Persistence may depend to some extent on the economic benefits, as generated, for example, by tourism, but protected areas tend to degrade, even in the best of circumstances, and few, if any are large enough to maintain viable populations of large predators and omnivores without ex situ supplementation (16, 19, 26, 55).
- 2) Inter situ refers to conservation systems or activities in regions where native species still persist, but which are outside the boundaries of established protected areas. Most of the lands belonging to this category are nonarable; typically, they are relatively infertile, cold, steep, rocky, or arid. In the United States, most such regions are administered by the Bureau of Land Management and the U.S. Forest Service.
- 3) Extractive reserves permit certain kinds of resource harvesting on a (theoretically) sustainable basis. Examples include rubber tapping, the collection of edible fruits and nuts, thatch grasses, and, perhaps, even limited logging and hunting. Sustainability of such practices, however, depends on a low population density, a stable economy, and careful management (56). In practice there may be little difference between extractive reserves and inter situ projects, except that the latter are more circumscribed.
- 4) Ecological restoration projects refers to intensive management activities intended to increase species richness or productivity in degraded habitats. Among the necessary conditions for such activities are political and institutional stability.
- 5) Zooparks refers to facilities in secure locations where a mix of local and exogenous species can be maintained under seminatural conditions—in other words, sanctuaries for sensitive species of diverse provenance (57). The assumptions underlying the establishment of such reserves are that protected areas, in many places, are not viable for social

Table 2. The relative potential significance of eight different conservation systems for the protection and maintenance of natural biological diversity. The "0" indicates little or no role; "X, XX, and XXX" indicate low, moderate,

and high significance, respectively. The order of the systems does not imply a ranking of value.

	Conservation system							
Targets of conservation	In situ	Inter situ	Extractive reserves	Restoration projects	Zooparks	Agroecosystems & agroforestry	Living ex situ	Suspended ex situ
Entire systems (ecosystems)								
Processes or functions	XXX	XX	XX	XX	XX	X	0	0
Biosocial (traditional human uses)	X	XX	XXX	XX	X	X	0	0
Biogeographic assemblages	XXX	XX	XX	X	XX	0	0	0
Indigenous and endemic species	XXX	XX	XX	X	XX	. X	XX	X
Local populations of species	XXX	XX	XX	X	XX	X	X	X
Genetic variation within species								
Wild relatives of domesticates	XXX	XX	XX	X	X	X	XXX	XX
Traditional domesticated varieties	X	X	X	0	X	XX	X	XXX
Noneconomic genetic variation	XXX	XX	XX	X	X	0	Х	X
Ownership	Public & private	Private & public	Public & private	Private & public	Private	Private	Private & public	Private & public

Fig. 4. Descriptive distribution of conservation tactics according to the degree of social integration at the local level, and the degree of technological input or management intensity. Shading indicates relative degree of human interference with natural processes; darker shades indicate less interference.



The positions shown for each tactic are meant to suggest the center of the probable zone of action for the tactic. The term "Biosphere Reserves" refers to multiple use, production-oriented projects, with a relatively sacrosanct core protected area.

or political reasons and the inevitability of highly recombined biotic communities in the future given current rates of species introductions (58). This category differs from in situ reserves because of the conscious introductions of target species.

6) Agroecosystems and agroforestry projects are highly managed, production-oriented systems with a wide range of dependence on artificial chemical and energy inputs (59). The number of native species that can survive in such systems is highly variable, depending mostly on the proximity of garden, farm, and plantation to wildlands, the use of artificial chemical inputs, and the tolerance of farmers to wildlife (60).

In addition to zooparks, there are two kinds of ex situ tactics or backup systems (14). These are essential where particular reserves are likely to fail or lose significant numbers of their species.

7) Living ex situ programs refers to botanical gardens, zoos, aquaria, and similar institutions that maintain and propagate living organisms for noncommercial (education, research, conservation) purposes in a highly controlled, usually urban, context.

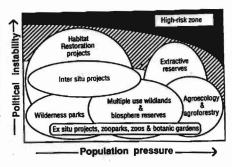
8) Suspended ex situ programs are completely artificial; living material is metabolically slowed or arrested. Among these projects are germplasm storage facilities such as seed banks, tissue culture collections, and cryopreserved collections of gametes, zygotes, and embryos.

As shown in Table 2, this typology of tactics manifests a current trend—the privatization of conservation. For many reasons, non-profit groups and individuals increasingly are complementing if not supplanting government agencies in protecting biodiversity. Private zoos, botanical gardens, and others are taking responsibility for the captive propagation of endangered species. Responsibility for the restoration of degraded forest, pastures, and farmlands on both public and private lands is being assumed by private groups. Organizations like The Nature Conservancy and Conservation International are acquiring new sites for protected areas (61), though governments are usually the ultimate owners.

Social Context and the Debate over Tactics

Current discussions have tended to oversimplify the diversity in conservation approaches by exaggerating the differences between the so-called species approaches and ecosystem approaches. The former emphasizes the protection, both in situ and ex situ, of endangered, often charismatic vertebrates, whereas the objective of the latter is to set aside and manage natural areas based on systems of landscape classification that will capture as much species and ecological diversity as possible (62). Critics of species-level approaches have emphasized the shortcomings of the Endangered Species Act and point out that most of the federal dollars are directed at a few birds and mammals (62). Some of these critics

Fig. 5. Prescriptive distribution of conservation tactics based on the probability of increasing population pressure and the likelihood of political instability or violent conflicts. Backup, ex situ facilities are placed in relatively secure, politically stable locations.



argue that success in captive breeding and cryopreservation will lead to complacency about the need for more and better protected areas. Supporters of endangered species might counter that if it were not for the charismatic species, the public appeal of conservation would be much less, that endangered species justify many of the larger protected areas in the United States and elsewhere, and that endangered species legislation is providing the economic leverage to bring developers and government agencies into negotiations about the preservation of large areas of habitat for general biodiversity conservation in the United States (63).

Such adversarial discussions, however, often ignore social context. As shown in Fig. 4, conservation tactics can be ranked according to the degree each is integrated into the local human community and the degree that each is dependent on artificial (technological) means and invasive management practices. Implicit is idea that different tactics require different degrees of social and technical sophistication.

A more prescriptive classification is shown in Fig. 5. It distributes the tactics in a plane of human population pressure and political stability. It is based on the untested assertion that the persistence of conservation projects, particularly protected areas, is related to the frequency and degree of political unrest and the rate of population growth. The combination of the two figures suggests that the choice of tactics should be influenced by the probable impact of demographic, economic, and social conditions as discussed above. For example, ex situ tactics are prescribed where political instability is frequent and where population pressure is building.

Much of the debate in the United States over approach and tactics stems from uncertainty and bias about landscape and geography, the importance of socioeconomic conditions and the stability of political structures, confidence in new legislative and legal remedies, and the identity of target organisms. For example, conservationists with experience in the species-rich tropics—where infrastructure is fragile at best, episodes of social chaos inevitable, human populations are doubling every few decades, laws are ignored, and hunting of rare animals and deforestation are a way of subsisting-should support a pluralistic approach that includes ex situ backup for protected areas. On the other hand, those with experience in wealthy, stable, temperate zone regions—where most species have wide geographic ranges and where there exists extensive areas of low productivity, government-owned lands-are more likely to promote systems of protected areas linked by corridors in multiple use zones that can be managed for conservation and sustainable forms of exploitation (64). They will also have more faith in legislative remedies and law enforcement. Figure 5 illustrates this tactical pluralism.

Conclusions

Today, the conservation of biodiversity is virtually equivalent to the ex situ protection of wildlands. In the future, however, such reserves will come to be seen actuarially, their life times dependent on many biogeographic, social, and political factors. Unless a much denser and more secure network of protected areas is established soon, the importance of less appealing alternatives will be greater than conservationists would wish.

This awareness has led some observers to call for a greater emphasis on adjunctive approaches, including inter situ projectsthe management of wildlife in nonarable lands outside of traditional reserves (65). Though appropriate in certain places, these lands are not immune to overexploitation, desertification, and to other forms of abuse, as the recent history of Tibet, the Sahel of Africa, and the American Southwest have shown. The inter situ tactic is an important backup, however, especially in socially and demographically stable nations and regions. The point is that every tactic has its limitations; sole reliance, for instance, on ecological restoration or on cryopreservation technologies would be premature, if not immoral, because these technologies could protect only a tiny fraction of species diversity for the foreseeable future, especially in tropical seas and forests.

Progress in conservation is hampered by the lack of a clearly articulated public policy on biodiversity. The United States and many other countries lack a coherent conservation strategy. In part, this may stem from confusion about tactics, as discussed above. The United States should join the nations that have developed a national conservation or biodiversity strategy. There is also a need for new institutions such as a National Institutes of the Environment (similar to the National Institutes of Health) to provide intellectual leaderhip and sustainable funding for planning and research in biodiverity. In addition, a high level review of federal agencies is necessary o that either the authority for the protection of biodiversity is rested in a new agency with clear directives, or the organic acts (if iny) of the agencies should be restructured, making conservation a orime directive of the U.S. Forest Service, the Bureau of Land Management, and the National Wildlife Reserve System.

Everywhere, nature reserves must be defended and bolstered by ocial experimentation in "sustainability." But there is too much at risk to gamble on any one social ideology, theory, or approach. All human institutions are transient expedients, and the conservation systems that are fashionable today will certainly undergo many changes in the next century. Opportunism and tolerance must be the watchwords of the science, the politics, and the art of nature protection (66). The issue, therefore, is not the "failure" of conservation; it is whether it can stay the course. During the construction of cathedrals in the Middle Ages, planners and artisans were not dismayed that "success" might require centuries. Like those workers, conservation scientists and practitioners must accommodate their objectives to the social complexity and temporal scale of their enterprise (67).

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An Evolutionary Basis for Conservation Strategies

TERRY L. ERWIN

ONSERVATION STRATEGIES HAVE BEEN REMARKABLY ANthropocentric from their inception in the Middle Ages to the present (1, 2). During dynastic and feudal times, parts of kingdoms were set aside as hunting grounds for the aristocracy, thus preserving everything that dwelled therein. This, plus severe natural and cultural control of human populations resulted in environmental protection for centuries. Today, with a burgeoning and expanding human population of 5.3 billion, no more than 4500 areas are protected globally (1); that is equivalent to a mere 3.2% of our planet's landmass. National parks, wildlife refuges, biosphere reserves, military reserves, Indian reservations, and other forms of legally protected areas have been established for aesthetic, political, or practical purposes in the last 150 years. Many reserves in less-developed nations are paper parks only; many in the more developed are lamentably endangered by touristic herds, and certain wilderness parks are threatened by short-sighted national energy policies.

The author is a curator of entomology (Coleoptera) at the National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.

Today, conservation strategy is based on a perceived impending loss of biodiversity due to tropical deforestation or disappearing habitats where populations of "interesting" species, subspecies, or even varieties (especially in temperate areas) reside. Campaigns usually focus on loss of potentially useful resources, such as plants with pharmaceutical properties or large animals that capture human interest. In practice, this results in saving fauna and flora in a few "available" acres where a well-known target taxon lives. Science has been too slow in providing inventory data to do much more; thus, what should be a major collective effort between conservation and science is often nonexistent, or in some cases, discord.

In the past 3 billion years, more species and their natural assemblies with their particular interactions have come and gone than are now present on Earth (3). One fact of evolution is that species go extinct, and others come into existence. Today, because of unprecedented human impact, species are increasingly going extinct and the speciation process, which creates future biodiversity, is being severely pressured through the removal of contiguous related biotic habitats. The pattern of continental habitats, often vast biomes, is being reduced to one of scattered island-like habitats and, just as on real islands, major extinctions are destined to occur. If this disruption of natural systems continues into the 21st century, we can expect the evolutionary process as we know it to become degraded and retarded.

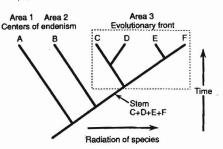
There is no unified scientific method behind conservation strategy that addresses the nature and quantity of biodiversity, nor what it means environmentally either to save it or lose it outside direct

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human interest. In fact, there is little altruism or science in the fight to save the rain forest, the spotted owl, or the Antioch blue butterfly. Rather, politics and economics weigh heavily on most decisions. It seems that degradation and conversion of the environment is proceeding so rapidly that getting something preserved—anything at all—is acceptable regardless of the yardstick. Worst of all is that legitimate arguments within the scientific and conservation communities allow decision-makers an out in politically difficult choices. In order to supplement positive conservation practices and provide an alternative to negative ones, an effort to establish a sound scientific underpinning must be made. Scientific rationale may transcend cultural changes through time, whereas economic and political grounds certainly will not.

What is biodiversity? Is it important, and if so, important to what? Is it possible to separate contemporary human needs from what is really necessary for the long-term environmental health of the planet? How can we hope to manage 30 or more million species? Given the myriad of societal demands and an ever-increasing population, what can realistically be achieved even if a global effort is sustained in environmental management? Should conservation strategy be scientifically or culturally based? These and others are the tough questions with which political systems must deal. For scientists, the question is what can we provide from our science that will help generate a long-term, transcultural foundation on which conservation strategy can be based?

Biodiversity can be equated with species richness, that is the number of species, plus the richness of activity each species undergoes during its existence through events in the life of its members, plus the nonphenotypic expression of its genome. Biodiversity evolves through numerous processes that vary from locality to ocality, habitat to habitat. Species richness at a site is a readily observable index of the number of interactions among and between species and how these species are grouped as a living unit at that site. A species richness index then is a reasonable and knowable tool that can be used in setting policy and making decisions about biotic conservation and management. To understand the significance of a biodiversity index across geography, one needs context. Relationships between species and a knowledge of lineages to



Flg. 1. Simple cladogram of seven species in a monophyletic lineage. More complex lineages may have more than one evolutionary front.

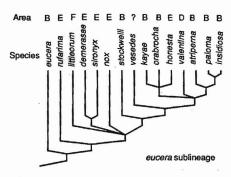


Fig. 2. Cladogram of the *eucera* sublineage of the carabid beetle genus *Agra* (9).

which they belong provide that context.

Radiation of lineages of organisms occurring on both continents and islands proceeds stepwise and requires contiguous habitats of various kinds through which sequences of phylogenetically related species pass as the lineage to which they belong rises to dominance (within the context of the occupied habitat) and ebbs to extinction (4, 5). Centers of endemism, or relict occurrences of organisms, are the last remaining footholds of past radiations. Elsewhere these endemic organisms have been replaced by better adapted lineages to an ever-changing contemporary environment. This model taken to its extreme, given current trends, indicates that within a few hundred years this planet will have little more than lineages of domestic weeds, flies, cockroaches, and starlings, evolving to fill a converted and mostly desertified environment left in the wake of nonenvironmentally adaptive human cultural evolution.

What should we know to aid in countering the planet's impending biotic destruction? Assuming that it is the species radiation part of the evolutionary process, the generator of biodiversity, which is endangered, and that is what we (altruistically) decide to protect through scientifically based choices rather than cultural ones, we need to know where lineages (not individual species) originate innovations in their evolution and how these become distributed over some part of the planet. The disciplines involved to achieve this are phylogenetics and biogeography, together referred to as systematics. We need to use this science to tell us where the critical areas are that need sound environmental management—that is, where we need to protect the active processes of contemporary evolution. The most powerful tool to emerge during the past 20 years as a robust and comparative science, with both practitioners and theoreticians, is phylogenetics (6, 7) and its methods and applications (8, 9). Phylogenetics is well suited to provide predictions of as yet unobserved qualities that are directly applicable to conservation decisionmaking (10) and because its tools are now computer-based it can be applied in a short time to many groups for detecting congruence in patterns of occurrence of radiating lineages (9). Site congruence, which can be mapped easily, of many evolving lineages can then become the target of conservation activities.

A cladogram illustrating the hypothetical phylogenetic relationships among seven known species that make up a monophyletic lineage of organisms is shown in Fig. 1. According to such an analysis, species A and B have not demonstrated radiation—that is, the ability to evolve into a more broadly adaptive and widespread lineage through time. Both are found to be geographically restricted endemic forms (relics) occupying small areas. Current conservation strategy places highest priority for protection on such areas as 1 and 2 (11). Endemic forms such as A and B are often unusual or rare, and even interesting to many scientists (12), but they are predictably on their way to extinction. These forms carry information about past evolutionary flourishes; they are important to protect, but they are only half the picture. The relatively more recent sublineage in Fig. 1 (stem C + D + E + F) is where phylogenetic theory predicts radiation and dynamic changes in taxa are occurring today and will occur in the future. Species such as C, D, E, and F are sometimes widespread and may even be regarded as "weedy" species, but does that make them less important? Their stem has become the multispecies sublineage that holds the most promise for continued evolution of this line of biodiversity under natural conditions. For example, in the eucera sublineage of the carabid beetle genus Agra (9) (Fig. 2), current interest would focus on areas D and F, each of which contains a relatively primitive and rare species. The cladogram (Fig. 2) shows that areas B and E contain both recent radiation and older species of the sublineage. If the eucera sublineage were something of general conservation interest, then the investment for protection would be better put into areas B and E to maximize

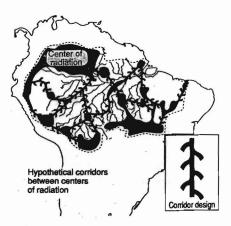


Fig. 3. Future corridors of ecological reconstruction between hypothetical centers of radiationfor example, in the Amazon Basin, to allow species movements and radiation. Inset is a design for a corridor that maximizes soil and habitat types in small areas.

salvaging this kind of beetle diversity now and in the future. Vane-Wright et al. (13) provide a novel index for cladogram analysis that needs careful testing in its application to making choices in conservation of taxic diversity. Congruence across many groups with their method may be the best way to find centers of radiation for conservation purposes.

Conservation strategy should incorporate methods to detect such contemporary evolution for the good of future maximum biodiversity. Conservation of only an accumulation of mostly nonradiating endemic taxa, the current conservation strategy (11), is like saving living fossils, something of human interest, but perhaps not beneficial to the protection of evolutionary processes and environmental systems that will generate future biodiversity.

Through analyses of diverse groups and detection of congruent patterns among radiating lineages (8), evolutionary fronts (centers of radiation) can be detected and targeted for long-term protection. Site protection and future ecological reconstruction of natural corridors (Fig. 3) between important centers will be essential to allow continued species radiation because climatic shifts may displace species' ranges (in isolated parks great extinction will occur); evolution proceeds from centers of radiation outward through

sequences of contiguous habitats latitudinally and altitudinally and there become disrupted from time to time allowing speciation.

Evolutionarily dynamic lineages today create future biodiversity. Such lineages are the cornerstone of natural environmental health. Science has the philosophy and tools to detect these lineages through phylogenetic systematics. Conservation strategy can use the patterns detected in cladistic studies to defend contemporary centers of radiation from destruction on the premise that today's maximum biodiversity, as well as tomorrow's, are in and stem from such centers. Acceptance of a nonhuman yardstick to measure environmental health—that is, evolutionary processes—and implementation of a scientific approach in conservation policies will provide a strategy to achieve a lasting stability for global environmental health because the basis for conservation will not be tied to the whims of human culture. The goal of conservation strategy should be the protection of future maximum biodiversity as well as preservation of contemporary species of human interest.

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Balancing Species Preservation and Economic Considerations

HAROLD J. MOROWITZ

OW MUCH IS A SPECIES WORTH? WE GENERALLY TAKE AN anthropocentric view of that question. The species Homo sapiens, as judged by the lives and well-being of individuals, is infinitely precious in our public ethic. A tiny arachnid, found only in the sands of Suvarov Islands, isolated in the mid-Pacific, is likely to get a much lower rating. The question becomes, "What is the value of a given species to human society?" Once the term "value" is introduced, the question moves to economics and ethics, both of which use that construct, but in very different senses. From a narrow economics point of view, we need a monetary metric of a species value to balance benefits against costs of preservations (1). Viewed from environmental ethics no such direct measure is possi-

ble (2). These considerations apply to ecosystems as well as to individual taxa. We are often left trying to balance the "good" of ethics with the "goods" of economics.

Some conservationists have argued for the virtue of the preservation of almost all species (3). There are techno-optimists who downplay the species problems (4). Extremist advocates of artificial intelligence envision a silicon chip-based "life" to succeed carbonbased humans (5). Some traditional economists might argue that the amount we are collectively willing to expend to preserve a species is an appropriate utility measure. But traditional theory does not deal effectively with goods not exchanged in organized markets. Free air and water pollution are examples of this approach. One senses that there has been far too little dialogue between environmental biology and economics.

The National Academy Forum on Biodiversity (3) devotes 30 of its 500 pages to economic issues, and the newly formed Society for Ecological Economics has begun to approach value problems. But one senses that there is not a full engagement of either of the contributing disciplines. Economics students are not required to study biology, and the curriculum of ecologists does not usually include economics. As noted in a recent business publication, "Environmental economics has been relegated unfairly to the mar-

The author is Robinson Professor of Biology and Natural Philosophy at George Mason University, Fairfax, VA 220307–4444.

gins of the economic community" (6). Difficult concepts such as the irreversibility accompanying species extinctions, the preferences of future generations, the problem of present benefits and future costs, and the distinction between commodity value and moral value render the economic mensurability of species preservation extremely difficult. Some conservationists argue that such an approach is wrong from a philosophical perspective (2). We are often left contrasting what is economically beneficial to individuals versus what is beneficial to society as a whole.

A few ideas are basic to our considerations. Species have almost certainly existed for over 3.7 billion years. It is in the nature of these taxa to arise, flourish for a time, and perish. For many biological groupings, the majority of species are no longer extant. Even the notion of what constitutes a species is not universally agreed on.

At some time in the last several million years, along the evolutionary line of hominids, reflective thought arose, coming to fruition in *Homo sapiens*. The appearance of a species with this novel noetic property is a discontinuity, a biological event of catastrophic impact and, of necessity, it profoundly changed the development of local and global ecosystems. In our reductionist fervor we sometimes have been remiss in underestimating the effect of reflective thought on global ecology. Environmentalists have not focused on how strange and different organisms human beings really are.

The agrarian revolution during the past 10,000 or more years converted vast land areas from forests, savannahs, and plains to fields and pastures. The large accompanying species loss was an inevitable sequela of the emergence of human civilization as we know it. This epoch, which was devastating in terms of biological diversity, is nevertheless referred to as "the humanization of the earth" by Dubos (7). Human society in the present context is inextricably intertwined with agricultural monoculture, the worst of all worlds from a diversity perspective. As the Irish potato famine and the desertification of the Sahal show, agricultural practices may also have devastating social and economic consequences. Humans, because of their engineering abilities, create another geosphere, the technosphere, to add to the traditional lithosphere, hydrosphere, atmosphere, and biosphere.

The continuing growth of human population requires ever more land for housing and agriculture, resulting in progressively increased habitat destruction. The conclusion is clear: the amount of unexploited lands and waters will decrease with increasing human population. Although the exact function is uncertain, the sign of the first derivative is ensured. Similarly, the total number of planetary species will be some monotonic function of unused habitats. Ergo, biodiversity decreases with increasing human population.

No discussion of managing global habitats and preserving species can avoid the population imperative. Ignoring this problem, whether for political, ideological, or theological reasons, which is the present stance of many world political leaders, is a policy that inevitably leads to habitat loss and species depletion. There has been an unwillingness to face the conclusion that environmental planning and concern for conservation in the absence of population control are tasks worthy of the metaphor of Sisyphus.

Following agriculture, a second great change has occurred: the industrial revolution and burning of fossil fuels. In chemical terms, for several hundred million years there has been a dehydration and reduction of buried biogenic CH₂O converting it to CH₄, CH₂, and C. The sudden reversal of this process to yield CO₂ is a major global consequence of industrialization. The acquisition and use of fossil fuels has resulted in habitat changes and loss of species.

From a direct economic perspective, the most severe changes in biota would be those that alter the global climate or geochemical distribution of essential materials or impact severely on cosmopolitan taxa. For example, loss of the genus *Rhizobium* (a most unlikely happening) would change the entire global nitrogen balance to a degree that would

require industrial nitrogen fixation or the farming of reduced nitrogen, which are clearly energetically expensive operations. If the loss of the Amazon rain forest were to lead to widespread deleterious climatological effects or major global mineral nutrient imbalance, then this would similarly be of direct economic importance.

Let us examine some of the more difficult to evaluate public goods. Species preservation has been argued from the viewpoint of potential future sources of natural products. Here the costs might be compared with those of the chemical research and biotechnology required to synthesize and test new compounds and produce them industrially. This is a case where conservationists are making direct economic assertions whose strength is subject to analysis by economic methods. Even this is complicated by the unknown future value of such commodities as tropical plant—based medicinals, which are now a rapidly expanding growth industry (8).

Much more difficult to deal with as a public good is the value of knowledge. A lost species may potentially possess some novel biological features that will forever be inaccessible to study. For example, the sperm and blue whales and the elephants, as the largest marine and terrestrial mammals, certainly merit extreme efforts of preservation on grounds of physiological uniqueness. It is difficult to put knowledge arguments in economic terms, but such knowledge is certainly part of my utility function and ultimately may influence agriculture, medicine, and industrial processes.

On the grounds just discussed, I would also argue for the careful conservation of primates, prosimians, and their immediate predecessors. The transition along the primate line to hominids is an ill-understood, vastly profound, and clearly globally overwhelming phenomenon. The anatomy, physiology, and behavioral biology of the primates are clearly major avenues to understanding aspects of ourselves and our culture.

The search for physiological uniqueness centers on larger organisms, whereas the search for novel biochemical features extends over all sizes. In the center of the size range is a vast array of insect species dominated by the Coleoptera and Diptera. In any case, if an argument is to be made to undertake the study of economic costs of preserving an individual species, the uniqueness or lack of uniqueness of that taxon should certainly be a component of the reasoning. Biodiversity per se may be of great intellectual importance to biologists, but to a broader society the argument hinges on something of more public value than our desire as biologists to understand all life, as laudable as that desire might be. The politics of species preservation should perhaps be shifted to the politics of habitat preservation.

Another group of taxa have a special but difficult to assign value because of cultural reasons or because they inspire a sense of awe and wonder. This has been referred to as amenity value. The mammals of Africa, the redwood trees of the western United States, and the Antarctic penguins are in this category. It is hard to develop a metric of awe and wonderment, yet it clearly is a factor in human response. If a habitat draws paying tourists to observe the flora and fauna, then we have some measure of human response. An example of a culturally significant species is the American bald eagle, which has acquired a symbolic importance far beyond the purely biological.

In dealing with issues of knowledge or cultural association, we clearly deal with public goods or collective goods as distinguished from the private goods of market economics. Here the market analogy becomes less useful and the invisible hand has to be replaced by aspects of the social compact. Regulation may be introduced for other than economic reasons, but this requires some kind of consensus. Bossons (9) argues,

Difficulties created by the public nature of ecological resources and their externalities suggest that the approach needed to rationalize protection of these resources must be reversed with respect to the approach used by competitive markets to satisfy consumers' demands.

Many environmental battles are being fought on these grounds.

There is a school of economic analysis (10, 11) that maintains that environmentally unsound practices are often economically unsound and involve governments fostering habitat destruction to protect politically influential industries. This leads to (11) "the use of limited natural resources at practically no cost." A number of examples are given (10) from the logging industry in the United States. The author maintains that in many cases the government is in fact subsidizing the clear-cutting of forests to produce a product that would be noncompetitive in the market without the subsidy. This is the reverse of the role a government should play in dealing with public goods.

What becomes clear is that it is not true that a species is a species is a species. The debate about preservation and management versus letting nature take its course must be argued for each taxon and habitat in some detail based on an understood and agreed upon way of assigning values. If preserving a species is to be used as a cover statement for preserving a habitat, it would be better to get the actual reasons up front so they can be debated on merits. Except in those very few cases where cost and benefit have calculable monetary values, conversion factors will have to be developed in terms of more abstract benefits. As has been pointed out by Baden (12), "not all values can be denominated on a spreadsheet."

It is necessary to stress that none of the trade-offs necessary to establish the relations between different value systems can be accomplished until biologists, economists, and technologists are willing and able to carry out discussions. A rational approach to problems demands this kind of communication. One would envision that the recently proposed National Institute for the Environment would be a locus for this activity, which at present lacks a home.

At the beginning of this century, humankind inherited a great

diversity of biota. The industrial revolution inevitably compromised habitats and led to large-scale extinctions. We have reached a stage where there is general agreement that ecosystems, including the global ecosystem, must be managed (13). This requires, at the very least, more effort devoted toward an improved understanding of ecological theory. It also urgently requires some national and international consensus as to the goals of that management. Public goods are clearly the province of governments.

We would be remiss not to repeat the assertion that as human population goes up, biological species diversity goes down. We might be able to moderate the rate of decline, but we cannot fend off the inevitable. As species number goes down, we might, of course, change our valuation system and subsequent responses; they are, after all, cultural, not metaphysical. The answer to "How much is a species worth?" is "What kind of world do you want to live in?"

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Extinctions: A Paleontological Perspective

DAVID JABLONSKI

HE FOSSIL RECORD IS RICH IN EXTINCTION: THE STAGGERing diversity of the present-day biota (1) represents a minute fraction of the taxonomic and morphologic variety that has populated the earth since the explosive diversification of multicellular organisms at the beginning of the Phanerozoic. Compilation and statistical analysis of temporal ranges of fossil taxa have verified that extinction intensities per unit time have varied widely, with a continuum from low to high intensities. Background extinction is recognized operationally as the troughs between extinction maxima in time series, and may involve the loss of only a few species. At higher intensities, extinctions may affect only a narrow subset of species (as in the late Pleistocene megafaunal extinction), or may be taxonomically and geographically pervasive (as in the mass extinctions as currently defined) (2-7). Paleontologists have learned much about the timing, magnitude, selectivity, and recovery patterns of the major extinction events (8), but the implications of these data for present biodiversity are still not fully understood. The fossil record is, however, our only direct source of information on how biological systems respond to large-scale perturbations and thus can provide

important insights into potential outcomes if habitat destruction or climate change proceeds unchecked (9, 10).

The most basic observation is simply that mass extinctions have happened: irreversible biotic upheavals have occurred repeatedly in the geological past. Marine and terrestrial biotas are not infinitely resilient, and certain environmental stresses can push them beyond their limits (11). This basic message derives not only from the fossil record of the five major mass extinctions of the Phanerozoic, but from smaller events like the end-Cenomanian and end-Eocene events (Table 1), and regional extinctions like the Pliocene loss of more than 50% of northeastern Atlantic and 75% of northwestern Atlantic bivalve species (12). The major mass extinctions have apparently mediated faunal replacements that were once attributed to a more classically Darwinian competitive process (13, 14): dominant groups decline or disappear and previously unimportant taxa rise to prominence in the aftermath, as seen in the successive reef biotas of the Phanerozoic (15, 16) and the successive terrestrial vertebrate dynasties from mammal-like reptiles to dinosaurs to mammals (13). Terrestrial plants have sometimes been described as exempt from ancient mass extinctions (17), but this is true only at the highest taxonomic levels. Detailed work on species and genera, for example, suggests that the end-Cretaceous extinction removed more than 50% of plant species and may have played a pivotal role in structuring the Cenozoic flora, at least in the Northern Hemisphere (18).

Survival of species or lineages during mass extinctions is not strictly random, but it is not necessarily closely tied to success during times of normal background extinction. Analyses of selectivity during mass extinctions are still scarce, and patterns emerge more

The author is in the Department of the Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, IL 60637.

Table 1. Extinction intensities at the genus and species level for the five major mass extinctions of the Phanerozoic and selected smaller post-Paleozoic extinction events. Generic values are calculated empirically from the marine fossil record (3); species loss inferred by rarefaction from generic data (3, 65). Age values from Harland et al. (42).

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Extinction	Age (× 10 ⁶ years)	Genera (%)	Species (%)		
Late Eocene (Priabonian)	35.4	15	35 ± 8		
End-Cretaceous (Maastrichtian)	65.0	47	76 ± 5		
Late Cenomanian	90.4	26	53 ± 7		
End-Jurassic (Tithonian)	145.6	21	45 ± 7.5		
Pliensbachian	187.0	26	53 ± 7		
Late Triassic (Norian)	208.0	47	76 ± 5		
Late Permian	245.0	84	96 ± 2		
Late Devonian (Frasnian)	367.0	55	82 ± 3.5		
Late Ordovician (Ashgillian)	439.0	61	85 ± 3		

clearly at lower taxonomic levels than at high ones, but some generalizations can be drawn. Among terrestrial vertebrates, for example, large-bodied lineages appear to suffer more severely than small-bodied forms {witness the end-Cretaceous dinosaurs [though juvenile and small adult forms also vanished (19)] and the end-Pleistocene megafauna (vertebrates over 44 kg)}; this makes biological sense, in terms of such factors as expected population sizes and densities (low), home range requirements (large), generation times (long), and trophic requirements (large) (20). The ecological consequences of the removal of these large vertebrates are only beginning to be explored, and the exploration requires reciprocal neontological-paleontological study, but may be far-reaching. In part on the basis of ecological research in Africa, the one continent that retains much of its Pleistocene megafauna, Owen-Smith (21) suggests that the end-Pleistocene extermination in North America of the species most attractive as human prey, such as mastodon and mammoth, would have brought extensive vegetational changes that in turn would explain the concomitant disappearance of so many other vertebrates. Such cascading ecological effects have long been suspected for the major mass extinctions [for example, the probable collapse of marine food chains with the end-Cretaceous phytoplankton crisis (22)], and may provide a useful model for the potential consequences for local or total extermination of present-day elephants and some of the other African megaherbivores (23). Controlled ecological experiments are still the most powerful way to predict responses of particular communities to species removals (24), but this approach would be particularly valuable if designed around removal of species likely on demographic or paleobiological grounds to be most extinction-prone.

Among marine invertebrates, where the fossil record is more completely known and more readily quantified (25), at least one strong generalization has emerged: widespread genera preferentially survive mass extinctions, whereas geographically restricted genera are particularly vulnerable (14, 26-29); during background extinction geographical range more demonstrably plays a role at the species level (30). Some factors that contributed to genus survival during background times, such as species richness, were ineffective during the end-Cretaceous mass extinction, so that molluscan and echinoderm taxa were lost that ordinarily were extinction-resistant (14, 26, 31); the same holds for early Paleozoic trilobites (28), late Devonian corals (32), and Paleozoic ammonoids (33) but not, apparently, for end-Permian gastropods (29). Major extinction events also preferentially or indifferently removed taxa normally at low risk among Paleozoic bryozoans (34), Late Cenozoic Foraminifera (35), and Late Cenozoic bivalves (35). Evidence is thus accumulating that taxa and morphologies may have been lost not because they were poorly adapted by the standards of background processes, but because they occurred in lineages lacking the environmental tolerances or geographic distributions necessary for surviving the mass extinction.

The paleontological data, then, corroborate suggestions (9, 10) that present-day perturbations are likely to impinge most heavily on rare, geographically restricted species, and can be indifferent to adaptations honed by prolonged intervals of natural selection under background extinction. In the face of ongoing habitat alteration and fragmentation, this implies a biota increasingly enriched in widespread, weedy species-rats, ragweed, and cockroaches-relative to the larger numbers of species that are more vulnerable and potentially more useful to humans as food, medicines, and genetic resources. However, we have little means of translating paleontological data into predicted rates or patterns of species loss for any given present-day locality or region. Data are needed on living species that allow direct comparison with the fossil record. For example, frequency distributions of geographic ranges for local faunas and floras would provide a framework for inferring the most vulnerable taxa, and for assessing possible impacts of losses at the more extinction-prone end of the geographic range spectrum. Such an approach will, of course, provide only a first approximation of extinction probability; some species, for example, are widespread but have narrow requirements (36), such as a herbivore dependent on a complex of geographically restricted (and thus extinctionprone) plant species. Nevertheless, the high rate of habitat disturbance or fragmentation, particularly in the tropics, lends urgency to the development of efficient approaches to estimating potential biotic consequences.

The fossil record also suggests that tropical biotas are the most vulnerable to extinction (37). The general impression, however, needs to be more fully explored: few data are available for terrestrial organisms, and the underlying marine data derive mainly from the striking demise of reef communities at each of the major mass extinctions (15, 16), combined with some evidence for relatively low extinction intensities at high latitudes (38). Whether this boom-andbust history reflects the vulnerability of the tropical marine biota in general, the vulnerability of the reef community in particular, or a chain of events put in motion by the extinction of geographically restricted species, as elsewhere on the globe, is not known (14). Reef biotas survived Pleistocene climate and sea-level fluctuations with few losses (39), but this may be an unreliable model for the present-day situation. Pleistocene reef species depended not upon withstanding in situ stresses but on shifting to or persisting in benign refugia (39, 40) now becoming increasingly scarce as human activities impinge on these environments.

Biotic recoveries after mass extinctions are geologically rapid but immensely prolonged on human time scales. New reef communities are not recognizable until 5 million to 10 million years after extinction events (15), and Talent (16) argues that the re-invasion and re-invention—of these habitats postdates by millions of years the slackening of the environmental perturbations associated with the demise of the preceding community. Further testing is needed, but the delay evidently reflects constraints on the evolution of species or assembly of communities capable of occupying these habitats rather than on continuing environmental stresses. Similarly, marine bivalves show episodes of accelerated diversification in the wake of mass extinctions, with recovery to pre-extinction levels of generic diversity requiring at least 10 million years (41). Whatever the exact magnitude of present-day diversity losses, rebounds in the fossil record suggest that they will not be recouped in the next thousand years, even in the absence of further disturbance. Comparative analysis of geologic intervals with intense turnover but modest drops in standing diversity might reveal taxon-specific or habitat-specific thresholds below which "instantaneous recoveries"

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are not possible. Such estimates could be used to weigh the risk of incurring truly long-term consequences under alternative management schemes.

Comparisons between present conditions and the fossil record are severely hindered by problems of temporal and taxonomic scale, and by a basic nonequivalence between the kinds of data available for the two systems. Reliable predictions on the decade or century scale are urgently needed today, but temporal resolution in the pre-Pleistocene fossil record is at least two to three orders of magnitude coarser, due to problems such as gaps in the record and vertical mixing of successive populations (42). Thus, even truly instantaneous events cannot be distinguished from processes encompassing 10⁵ to 10⁶ years, particularly on a global scale. Moreover, highresolution data suggest some measurable duration for most, if not all, major extinctions. Even the end-Cretaceous event, the one most likely to have been triggered suddenly by bolide impact or other environmental shock, apparently involved at least 10⁴ to 10⁵ years of oceanographic and atmospheric turmoil when analyzed at single sites (an approach that sacrifices global generality for refined local resolution) (43). The best-dated extinction of the geologic record, the terminal Pleistocene extinction of large mammals, is currently estimated as spanning about 9,000 years (with onset about 18,000 years ago) (44, 45).

The best paleontological extinction data, in terms of geographic coverage and temporal resolution, are for marine invertebrates and microplankton. Most workers consider large databases to be more robust to sampling biases when compiled at the genus level or above, and many argue that the behavior of genera is useful as a damped proxy for species-level processes (3, 46). These factors alone would hamper quantitative comparisons to present-day extinctions, but a subtler bias is also at work: the extinctions detected by paleontologists primarily involve taxa that are more widespread and abundant (and thus more likely to be fossilized) than the extreme endemics that constitute some fraction of present-day estimates for endangered tropical species. Many uncommon, localized taxa do enter the fossil record, but species such as those restricted to the now deforested Centinela Ridge, Ecuador [≤20 km² (47)], would almost certainly fail to be fossilized or collected, and this renders overall comparisons to fossil data problematic. Estimated paleontological background rates are so low [averaging only about 1 to 10% per million years for marine invertebrate species (48) but less fully analyzed for terrestrial animals or plants] that tropical extinctions corrected to their potential fossil record would still probably exceed paleontological background rates, but this question requires careful analysis.

One approach to scaling present-day extinction estimates to the fossil record would be to assess how many living species and genera described thus far (which in turn are just a fraction of the 5 million to 30 million living species estimated) actually, or even potentially, have a fossil record. More than 77% of 700 species of shelly marine mollusks of the Californian province occur as Pleistocene fossils (49), and comparable proportions probably obtain for vertebrates and plants, particularly for pollen taxa. Given a particular scale of perturbation, then, what is the expected fate of those groups for which the fossil record provides the most robust predictions?

Finally, the disparity of the unknowns in the two systems also hinders detailed use of the fossil record to predict present-day biodiversity losses and their consequences. Paleontologists have a partial record of taxon loss in time and space, and attempt to infer the nature of the disturbances that caused the observed magnitudes and patterns of differential extinction. Linkages between a particular extinction episode and climatic or other potential forcing factors are hypotheses to be tested. In contrast, biologists have partial data on environmental disturbances such as rain forest conversion and

attempt to infer or predict magnitudes and patterns of extinction. Again, compiling data on living species that are analogous to paleontological data might be the most efficient means of generating rigorous interdisciplinary extrapolations.

All of these problems are minimized in the youngest part of the fossil record: the last 5.2 million years since the start of the Pliocene, with their oscillations between glaciations and global warming trends, are being explored in increasing stratigraphic, geochemical, and paleobiological detail (12, 50). Data on differential survivorship and geographic shifts of late Tertiary vertebrate and plant species in response to increasing aridity and habitat patchiness (50, 51) should be useful in inferring potential effects of present-day perturbations. The analogy is imprecise because the late Tertiary changes seem tied ultimately to the onset of global cooling, an unlikely scenario for the immediate future, but faunal and floral dynamics can still be used to good predictive effect given the diversity of present and impending environmental alterations independent of the overall vector of global climate change. Further, the repeated oscillations between glacial and interglacial states that characterize global climates over the past 2 million years provide replicated natural experiments on biotic consequences of rapid shifts in global temperature and rainfall

The past 50,000 years in particular offer extraordinary opportunities for predicting upcoming biotic changes. Time resolution is on the order of centuries, geochemical tracers permit fine-scale calibration of paleotemperature and other factors, and many of the plant and animal species are still extant, so that past performances can be projected into the future with some confidence. In addition to encompassing the end-Pleistocene extinction of large terrestrial vertebrates (45), this interval provides invaluable data on the behavior of species and communities in response to climatic changes, most notably the most recent post-glacial global warming trend. The most important message of this still underexploited record is that ecological communities do not respond as units to environmental change. Pollen and skeletal data show that species are highly individualistic in their behavior, so that few, if any, modern terrestrial communities existed in their present form 10,000 years ago. Instead, they originated in piecemeal fashion by means of shifts in abundance or geographic range of their constituent species and will presumably continue to change composition in response to anthropogenic or natural climatic changes.

The individualistic behavior of terrestrial species in response to Pleistocene and Holocene climate changes is evidently a general phenomenon, known for plants in eastern and western North America (52, 53), Europe (54), South America (55), Australia (56), and Africa (57), North American vertebrates (58), and invertebrates (59). This fundamental paleontological insight cannot be ignored in designing nature reserves (60): reserves must be sufficiently large and environmentally complex to accommodate the array of disparate geographic range shifts that any climatic change will evoke from the resident species assemblage. Any other attempts to anticipate species behavior—cultivars or pest species, for example—must take these discoveries into account as well.

Late Pleistocene–Holocene extinctions are still controversial, but most authors now assign humans at least an accessory role for the end-Pleistocene megafaunal extinctions (61). The Holocene fossil or archeological record has also revealed significant extinction due primarily or exclusively to pre-European human disturbance, particularly in island biotas [for example, more than 50% of the avifauna in Hawaii and other Polynesian islands (62), and 49% of West Indies land mammals (63)]. These data force a substantial upward revision of estimated post-Pleistocene human impacts and offer rich possibilities for testing hypotheses on causes and consequences of special loss. They also undermine attempts to predict biotic respons-

es to habitat reduction or fragmentation, which are commonly based on species-area relations in modern island biotas that are assumed to be at evolutionary equilibrium. In any case, the fossil data on individualistic species behaviors support arguments that habitat diversity is more important than area per se in refuge design (60, 64).

The lessons of the past are inevitably blurry and at a coarse scale. At the present state of knowledge, the fossil record is more revealing of potential long-term consequences than of immediate solutions. However, the history of life on Earth provides an array of worst-case scenarios-including even the mildest of the extinction events in Table 1—that are sufficiently spectacular to militate against inaction. Coordinated research on fossil and extant biotas should yield very real benefits for understanding, anticipating, and perhaps managing the biological changes driven by human activities.

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Article

Biodiversity Studies: Science and Policy

PAUL R. EHRLICH AND EDWARD O. WILSON

Biodiversity studies comprise the systematic examination of the full array of different kinds of organisms together with the technology by which the diversity can be maintained and used for the benefit of humanity. Current basic research at the species level focuses on the process of species formation, the standing levels of species numbers in various higher taxonomic categories, and the phenomena of hyperdiversity and extinction proneness. The major practical concern is the massive extinction rate now caused by human activity, which threatens losses in the esthetic quality of the world, in economic opportunity, and in vital ecosystem services.

TROM LINNAEUS TO DARWIN TO THE PRESENT ERA OF cladograms and molecular evolution, a central theme of biology has always been the diversity of life. A new urgency now impels the study of this subject for its own sake: just as the importance of all life forms for human welfare becomes most clear, the extinction of wild species and ecosystems is seen to be accelerating through human action (1). The dilemma has resulted in the rise of biodiversity studies: the systematic examination of the full array of organisms and the origin of this diversity, together with the methods by which diversity can be maintained and used for the benefit of humanity. Biodiversity studies thus combine elements of evolutionary biology and ecology with those of applied biology and public policy. They are based in organismic and evolutionary biology in the same manner that biomedical studies are based in molecular and cellular biology. They include the newly emergent discipline of conservation biology but are even more eclectic, subsuming pure systematic research and the practical applications of such research that accrue to medicine, forestry, and agriculture, as well as research on policies that maximize the preservation and use of biodiversity. In biodiversity studies, the systematist meets the economist and political scientist. In this article we will present some of the key issues that newly link these two principal domains.

Species Formation

A rich medley of models has been constructed to account for the origin of species by reproductive isolation. Two broad categories have been substantiated by empirical evidence. The first is poly-

ploidy, the multiplication of entire chromosome numbers within individual species or within hybrids of species, a process that isolates the new breed from its ancestor in one step. This instantaneous mode has generated 40% of contemporaneous plant species and a much smaller number of animal species (2). Of comparable importance is geographic (or allopatric) speciation, the origin of intrinsic isolating mechanisms in two or more daughter populations while they are isolated by a geographic barrier, such as a sea strait, desert basin, or mountain range. Evidence of this two-step process, which occurs widely in plants and animals, has been documented minutely, often to the level of the gene, in birds, mammals, and a few groups of insects such as drosophilid flies and butterflies (3).

The diversification processes of polyploidy and geographic isolation are generally appreciated because they follow an easily traced pathway of measurable steps. Other modes of speciation are more difficult to conceive and test, but this does not mean they do not occur widely. Perhaps the most common is nonpolyploid sympatric speciation, in which new species emerge from the midst of parental species even when individuals of both populations are close enough to intermingle during part of their life cycles. The dominant process of this category, at least the one most persuasively modeled and documented, is by intermediate host races. Members of the parental species feed upon and mate in the vicinity of one kind of plant; they give rise to an alternate host race that shifts to a second species of host plant growing nearby; the two races, thus isolated by their microhabitat differences, diverge further in other traits that reinforce reproductive isolation. Sympatric speciation may play a key role in the origin of the vast numbers of insects and other invertebrates specialized on hosts or other types of microhabitats. The early stages are difficult to detect, however, and few studies have been initiated in the invertebrate groups most likely to display them (4).

Certain forms of speciation can thus occur very rapidly, within one to several generations. And when species meet, they can displace one another genetically within ten or fewer generations, reducing competition and the likelihood of hybridization (5). A question of central importance is the impact of high speciation rates on standing diversity. Although the probability of extinction of species within a particular group at a particular place (say, the anole lizards of Cuba) eventually rises with the number of species, the number of species should increase with greater speciation rates at all levels up to equilibrium. But does it really? And if so, in which groups and to what degree?

Current Levels of Biodiversity

Also in an early stage, and surprisingly so, is the elementary taxonomic description of the world biota. At the present time approximately 1.4 million species of plants, animals, and microorganisms have been given scientific names (1, 6). Terrestrial and freshwater species diversity is greater than marine diversity. The

P. R. Ehrlich is Bing Professor of Population Studies and Professor of Biological Sciences at Stanford University, Stanford, CA 94305. E. O. Wilson is Baird Professor of Science and Curator in Entomology at Harvard University, Museum of Comparative Zoology, Cambridge, MA 02138–2902. This article is based on their Crafoord Prize lectures given at the Royal Swedish Academy of Sciences, Stockholm, 26 September 1000

overwhelming elements are the flowering plants (220,000 species) and their coevolutionary partners, the insects (750,000 species). The reverse is the case at the highest taxonomic levels, with all of the 33 living animal phyla present in the sea and only 17, or half, present on land and in fresh water (7).

Known species diversity is only a small fraction of actual species diversity, especially in the invertebrates and microorganisms. In this century the class Insecta has always been considered the most speciose group at the class level. As early as 1952, Sabrosky estimated that the number of living species is as high as 10 million (8). In 1982, Erwin found that beetle diversity in Neotropical trees, revealed in samples knocked down by insecticidal fogs, suggest far higher levels of insect and other arthropod diversity in tropical rain forests than had previously been estimated for the entire world fauna and flora (9). His figure, 30 million, was reached by extrapolating from counts of beetle species (1200) in a Panamanian tree species through estimates of total arthropod diversity per tree species to the percentages of species limited to each tree species to the total of tree species in tropical rain forests. Stork (10) reassessed this bold extrapolation, and in essence agreed with it, adding data of his own from Indonesian forests to produce a possible range of 10 to 80 million tropical forest arthropods. The most sensitive parameter remains the degree to which species of beetles and other arthropods are found uniquely on individual tree species.

In fact, because the life of the planet remains mostly unexplored at the species and infraspecies levels, systematists do not know the species diversity of the total world fauna and flora to the nearest order of magnitude. It is easily possible that the true number of species is closer to 10⁸ than 10⁷. Relatively little effort has been expended on nematodes, mites, or fungi, each highly diverse and containing undescribed species that could easily range into the hundreds of thousands or millions. Bacteria, with only about 4000 described species, remain a terra vitae incognita because of the astonishingly small amount of research devoted to their diversity, as opposed to the genetics and molecular biology of select species.

Hyperdiversity

Certain taxa are hyperdiverse, that is, they contain more species, genera, or higher ranked groups within them than expected by a null model of random assortment (11). Examples include arthropods among animal phyla, insects among arthropods, rodents among mammalian orders, orchids among monocotyledonous plant families, Sciurus among the genera of Sciuridae (squirrels), and so forth. It can be expected in a Darwinian world, where chance and opportunism prevail, that production of great diversity depends to substantial degree on special adaptations allowing penetration of multiple niches, such that each hyperdiverse group has its own magic key. For example, the ants appear to have expanded by virtue of fungistatic secretions, series-parallel work operations, and a highly altruistic worker caste (12). But recent research has also begun to identify properties possessed by many groups: small size, permitting fine niche subdivision (7, 13, 14); phytophagy and parasitism with specialization on hosts (15); specialized life stages that allow species to occupy multiple niches; entry into new geographic areas with subsequent adaptive radiation and preemption; and greater dispersal ability, promoting the colonization of empty areas. Southwood has neatly summarized the likely causes of the extreme hyperdiversity of insects as "size, metamorphism, and wings" (13).

Hyperdiversity also occurs in certain habitats and geographical areas. The strongest trend worldwide is the latitudinal diversity gradient, with group after group reaching its maximum richness in the tropics and most particularly in the tropical rain forests and coral reefs. (Exceptions include conifers, salamanders, and aphids.) The hyperdiversity of continental rain forests is legendary. Gentry found about 300 tree species in single-hectare plots in Peru (16), to be compared with 700 native tree species in all of North America. A single tree in the same area yielded 43 species of ants in 26 genera, about equal to the ant fauna of the entire British isles (17). Explaining the latitudinal diversity gradient has proven an intractable problem. But clues exist which when pieced together suggest the possibility of a general explanation, involving climatic stability and extreme biological specialization and niche division (18).

Natural Extinction

One of the qualities reducing diversity in particular groups is extinction proneness, which renders populations vulnerable to environmental change and reduces taxonomic groups to one or a very few threatened species. A threatened or endangered species (the two grades commonly employed by conservationists) is one with a high probability of extinction during the next few years or decades. The principal demographic properties contributing to the status are a low maximum breeding population size and a high coefficient of variation in that size (19). When the breeding size drops to a hundred or less, the likelihood of extinction is enhanced still further by inbreeding depression (20).

The overall natural extinction rate (at times other than mass extinction episodes) estimated from fossil data to the nearest order of magnitude is 10^{-7} species per species year (21). This estimate refers to true extinction, from the origin of a species to the extinction of that species and any species descended from it (altogether, called the clade) and excludes "pseudoextinction," the evolution of one species into another. Wide variation exists among major taxonomic groups in the longevity of clades. Mesozoic ammonoid and Silurian graptolite clades lasted only 1 million to 2 million years, whereas most other Paleozoic and Mesozoic invertebrate clades lasted closer to 10 million years (21). In general, planktonic and sessile marine animals, including corals and brachiopods, have had higher extinction rates than mobile benthic animals such as gastropods and bivalves (22). Using anatomical evidence from fossils and comparisons with related living species, paleobiologists have begun to infer the determinants of clade longevity by relating the adaptations of the organisms to maximum population size, population fluctuation, and dispersal ability (23).

Human-Caused Extinction

Biodiversity reduction is accelerating today largely through the destruction of natural habitats (1). Because of the latitudinal diversity gradient, the greatest loss occurs in tropical moist forests (rain forests) and coral reefs. The rate of loss of rain forests, down to approximately 55% of their original cover, was in 1989 almost double that in 1979. Roughly 1.8% of the remaining forests are disappearing per year (24). By the most conservative estimate from island biogeographic data, 0.2 to 0.3% of all species in the forests are extinguished or doomed each year (25). If two million species are confined to the forests, surely also a very conservative estimate, then extinction due to tropical deforestation alone must be responsible for the loss of at least 4000 species annually.

But there may well be 20 million or more species in the forests, raising the loss tenfold. Also, many species are very local and subject to immediate extinction from the clearing of a single habitat isolate, such as a mountain ridge or woodland patch (26). The absolute

extinction rate thus may well be two to three orders of magnitude greater than the area-based estimates given above. If current rates of clearing are continued, one-quarter or more of the species of organisms on Earth could be eliminated within 50 years—and even that pessimistic estimate might be conservative (25). Moreover, for the first time in geological history, plants are being extinguished in large numbers (27).

Another data set illuminating the urgency of dealing with the extinction problem measures the human impact on global net primary productivity (NPP) (28); global NPP is roughly the total food supply of all animals and decomposers. Almost 40% of all NPP generated on land is now directly used, coopted, or forgone because of the activities of just one animal species—Homo sapiens.

Since the overwhelming majority (possibly more than 90%) of species now exists on land, the 40% human appropriation there alone shows why there is an extinction crisis. Furthermore, the human population is projected to double in the next half-century or so—to more than 10 billion people. Most ominous of all, the widely admired Brundtland Report speaks of a five- to tenfold increase in global economic activity needed during that period to meet the demands and aspirations of that exploding population (29). If anything remotely resembling that population-economic growth scenario is played out, with an acceleration of habitat destruction, most of the world's biodiversity seems destined to disappear.

Why Should We Care?

The loss of biodiversity should be of concern to everyone for three basic reasons (1, 30). The first is ethical and esthetic. Because *Homo sapiens* is the dominant species on Earth, we and many others think that people have an absolute moral responsibility to protect what are our only known living companions in the universe. Human responsibility in this respect is deep, beyond measure, beyond conventional science for the moment, but urgent nonetheless. The popularity of ecotourism, bird-watching, wildlife films, pet-keeping, and gardening attest that human beings gain great esthetic rewards from those companions (and generate substantial economic activity in the process).

The second reason is that humanity has already obtained enormous direct economic benefits from biodiversity in the form of foods, medicines, and industrial products, and has the potential for gaining many more. Wheat, rice, and corn (maize) were unimpressive wild grasses before they were "borrowed" from the library and developed by selective breeding into the productive crops that have become the feeding base of humanity. All other crops, as well as domestic animals, have their origins in the genetic library, as do many medicines and various industrial products, including a wide variety of timbers (1, 30). Throughout the world almost a quarter of all medical prescriptions are either for chemical compounds from plants or microorganisms, or for synthetic versions or derivatives of them (31). One plant compound, quinine, is still a mainstay of humanity's defense against its most important disease, malaria.

Biodiversity is a precious "genetic library" maintained by natural ecosystems. But the potential of the library to supply such benefits has barely been tapped. Only a tiny portion of plant species has been screened for possible value as providers of medicines (31), and although human beings have used about 7000 plant species for food, at least several times that number are reported to have edible parts (1).

The third reason, perhaps the most poorly evaluated to date, is the array of essential services provided by natural ecosystems, of which diverse species are the key working parts. Ecosystem services include maintenance of the gaseous composition of the atmosphere, pre-

venting changes in the mix of gases from being too rapid for the biota to adjust. In Earth's early history, photosynthesizing organisms in the seas gradually made Earth's atmosphere rich in oxygen. Until there was enough oxygen for an ozone shield to form, the land surface was bathed in ultraviolet-B radiation. Up to some 450 million years ago life was confined to the seas. Only with the protection of the ozone shield were plants, arthropods, and amphibians able to colonize the land.

Significant alteration of the atmosphere has signaled the arrival over the past few decades of *Homo sapiens* as a global force, one capable of destroying most of biodiversity. As a result of human activities (32), the ozone shield has thinned by as much as 5% over Europe and North America (33), and there is some evidence that the surface intensity of ultraviolet-B radiation has increased there (34). Each spring the shield is now reduced over the Antarctic by approximately 50%. The global impact of the human economy is even more evident in the prospect of climatic change in response to increasing concentrations of greenhouse gases (35).

The organisms in natural ecosystems influence the climate in ways other than the role they play in regulating atmospheric gases. The vast rain forests of Amazonia to a large degree create the moist conditions that are required for their own survival by recycling rainfall. But as the forest shrinks under human assault, many biologists speculate that there will be a critical threshold beyond which the remaining forest will no longer be able to maintain the climate necessary for its own persistence (36). Deforestation and the subsequent drying of the climate could have serious regional effects in Brazil outside of Amazonia, conceivably reducing rainfall in important agricultural areas to the south. There also appear to be regional effects on climate when semi-arid regions are desertified (37), but their extent remains unknown.

The generation and maintenance of soils is another crucial service supplied most efficiently by natural ecosystems. Soils are much more than fragmented rock; they are themselves complex ecosystems with a rich biota (38). The elements of biodiversity in soil ecosystems are crucial to their fertility—to their ability to support crops and forests.

Many green plants enter into intimate relationships with mycorrhizal fungi in the soil. The plants nourish the fungi, which in turn transfer essential nutrients into the roots of the plant. In some forests where trees appear to be the dominant organisms, the existence of the trees is dependent upon the functioning of these fungi. On farms, other microorganisms play similar critical roles in transferring nutrients to crops such as spring wheat.

Organisms are very much involved in the production of soils, which starts with the weathering of the underlying rock. Plant roots can fracture rocks and thus help generate particles that are a major physical component of soils; plants and animals also contribute CO₂ and organic acids that contribute to the weathering of parent rock. More importantly, many species of small organisms, especially bacteria, decompose organic matter (shed leaves, animal droppings, dead organisms, and so on), releasing carbon dioxide and water into the soil and leaving a residue of humus, or tiny organic particles. These are resistant to further decomposition, help maintain soil texture and retain water, and play a critical role in soil chemistry, permitting the retention of nutrients essential for plant growth.

Soil ecosystems themselves are the main providers on land of two more essential ecosystem services: disposal of wastes and cycling of nutrients. Decomposers break wastes down into nutrients that are essential to the growth of green plants. In some cases, the nutrients are taken up more or less directly by plants near where the decomposers did their work. In others, the products of decomposition circulate through vast biogeochemical cycles before being reincorporated into living plants.

Another critical service provided by natural ecosystems is the

control of the vast majority of species that can attack crops or domestic animals. Most of those potential pests are herbivorous insects, and the control is provided primarily by numerous species of predacious and parasitic insects that naturally feed upon them.

While natural ecosystems are providing crop plants with stable climates, water, soils, and nutrients, and protecting them from pests, they also often pollinate them. Although honeybees, essentially domesticated organisms, pollinate many crops, numerous other crops depend on the services of pollinators from natural ecosystems. One such crop is alfalfa, which is most efficiently pollinated in cooler areas by wild bees.

The biodiversity in natural ecosystems also supplies people with food directly—most notably with a critical portion of their dietary protein from fishes and other marine animals. This service is provided by oceanic ecosystems in conjunction with coastal wetland habitats that serve as crucial nurseries for marine life.

The ecosystem services in which biodiversity plays the critical role are provided on such a grand scale and in a manner so intricate that there is usually no real possibility of substituting for them, even in cases where scientists have the requisite knowledge. In fact, one could conclude that virtually all human attempts at large-scale inorganic substitution for ecosystem services are ultimately unsuccessful, whether it be introductions of synthetic pesticides for natural pest control, inorganic fertilizer for natural soil maintenance, chlorination for natural water purification, dams for flood and drought control, or air-conditioning of overheated environments. Generally, the substitutes require a large energy subsidy, thereby adding to humanity's general impact on the environment, and are not completely satisfactory in even the short run (39).

It is important to note that in supplying ecosystem services the species and genic diversity of natural systems is critical. One might assume that one grass or tree species can function as well as any other in helping control the hydrologic cycle in a watershed, or that one predator will be as good as another in controlling a potential pest. But, of course, organisms are generally highly adapted to specific physical and biotic environments-and organic substitutions, like inorganic ones, are likely to prove unsatisfactory.

In sum, much of biodiversity and the quality of ecosystem services generated by it will be lost if the epidemic of extinctions now under way is allowed to continue unabated.

Public Policy

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Many steps can be taken to preserve biodiversity, if the political will is generated. Perhaps the first step, which would be seen as especially extreme by Americans, would be to cease "developing" any more relatively undisturbed land. Every new shopping center built in the California chaparral, every hectare of tropical forest cut and burned, every swamp converted into a rice paddy or shrimp farm means less biodiversity.

In rich countries, stopping the more destructive forms of "development" is relatively simple in principle. Age structures are such that population shrinkage in most rich nations could be achieved with little effort (a few are already in that desirable mode). When new facilities are needed, they should replace deteriorating old ones. Forestry should be placed on a sustainable basis with careful attention to the conservation of precious reserves of old growth. And much more scientific effort and public support should go into biodiversity studies, including the cataloging of the genetic library and national biological inventories (1, 31).

In poor nations, the task is both more urgent and vastly more difficult. It cannot be accomplished immediately, and will not be accomplished at all without massive assistance from the rich. For instance, stopping the expansion of cropland and pasture into virgin areas cannot be accomplished unless birth rates can be dramatically lowered and the development of sustainable high-yield agricultural systems is backed by land reform and a sound agricultural infrastructure and economy. In many cases, new social and economic systems must be developed in which preservation of biodiversity and its sustainable exploitation go hand in hand. The social, political, economic, and scientific barriers to achieving the goal are so formidable that nothing less than the kind of commitments so recently invested in the Cold War could possibly suffice to accomplish it. And we are 45 years late in starting.

But ending direct human incursions into remaining relatively undisturbed habitats would be only a start. Simultaneously, global cooperative efforts to reduce anthropogenic impacts on ecosystems, such as those directed at a reduction of emissions of greenhouse gases and ozone-destroying compounds, must be greatly enhanced. They are much more likely to be successful if population growth can be halted and the cessation of forest destruction can be achieved.

Finally, because humanity already occupies so much of Earth's surface, substantial effort should be directed at making areas already used by people more hospitable to other organisms. Those efforts can range from the substitution of game ranching for cattle and sheep ranching in many areas to the substitution of native vegetation for European-style lawns in desert cities.

If there is to be any chance of abating the loss of biodiversity, action must be taken immediately. The essential tactics of conservation are being developed within conservation biology, as a subdiscipline of biodiversity studies. The indispensable strategy for saving our fellow living creatures and ourselves in the long run, is, as the evidence compellingly shows, to reduce the scale of human activities. The task of accomplishing this goal will involve a cooperative worldwide effort unprecedented in history. Unless humanity can move determinedly in that direction, all of the efforts now going into in situ conservation will eventually lead nowhere, and our descendents' future will be at risk.

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Research Article

Convergence of Ets- and Notch-Related Structural Motifs in a Heteromeric DNA **Binding Complex**

CATHERINE C. THOMPSON, THOMAS A. BROWN, STEVEN L. McKNIGHT

Analysis of the heteromeric DNA binding protein GABP has revealed the interaction of two distinct peptide sequence motifs normally associated with proteins located in different cellular compartments. The a subunit of GABP contains an 85-amino acid segment related to the Ets family of DNA binding proteins. The ETS domain of GABP α facilitates weak binding to DNA and, together with an adjacent segment of 37 amino acids, mediates stable interaction with GABPβ. The β subunit of GABP contains four imperfect repeats of a sequence present in several transmembrane proteins including the product of the Notch gene of Drosophila melanogaster. These aminoterminal repeats of GABPB mediate stable interaction with GABPα and, when complexed with GABPα, directly contact DNA. These observations provide evidence for a distinct biochemical role for the 33-amino acid repeats, and suggest that they may serve as a module for the generation of specific dimerization interfaces.

INCE THE INITIAL RECOGNITION OF A COMMON PROTEIN sequence motif in the SWI6 gene product of Saccharomyces cerevisiae and the Notch gene product of Drosophila melanogaster (1), similar sequences have been identified in different biologically interesting proteins. The motif, variously termed the cdc10/ SWI6 or ankyrin repeat, consists of a 33-amino acid sequence often present in tandem arrays. This motif has been observed in the products of the Notch, lin-12, and glp-1 genes, putative transmembrane proteins of Drosophila melanogaster and Caenorhabditis elegans that transmit signals critical for specification of cell fate (2); the product of fem-1, a Caenorhabditis elegans gene that regulates sex determination (3); cdc10, SWI4, SWI6, yeast proteins involved in cell cycle control (1, 4); ankyrin, a multifunctional protein of the red blood cell cytoskeleton (5); the product of bcl-3, a human gene located near a translocation breakpoint associated with some leukemias (6); the 105-kD precursor to the active 50-kD subunit of NFkB/KBF1 (7); and IkB, a regulatory subunit of NFkB that inhibits DNA binding and has been implicated in cytoplasmic sequestration (8). Despite the widespread occurrence of the 33amino acid motif, its functional role has heretofore remained obscure.

Our interest in the 33-amino acid repeat arose from studies of GA binding protein (GABP), a multisubunit DNA binding protein purified from rat liver nuclei (9). GABP was originally identified as a factor that binds to a cis-regulatory element required for VP16mediated activation of herpes simplex virus (HSV) immediate early genes (10). Biochemical and molecular biological experiments have shown that GABP is composed of two distinct polypeptides, both of which are required for avid interaction with DNA (9, 11). The amino acid sequence of the GABPa subunit exhibits similarity to the Ets family of nuclear proteins, whereas that of GABPB contains a tandem series of 33-amino acid, cdc10/SWI6 repeats (11). We now demonstrate that it is these two distinct protein sequence motifs that form the heteromeric interface between GABPα and GABPβ.

We view the 33-amino acid repeat as a versatile module for the

The authors are in the Howard Hughes Research Laboratories, Carnegie Institution of Washington, Department of Embryology, Baltimore, MD 21210.

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KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 12
GENOME BANKS & REPRODUCTIVE TECHNOLOGY

PROPOSED IUCN RESOLUTION STATEMENT ON ANIMAL GENETIC RESOURCE BANKING FOR SPECIES CONSERVATION

Captive Breeding Specialist Group Annual Meeting Singapore, September 29, 1991

PROBLEM STATEMENT

The IUCN holds that the successful conservation of species requires integrated management efforts to sustain available genetic diversity. These efforts include programs to protect and manage animal populations within their natural, native habitat (in situ conservation) and supporting programs that manage individuals, gametes and/or embryos outside of natural environments (ex situ conservation).

The IUCN recognizes that, although habitat protection is the most desirable approach for conserving biological diversity, supportive ex situ programs are essential in many cases. For example, such programs can deal effectively with short-term crises and with maintaining long-term potential for continuing evolution.

The IUCN further recognizes that the efficiency and efficacy of ex situ conservation can be increased many fold by applying recent advances in reproductive technology. These include assisted or 'artificial' breeding and the low temperature storage (banking) of viable animal germ plasm, namely spermatozoa, embryos and oocytes. Germ plasm banks: 1) offer a high degree of security against the loss of diversity and, therefore, entire species from unforeseen catastrophes; 2) minimize depression effects of genetic drift and inbreeding; and 3) provide a powerful method for managing the exchange of genetic diversity among populations. Other conservation benefits include banks of serum, DNA and cultured cell lines from germ plasm donors which permit studies on disease status, detection of microbial antibodies, pedigree determination, taxonomic status, geographical substructure and cellular physiology.

The IUCN also recognizes that the establishment of a genetic resource bank must, through basic research, be matched by the development of technologies for its use as a genuine and practical conservation asset.

The development of genetic resource banking programs is hampered by the lack of guidelines for establishing such banks and for integrating them with overall conservation programs. As yet, no single organization with a role in the international coordination of conservation efforts has provided guidance.

RECOMMENDATION

The IUCN regards development of genetic resource banks as an essential component of integrated conservation programs. Therefore, the Captive Breeding Specialist Group recommends that a formal process be developed to formulate global guidelines to establish, operate, use and review animal genetic resource banking programs for species at risk. The framework for international coordination of this type of program must be based upon agreements to cooperatively manage such species for demographic security and genetic diversity.

To achieve this recommendation, a Coordination Committee under the auspices of the Captive Breeding Specialist Group and others to be identified will:

- a) Coordinate animal genetic resource banking activities within the Species Survival Commission and among regional captive propagation groups. This will be accomplished by integrating the genetic resource banks directly into the framework of population viability assessments and conservation Action Plans. These activities require an expert resource network to provide advice on all technical matters.
- b) Establish guidelines for identifying taxa, species or populations that would benefit from genetic resource banks. These guidelines should be detailed and assist in the development of strategic Action Plans for conserving targeted animal populations. The single most important consideration is to ensure that there is a defined conservation goal that requires the collection and storage of biological materials. This requires that an integrated plan for a goal-orientated conservation program be established prior to initiating banking activities,
- c) Establish a globally-standardized, record-keeping database for cataloging, managing and pooling data on banked materials. It will be essential that these biological materials are linked to individually identifiable source animals.
- d) Provide expert technical advice to the appropriate taxon groups to assist in developing animal genetic resource Action Plans. The primary responsibility for developing Action Plans resides with those groups with specific responsibilities for *in situ* and *ex situ* conservation of specific taxa, species and populations. These groups should be encouraged by the Coordination Committee to include genetic resource banks as an integral component in their strategic conservation planning. The Coordination Committee will support the appropriate taxon groups to integrate information on: reproductive and genetic histories of *ex situ* and *in situ* populations; efficiency of reproductive technologies; areas requiring further research; types of biological materials requiring storage; appropriate protocols for banking biological materials; primary and secondary repository sites; strategies for using banked materials; and sources of funding.
- e) Provide a mechanism for approval and periodic review of animal genetic resource banking Action Plans.

DRAFT

Cryopreservation and Banking of Animal Germ Plasm for Species Conservation: An Imperative for Action by the Captive Breeding Specialist Group

W.F. Rall, J.D. Ballou and D.E. Wildt National Zoological Park, Smithsonian Institution Washington, DC 20008-2598 USA

SUMMARY .

Conservation efforts for rare animal species currently focus on programs to protect populations in natural habitat (in situ) and in captivity (ex situ). The ultimate aim of both approaches is to maximize both global biodiversity and genetic diversity. The systematic cryopreservation and banking of germ plasm from free-living and captive populations provide new opportunities to control and manage bio- and genetic diversity. Despite the widely acknowledged benefits of this approach, the development of genetic resource banking programs is hampered by the lack of a mechanism to integrate this activity with other conservation activities.

We propose that the CBSG act immediately to provide leadership for international coordination. The CBSG should assume responsibility for developing programs that encourage germ plasm banking as an integral component of in situ and ex situ conservation efforts. Specifically, the CBSG should: 1) draft and seek adoption of an IUCN Position Statement on the role of germ plasm banking in management and research programs to conserve endangered species; 2) establish a Genetic Resource Banking Oversight Committee to formulate global guidelines for the establishment, operation and review of animal genetic resource banking programs; and 3) develop a formal process that would assist the development of Genetic Resource Banking Action Plans. It is likely that extensive regional and international planning is required to establish and operate such banking programs and ensure the ultimate utility of the banked materials.

INTRODUCTION

Increasing numbers of species face extinction in their native habitat usually as a result of the direct or indirect actions of man. The survival of a species in the wild is thought to depend on a secure native habitat that is sufficiently large to support a population meeting certain genetic and demographic requirements (Soule 1987). Most of the important requirements are related to the properties and characteristics of the population as a whole, such as its size, life-history characteristics and the nature of the gene pool contained therein. The latter, especially genetic variations (i.e. polymorphism) within populations or communities of individuals, plays an important role in many of the critical biological processes related to species conservation, including

extinction (Ehrlich and Ehrlich 1981), inbreeding depression (Ralls et al. 1988), speciation (Templeton 1989) and natural selection (Frankel and Soule 1981). The loss of biological resources as embodied in species resulting from aeons of evolutionary adaptations is recognized as a major international concern. For this reason, it is generally recognized that every possible avenue should be taken to conserve bio- and genetic-diversity (Wilson 1988).

Conservation efforts consist of both: 1) 'in situ' conservation programs that protect and manage animal populations within their natural, native habitat; and 2) 'ex situ' conservation programs that remove individuals, gametes or embryos from wild populations for controlled breeding and management in captivity. Although habitat protection is acknowledged to be the most efficient approach for conserving bio-and genetic-diversity, for some species, in situ conservation alone can not be relied upon to ensure the long-term viability of species at risk (Conway 1988, Soule 1991). Continued human population growth and the biopolitical, environmental and social consequences of that growth require ex situ approaches as critical components of integrated conservation (McNeely et al. 1990).

Currently, ex situ efforts for animal species at risk of extinction focus on captive propagation (Soule et al. 1986, Foose et al. The immediate goal of such programs is to manage populations of a species so as to retain maximum genetic diversity. Ultimately, such captive populations would serve as a source of individuals for release into restored habitat or to infuse genetic diversity into inbred, free-living populations. This can be accomplished only if a significant fraction of the overall genetic diversity existent in the wild population is incorporated into and retained by the captive population. Most captive breeding programs seek to maintain 90% of the captive population's initial genetic diversity for 200 years (Ballou 1991), as recommended by Soule et al (1986). Unfortunately, the world's zoos and bioparks do not have sufficient capacity to house the numbers of animals needed to meet the habitat crisis facing wild animals. For example, estimates suggest that space currently is available in North America for only about 100 mammalian species in populations large enough to meet the required genetic and demographic goals (Conway, This compares to the 815 mammalian species estimated by Soule et al. (1986) that would require captive propagation programs during the next 200 years.

UTILITY OF GENETIC RESOURCE BANKS FOR IN SITU AND EX SITU CONSERVA-TION PROGRAMS

The efficiency and efficacy of captive breeding can be increased many-fold by applying recent advances in reproductive biotechniques (Wildt 1989, 1991). Perhaps the most important advance is germ

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plasm cryopreservation or the low-temperature storage and banking of spermatozoa, embryos and oocytes. Germ plasm cryopreservation currently plays an important role in domestic livestock agriculture, especially in the international movement of disease-free, genetically-superior individuals. The development of banks of cryopreserved germ plasm for nondomesticated species offers many important advantages for conserving and managing the genetic diversity within existing populations. Specifically, an animal genetic resource bank:

- 1. Reduces the number of animals that must be maintained in captivity by extending the generation interval of a species indefinitely. Thus, the genetic diversity of a founder does not die with the animal, but remains viable and available for use in future generations.
- 2. Provides a high degree of security against the loss of diversity or entire species from epidemics, natural disasters and social/political upheavals.
- 3. Serves a vital, interactive role between in situ and ex situ conservation programs. Such interactions prevent unintended selection pressures in captivity, preserve new diversity resulting from natural evolutionary processes in free-living populations, and permit 'infusions' of genetic diversity into fragmented populations suffering from genetic drift or inbreeding depression. This strategy also eliminates the need to remove additional animals from the wild or introduce captive animals into wild free-living populations.
- 4. Provides a method for improving food production and the economy of local communities by inter-species hybridization with domesticated species (e.g. hybridization of rare species of cattle with domesticated breeds).
- 5. Allows ready access to systematic collections of rare biological specimens for research in conservation biology or other 'life' sciences.

The importance of germ plasm resource banks for conserving the genetic diversity of wild fauna has been recognized since the first reports of successful cryopreservation of spermatozoa (Polge et al. 1949) and mammalian embryos (Whittingham et al. 1972). Over the past two decades, reports of various public- and privately-sponsored task forces have stressed the need for germ plasm repository programs to be established for conservation purposes. These include:

- 1. Conservation of Germplasm Resources: An Imperative. National Research Council, National Academy of Sciences, Washington DC, USA, 1978.
- 2. Animal Genetic Resources: Conservation and Management.

- Proceedings of the FAO/UNEP Technical Consultation, FAO Animal Production and Health Paper No. 24, Rome Italy, 1981.
- 3. Animal Germplasm Preservation and Utilization in Agriculture. Council for Agricultural Science and Technology, Report No. 101, September 1984, Ames, Iowa, USA.
- 4. U.S. Strategy on the Conservation of Biological Diversity.
 Interagency Task Force Report, U.S. Agency for International
 Development, Washington DC, USA, 1985.
- 5. Technologies to Maintain Biological Diversity. U.S. Congress, Office of Technology Assessment, Report OTA-F-330, U.S. Government Printing Office, Washington DC, USA, 1987.
- 6. Research Priorities for Single Species Conservation Biology.
 A workshop sponsored by the U.S. National Science Foundation,
 Washington, DC, 1989.

STATEMENT OF THE PROBLEM

Despite all the publicity directed at the issues of declining habitat, species extinction, loss of genetic diversity and the potential contributions of germ plasm banking, it is remarkable that no organized programs exist to sample, evaluate, cryopreserve, maintain and use germ plasm from wild animal species. Furthermore, there are no guidelines for establishing such germ plasm banking programs or integrating them with other conservation programs. As yet, no single organization with a role in the international coordination of conservation efforts has provided guidance or oversight.

There are several organizational and procedural matters that must be addressed before the full potential of genetic resource banks can be realized for international conservation purposes. propose that the CBSG immediately provide a leadership role to remedy the lack of international oversight and coordination. CBSG should assume responsibility for developing programs that encourage germ plasm banking as an integral component of <u>in situ</u> and ex situ conservation efforts. Specifically, the CBSG should: draft and seek adoption of an IUCN Position Statement on the role of germ plasm banking in management and research programs to conserve endangered species; 2) establish a Genetic Resource Banking Oversight Committee to formulate global guidelines for the establishment, operation and review of animal genetic resource banking programs; and 3) develop a formal process that would assist the development of Genetic Resource Banking Action Plans. important elements of these overall activities include the coordination of activities within the Species Survival Commission to identify species conservation programs that would benefit from germ plasm banking, and assisting efforts to secure sources of funding for international germ plasm banking activities. Discussion of each of these critical needs follows.

ENCOURAGE INTERNATIONAL GERM PLASM BANKING ACTIVITIES

Germ plasm banking activities can best be encouraged by education programs to inform the public, conservation managers and conservation researchers of the benefits resulting from the systematic banking of genetic resources. Examples of current applications and the conservation and research benefits of germ plasm banking can be drawn from type-culture collections of microorganisms and cell cultures (Colwell 1976, Edwards 1988), the commercial cattle breeding industry (Seidel, G.E. 1990) and banks of embryos from genetically-defined strains of laboratory rodents (Mobraaten 1981).

Ongoing international programs for the f ex f situ conservation of \cdot plant genetic resources provide a useful model (Cohen et al. 1991). Efforts for developing collections of crop germ plasm are well International coordination of crop germ plasm conservation is provided by the International Board for Plant Genetic Resources (IBPGR) and the Consultative Group on International Agricultural Research (CGIAR). At present, 14 major agricultural research centers have been established in developing regions, each developing base collections of germ plasm for the major food crops. Funding for these activities is approximately US\$300 million per year. Comparable efforts for domestic animal species are modest. Currently there is no 'International Board of Animal Genetic Resources' to coordinate international efforts to conserve agriculturally-important sources of animal germ plasm. However, the Food and Agriculture Organization (FAO) of the United Nations has established an initiative to establish germ plasm banks in developing regions. Coordination of FAO and wild animal conservation and germ plasm banking activities would be best provided through the CBSG.

IUCN POSITION STATEMENT ON ANIMAL GENETIC RESOURCE BANKING

One method of highlighting the potential benefits of active genetic resource banking programs is to seek an official position statement The statement should be drafted jointly by the CBSG and the Chairman of the Species Survival Commission (SSC) of the Information and review of the statement should be solicited from other SSC Specialist Groups prior to submission to the IUCN We suggest that the statement emphasize the for approval. importance of coordinated in situ and ex situ conservation programs for endangered species. The role of germ plasm banking in preserving important sources of genetic diversity and in providing a means for moving genetic diversity between captive and freeliving populations should be stated. The CBSG should be designated to be responsible for oversight of germ plasm banking activities within the Species Survival Commission. Finally, the CBSG should be directed to coordinate and review international aspects of banking programs for nondomesticated animal species.

FORMULATE GLOBAL GUIDELINES FOR THE ESTABLISHMENT, OPERATION AND REVIEW OF ANIMAL GENETIC RESOURCE BANKS

A key factor to ensuring the success of animal genetic resource banks (GRBs) is to ensure that they are established using rigorous scientific criteria and state-of-the-art technology. Because limited resources are available, difficult choices will need to be made on which species can derive the maximum benefit from this approach. At present no guidelines exist to assist in formulating action plans for establishing and operating a genetic resource bank.

To assist the CBSG in developing such guidelines, we suggest the following sequence as a first attempt to address many of the 'important issues. This working plan was modified from one suggested recently by one of us (Rall 1992).

GENETIC RESOURCE BANKING OVERSIGHT COMMITTEE

STEP 1. The first step in establishing integrated GRBs is to establish a GRB Oversight Committee under the auspices of the CBSG. This committee should be composed of 8 to 15 members. The composition must include one or more experts from each of the following areas: 1) cryobiologist; 2) reproductive physiologist; 3) population biologist; 4) geneticist; 5) veterinarian; 6) in situ conservation biologist; 7) ex situ conservation manager; and 8) the chairmen of regional cryopreservation task force committees. Furthermore, the chairmen (or their representative) of all SSC specialist groups should serve as ad hoc members.

- STEP 2. The second step is to define the responsibilities of the committee and formulate a formal process for establishing GRBs. We propose five basic missions for the GRB Oversight Committee:
- 1. Coordinate GRB activities within the SSC and regional propagation groups. The GRB Oversight Committee would assist SSC taxon Specialist Groups, regional taxon advisory and captive propagation groups achieve their goals of conserving rare species. This can be accomplished by integrating the consideration of GRBs directly into the framework of strategic planning processes of population viability assessment and conservation action plan (PVA/CAP) workshops. These activities require that an expert resource network be established to provide advise on all technical matters related to GRBs and their utility.
- 2. Establish guidelines for identifying candidate taxa, species or populations that would benefit from a GRB program. These guidelines should be detailed and assist in the development of strategic GRB Action Plans for conserving specific animal populations. The single most important consideration is to ensure that there is a defined conservation goal that requires the collection and storage

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of biological materials. This requires that a integrated plan for a goal-oriented conservation program be established prior to initiating banking activities. We list three scenarios below to illustrate our proposed process.

- 3. Provide expert technical assistance to the appropriate taxon groups to assist in the development of GRB Action Plans. This would include identifying institutions with an interest in providing long-term repository storage space or local/regional assistance in collecting and preserving material. Furthermore, the GRB Oversight Committee would work with the CBSG, the SSC Financial Development Officer and other interested organization to identify sources for supporting international GRB activities. Proposals for funding might be submitted individually or jointly with these and other organizations to private foundations, national research granting agencies and multinational organizations.
- 4. Provide a mechanism for the review of proposed GRB Action Plans. Plans that meet recommended requirements should be approved formally by the CBSG. (Formal 'sanction' may assist in the securing of external funding.)
- 5. Develop a periodic review process for individual GRB programs. This would be best accomplished by shared responsibility with the appropriate regional GRB Task Force Committee. For example, the annual reports of individual GRBs could be presented by the chair of the appropriate regional GRB Task force for review of recent progress, problems and future directions of banking activities.

THREE SCENARIOS OF APPROPRIATE GENETIC RESOURCE BANKING PROGRAMS

Scenario 1. An ongoing captive propagation program seeks to increase safety and management options for maintaining genetic diversity in a population, and achieve the same goals with fewer animals. We propose that such a population would be a candidate for a GRB program if the following minimum requirements are met:

- a. Populations in captivity and/or the wild must be potentially viable by demographic and genetic criteria. This information is best obtained from a recent population viability assessment (PVA).
- b. Ongoing captive propagation (e.g. SSP, EEP), studbook and conservation research programs have been established for the candidate animal population(s).
- c. The current level of success of captive breeding must be sufficient to provide reasonable assurance that GRB-associated reproductive biotechniques will be successful.
- d. Animals with known genetic backgrounds should be available to serve as founders of a GRB.
- e. Sufficient numbers of 'surplus' females and males must be available to act as recipients to demonstrate the viability of cryopreserved germ plasm and serve as a source of material for

research and protocol development.

f. The effects of potential restrictions on the importation and exportation of animals and animal products must be evaluated.

g. And other factors as appropriate for the specific candidate species or population.

- Scenario 2. An animal population has declined to low numbers (<100) and is expected to recover slowly. The population is expected to lose heterozygosity rapidly (>0.5% per generation and be subjected to genetic drift. A propagation/management plan has been initiated with the goals of protecting current levels of genetic diversity, preventing the loss of diversity in specific elderly founders and increasing the size of the population. We propose that such a population would be a candidate for an emergency GRB program if the following minimum requirements are met:
- a. The populations must be potentially viable by demographic and genetic criteria. This information is best obtained from a recent population viability assessment (PVA).
- b. There is a reasonable expectation that captive propagation will be successful. For example, a taxonomically-related species or subspecies has been successfully bred in captivity.
- c. There is a reasonable expectation that GRB-associated reproductive techniques (e.g. germ plasm collection and cryopreservation, artificial insemination, embryo transfer) will be successful. For example, these procedures have been successfully applied in a taxonomically-related species or subspecies.
- d. And other factors as appropriate for the specific candidate species or population.
- Scenario 3. A free-living population has declined rapidly and satisfies the 'critical' or 'endangered' categories of the Mace-Lande criteria for threatened taxa (Mace and Lande 1991). Factors leading to the decline have been identified and a management plan has been initiated to maintain the population at low numbers (<2000) for many generations (5 to 20) before an increase in population size is expected. The population remains at risk to a further rapid decline that may reduce genetic diversity to unacceptable levels. One management goal is to develop a secure ex situ program to provide a reinfusion of genetic diversity in the event of a future decline. We propose that such a population would be a candidate for a GRB program if the following minimum requirements are met:
- a. There is a reasonable expectation that GRB-associated reproductive techniques (e.g. germ plasm collection and cryo-preservation, artificial insemination, embryo transfer) will be successful. For example, these procedures have been successfully applied in a taxonomically-related species or subspecies.
- b. Animals with known or identifiable genetic backgrounds should be available to serve as founders of a GRB.
- c. sufficient numbers of 'surplus' females and males must be available to act as recipients to demonstrate the viability of cryopreserved germ plasm and serve as a source of material for

research and protocol development.
d. And other factors as appropriate for the specific candidate species or population.

DEVELOPMENT OF ACTION PLANS FOR GENETIC RESOURCE BANKS

STEP 3. The primary responsibility for developing GRB Action Plans properly resides with those groups with specific responsibilities for in situ and ex situ conservation of specific taxa, species and populations (e.g. taxon Specialist Groups, Taxon Advisory Groups and regional captive propagation groups). These groups should be encouraged to include the development of GRBs as an integral component in their strategic conservation planning (e.g. Captive Action Plans, Taxon Action Plans). The first step in the process occurs when a group identifies a specific conservation goal for a taxon, species or population that requires the collection and storage of biological materials. The needs and characteristics of the candidate animal population(s) would be evaluated in terms of the requirements listed in the appropriate scenario listed above. If analysis of these factors suggest that conservation efforts would be enhanced or ensured by a GRB program, the group would petition the CBSG of their intent to develop such an action plan.

The GRB Oversight Committee would review the petition and, if approved, would assist the conservation group in organizing a working session meeting to further evaluate the conservation needs and develop a detailed action plan. The role of the Oversight Committee would be to identify technical experts who can assist in this effort. The specific goals of the meeting would be to:

- 1. Assemble and evaluate available information on the life-, reproductive- and genetic histories of ex situ and in situ populations of interest. Much of this information would be available for recent propagation/management (e.g. SSP, TAG) and PVA materials.
- 2. Evaluate the efficiency and efficacy of reproductive technologies for the candidate species, such as artificial insemination, embryo transfer, in vitro fertilization, gamete and embryo cryopreservation and collection of spermatozoa, oocytes and embryos. Areas requiring further research or development would be identified.
- 3. Identify the types of biological material requiring storage. It should be noted that a wide variety of different biological materials might be cryopreserved and stored depending on the goals and needs of the conservation program (see Table 1).
- 4. Specify the appropriate protocols for banking activities. These include:
- a. The criteria used to select material(s) for accession, determine the quantity of material from each donor and identify

appropriate uses of the material.

- b. Procedures for collection, processing, cryopreservation, shipping, thawing and other treatments. The minimum quality control standards for each process and overall viability would be identified.
- c. The appropriate repository equipment, facilities, security and management systems that ensure the ultimate utility of the banked materials would be identified.
- d. If any of the above items are unknown, specific areas requiring further research should be identified.
- 5. Determine the location of the primary repository for storage of cryopreserved materials and secondary backup sites.
- 6. Develop strategies for the use of banked materials in breeding and conservation research programs.
- 7. Identify sources of funding for the GRB Action Plan.

If analysis of the these factors indicates that a GRB program would benefit conservation, the petitioning organization would prepare a written Action Plan for developing a GRB program.

REVIEW AND APPROVAL OF PROPOSED ACTION PLAN FOR A GENETIC RESOURCE BANK

STEP 4. Identifying the appropriate authority for reviewing GRB Action Plans is complicated by the overlapping purviews of national, regional and international organizations and their animal propagation/management programs. We suggest that the proposed GRB Oversight Committee is the most appropriate organization because of the very nature and responsibilities of the CBSG. First, by definition, genetic resource banking programs represent a form of ex situ captive propagation. Second, GRB activities are international in that technical experts and populations of most rare species are located on several continents. Third, GRB programs require integration with other in situ and ex situ conservation programs. However, in many cases, regional cryopreservation task force committees will play an important role in regional coordination and development of these programs. In those cases, we propose that the GRB Action Plan be reviewed by both the regional banking authority and CBSG GRB Oversight Committee. After approval, the plan would be implemented and collection, storage and use of biological materials can begin.

CONCLUSION

The development of animal Genetic Resource Banks offers unique opportunities to control and manipulate the effects of time in the management and conservation of rare species. The ideas proposed

here are intended to help stimulate discussion about the process on a formal basis. Many important questions remain to be resolved, including the translation of banking germ plasm into live off-spring. However, many recent reports of successes using artificial breeding techniques indicate the potential of reproductive biotechnology. The further development of strategies proposed here will ensure that GRBs are not merely an interesting idea or static warehouses of biological materials but facilitators for conservation.

Table 1. Biological Materials for Germ Plasm Banking and Conservation Research.

•	Material Type	Long-term Storage <u>Conditions</u>	Examples of Potential Uses
	Sperm, oocytes	below -130°Ca	Controlled breeding; international shipment; gene banking
	Embryos	below -130°C	Control of generation interval and gene flow; population amplification; international shipment
	Cell lines	below -130°C	Genetic and physiological research
	DNA -Isolated	dried, 4°Cb	Molecular biology: Sequence detection and identifica-
	-Isolated and frozen tissues	below -60°C°	tion (e.g. by PCR) Pedigree determination; genomic and mitochondrial libraries
	Serum, plasma	below -60°C	Disease status (detection of micro- bial antibodies and disease organisms); endocrine status (measure hormones or hormonal metabolites)
	Urine, milk	below -60°C	Endocrine and health status (measure hormonal and other metabolites)

^{*}Liquid nitrogen refrigerator.
*Refrigerator or cold room.

CLow-temperature mechanical refrigerator.
[from Rall 1992, with modifications]

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UTILIZATION OF SPERM BANKS TO MAINTAIN GENETIC DIVERSITY IN CAPTIVE POPULATIONS OF WILD CATTLE

Leslie A. Johnston and Robert C. Lacy

INTRODUCTION

As a result of habitat fragmentation, wild cattle species of Southeast Asia are either threatened or endangered in their indigenous habitats, and soon will become extinct unless preservation efforts are undertaken immediately. Gaur, (Bosgaurus), a critically endangered species of wild cattle, historically ranged throughout Asia. Today, there are only remnant populations in Nepal, India, Thailand, Laos, Burma, Cambodia, Vietnam and Malaysia. Gaur, which are shy forest-dwelling creatures, are reluctant to use cleared areas as migration corridors to other forested areas. As a result, subpopulations are becoming highly isolated, resulting in genetic and demographic instability.

Recently, captive propagation has become an integral component of the conservation strategy to maintain wild populations through: 1) enhanced preservation of genetic diversity; 2) protecting gene pools against the effects of environmental and demographic fluctuations in the wild and 3) providing animals for reinforcement of wild populations or establishment of new wild populations. Soule et al. has suggested that approximately 815 mammalian species will all but disappear unless they are maintained in captivity [1]. to manage captive populations, effective breeding sizes need to be adequate to achieve specific genetic and demographic goals. In many cases this requires a minimum of 200 to 800 individuals/species maintained in captivity. Currently, there is enough space in zoos worldwide to house only 100 mammal species in populations large enough to be self-sustaining demographically and genetically [2].

Ballou has recently discussed the benefits of germ plasm cryopreservation (sperm, ova, embryos) for captive management programs [3]. Cryopreserved germ plasm enables the captive program to: 1) maintain a population's original genetic diversity indefinitely; 2) extend generation length of individuals/populations and 3) decrease the number of individuals required to achieve the defined genetic goals. Long term preservation of genetic diversity will enable the population to continue evolving through time. In addition, increasing generation length will provide fewer opportunities for losing genetic diversity. The combined effect of preserving genetic diversity and extending generation length is the ability to reduce population numbers and at the same time achieve genetic goals. Consequently, cryopreservation programs will allow additional space to become available for other species.

While there has been much speculation on the effectiveness of gamete cryopreservation as a conservation tool (ranging from discussions of completely frozen zoos to dismissal of the concept), little effort has been made to evaluate quantitatively

the role that reproductive technologies can play in wildlife conservation. Development of sampling and utilization strategies to guide selection of an optimal representation of the genetic diversity are required for a genome banking program. In this paper, we present a quantitative assessment of the likely efficacy of sperm banking in furthering the goals of the captive breeding program for gaur. Using computer simulation models, we examined a scheme proposed for the preservation of the gene pool of the North American gaur herd, and make recommendations for the optimal use of the sperm in the captive program.

Conceptually we have proposed the use of three sperm banks for gaur. The first one is established with semen collected from genetically valuable males in the current captive population. The second one is established with semen from wild-caught males. The third is a mirror of the captive population through time, with genetic exchange between the bank and the living population. The first and second banks will be used to replenish the living population. The intent of the third bank is to be used primarily as a reserve in case the other two banks are destroyed.

Frozen sperm banks offer promise for preserving much of the genetic variation in populations of wild cattle. Unlike the situation for most endangered species, reliable artificial insemination (AI) techniques already exist for cattle and are being applied to other bovid species, including gaur [4].

Gaur were brought into captivity between 1958-65, and in 1981, the North American Gaur Species Survival Plan was formed. Presently, the herd consists of 162 animals descended from 8 founders. Pedigree analysis indicates that the captive herd has 89.4% of the gene diversity (heterozygosity expected under Hardy-Weinberg equilibrium) of the ancestral wild stock from which founders were obtained. It is estimated that over 900 animals will be required to maintain this level of diversity through the next 100 years. Currently, there is limited space for expanding the herd beyond 150 individuals; therefore it is critical that a semen cryopreservation program is designed in order to limit further decline of genetic diversity.

The following variables were examined during individual simulations between the living gaur population and semen cryobank to assess their effects on retention of genetic diversity:

1) effective population size of the living herd; 2) sex ratio of the herd; 3) number of offspring required from each bank for each generation; 4) semen usage interval; 5) the minimum number of males required to establish the captive bank and 6) the interaction of both the captive and wild bank.

Methods

Computer simulations were done by using a modified version of Lacy's GENESIM computer simulation program of genetic diversity [5].

To simulate the fate of two alleles at a genetic locus, with the interactions of frozen banks, the program:

1. Prompts the user to enter the number of described conditions for a population: number of generations, population

size, sex ratio, initial gene frequency at a hypothetical locus (defining the initial gene diversity) and the use of any of 3 sperm banks. If any of the banks are selected, the user is prompted to enter the initial gene frequency of the bank, the generation usage of the bank, number of offspring produced per generation. The use of sperm bank 3 also allows the user to define how many males are used to establish the bank and the number of males each generation to be used to augment the bank. The simulation program assumes that each sperm sample can be infinitely extended, so that the lack of sufficient frozen sperm does not interfere with planned matings.

2. Creates a population of living diploid individuals, assigning 2 alleles to each individual with the probability p that each allele is of one type (A), where p is the initial

allele frequency as specified by the user.

3. Either: selects two parents at random from the living population, or selects a male from the bank and female from the living population. The decision to select two living parents vs. a female and frozen sperm from a sperm bank is determined by the designated frequency of use of each sperm bank.

4. Randomly selects one allele from each of the two parents

and assigns that allele pair to the offspring.

- 5. Calculates allele frequencies and % expected heterozygosity that would be observed if the population was in Hardy-Weinberg equilibrium.
- 6. Steps through the specified number of generations, randomly mating all females of the herd.
- 7. Repeats the simulation 1000 times to generate a distribution of outcomes.
- 8. Averages overall heterozygosity for each generation over all repetitions.

RESULTS

Population size:

One of the primary benefits to the use of frozen germ plasm is the ability to reduce the population size and still achieve the genetic goals. Figure 1 compares the genetic variation present after 1000 years in the living herd with genetic replenishment from either of two cryo-banks (wild, captive) or without either bank, using populations of sizes: 40, 80, 120, 160, 200 and 500 individuals. As expected, without infusion of genetic material, genetic diversity was dependent upon population The mean heterozygosity dropped to a low of 18.0% (after 1000 years with an Ne = 40) and with Ne = 500 was maintained at 78.9%. By using the captive bank every generation, the herd was able to retain 80.9% to 82.9% heterozygosity (SE = 0.61-0.52) over 125 generations (=1000 years). Utilization of the wild bank enabled the herd to increase its heterozygosity from 89.2% to above 90%. The population was able to maintain heterozygosity levels at 91% for Ne = 40, 80, 120, 160 and 200. With a effective population size of 500, the mean heterozygosity retained was 92% (SE = 0.31). All of the following simulations

assumed N=80.

Sex ratios:

Frozen banks, in principle, genetically augment the living population size. However, the use of sperm banks will increase only the effective male population size. While adding males to the breeding pool through the use of their sperm in the banks, the genetically effective population size (and the retention of genetic variation) might be increased by an offsetting skew of the living population toward females. Therefore, to manage the population effectively, it is important to determine the optimal sex ratio of the living population. Figure 2 depicts the percent of genetic diversity retained for 1000 years with either: 1) genetic replenishment from the wild or captive bank or 2) no infusion at all using sex ratios (proportion male) of: 0.1, 0.2, 0.3, 0.4, and 0.5. Without the use of either frozen bank, retention of genetic diversity was detrimentally influenced by sex ratios lower than 0.5. This is expected to occur since the small number of individuals of one sex will act as a bottleneck because half of the genetic information inherited by the next generation comes from each sex. With either the wild or captive cryo-bank replenishing the living population, the retention of genetic diversity appears almost independent of sex ratio. mean heterozygosity ranges from 87.4% (SE = 0.50) to 91.5% (SE = 0.34) when semen from the wild bank is used. With the captive bank replenishing the living population, mean heterozygosity ranges from 77.6% to 81.6%. However, there is a slight advantage to skewing the ratio toward 0.3 when using the wild bank.

Number of offspring:

Figure 3 shows the effect on genetic diversity retained by producing different numbers of offspring every generation from each cryo-bank. The following number of offspring produced were tested; 2, 4, 6, 8 and 10. Regardless of which bank was in use, 2 offspring per generation was insufficient to maintain heterozygosity above either 80% (captive bank - 75.1%) or 90% (wild bank - 86.3%). Producing 4 offspring per generation from the captive bank will enable the population to retain 81.7% genetic diversity. Additional offspring will maintain the population between 83.6% to 85.8% (n=6 and 10, respectively). If genes are only brought in from the original captive herd (bank 2), diversity can never increase above 89.4%. Production of 4 offspring using the wild cryo-bank will maintain heterozygosity However, production of 8 to 10 offspring using the wild bank will capture much of the diversity in the wild population, increasing heterozygosity to 95.5% and 96.2%, respectively.

Semen Usage Interval:

To assist in planning the amount of semen to be cryopreserved, it is important to determine how often during the course of management semen is required for optimal utilization of

the frozen banks. Generation intervals for semen usage were tested and the results are shown in Figure 4. Regardless of whether the living population is replenished with semen from the captive or wild bank, it is optimal to utilize the banks every generation (82.0%, 91.2%, respectively). Although, even with occasional use of either cryo-bank, it is still substantially better to use a bank on a limited basis, than no bank at all (recall that the population declines to just 38% heterozygosity when no bank is used).

Number of Captive Males to Establish a Bank:

For any management scheme to be set in place it is critical to determine the required number of males from which sperm needs to be frozen to utilize the frozen bank efficiently and to maintain maximum genetic diversity. The number of males tested to establish the cryo-bank from the captive population ranged from 5 to 100. A minimum of 20 males are required to maintain most of the heterozygosity present in the initial population (Figure 5). After banking sperm from 30 males, the incorporation of additional animals is unnecessary, and even with 100 males heterozygosity remains at virtually the same level as with 30 (80.7% vs 80.9%).

Interaction between captive and wild banks:

The establishment of the captive bank is operationally easier than establishing a wild bank. Therefore, to maximize resource and effort, there is the need to assess the benefits of using the wild bank immediately or in the future, assuming the captive bank is already functional. Usage of the captive bank alone will maintain genetic diversity at ~80% relative to the original wild population. Figure 6 shows the results of initially using the captive bank every generation and then incorporating the wild bank after 5, 10, 15, 20, 40, 60, 80, 100 and 120 generations. Once the wild bank is incorporated, the captive bank will no longer be used. It is apparent that as long as the captive bank is replenishing the living population, it is possible to postpone using the wild bank until at least generation 80 and still maintain 91.6% heterozygosity after 1000 years. From the data, (not shown), it appears that once the wild bank is initiated, it takes approximately 5 to 10 generations to increase the genetic diversity of the living population to greater than 90% of the wild population.

Discussion

In the preservation of maximum biological diversity, the use of reproductive technology may be the last resort. It has been estimated that the demographic winter and human control of wilderness areas will last at least the next 500-1000 years [1]. When human attitudes change and habitat regeneration becomes a goal of society, it will take a minimum of centuries to replenish the ecosystems destroyed in tropical and temperate regions. As a consequence, zoos will need to maintain the genetic and

demographic health of their charges for many centuries or millennia. Many Species Survival Plans provide management of populations with genetic goals of 90% for the next 100-200 years. It is estimated that after that time, advances in reproductive technology will be able to extend the program to at least 1000 years. Because reproductive technologies have already been well developed for cattle, we can now begin managing wild cattle species for that 1000 year goal.

The major problem facing long-term management of small populations is the loss of genetic diversity through drift. Genetic drift can be controlled by the maintenance of large breeding populations in which all animals contribute equally to future generations. In many cases, immigration of individuals into subpopulations can reduce genetic drift. In captive and, increasingly, in wild populations, the number of breeding individuals is so reduced and populations are so isolated that even short-term maintenance of genetic diversity is placed in jeopardy. Therefore, strategies will need to be designed to eliminate additional loss of heterozygosity. Sperm banks will increasingly play an important role in small population management by preserving original germ plasm indefinitely and reintroducing this material (as immigrants) through time to counter genetic drift.

With the modelling simulations shown, it is possible to sustain a genetically healthy gaur population for the next 1000 years with a sperm banking program. The loss of genetic variation is affected by a number of factors including: the number of breeding individuals in a population, sex ratio and number of offspring produced from AI. Excluding demographic constraints, it is possible to retain maximum genetic diversity with as few as 40 individuals in the population when offspring are produced from semen from either the captive or wild bank. fact, the retention of genetic variation becomes relatively insensitive to the captive population size when genetic material can be regularly infused from one or more sperm banks. capability to retain more diversity with smaller living captive populations should allow a dramatic expansion of the number of species that might be supported with living captive populations and genome banks.

When the wild bank is in use, there is also a tendency for optimal retention of genetic diversity when the sex ratio is skewed toward 0.3. The use of gametes from sperm banks in the production of offspring skews the effective sex ratio toward males. This effect can be countered by skewing the sex ratio of the living population toward females. It is possible that since the wild cryo-bank is genetically more unique than the living population, it is optimal to reduce the number of living and not as "genetically unique" males even more than might be estimated based on the number of frozen sperm samples utilized each generation. However, genetic diversity is affected detrimentally if the sex ratio is reduced further, as a result of decreased number of breeding animals (Ne).

Based on the generation length for gaur (T=8), essentially one offspring is required to be produced from either the wild or captive bank each year to maintain maximum genetic diversity. It

is also worthwhile to note that although it is optimal to use either bank every generation, there is still benefit to the living population if sperm banks can be used only intermittently. It is also important to note that once the wild bank becomes functional, use of the captive bank will no longer benefit the living population. Also, a third bank, which would mirror of the living population, will only be utilized if either of the other two banks fail. The genetic representation of this bank will be intermediate between either of the other two banks and the living population.

In many instances, it will be impossible to depend upon a wild bank initially; therefore efforts should be made to establish a captive bank before additional genetic diversity is Currently the North American gaur herd consists of 59 males. In order to establish an effective captive bank, one-third of these males are required to be banked (see Fig. 5). selection of which males to use will be based on the Mean Kinship values derived from pedigree analysis. The most genetically valuable males are those with the lowest mean kinship to the living population, i.e., those with the rarest genes. Kinship is the average relatedness of each individual to every other animal in the population, and is calculated from pedigree data. An animal with high average relatedness will share alleles with a number of other individuals in the population, and conversely an individual with no relatives will have an average relatedness of 0.

Finally, these simulations are based on a number of simplifying assumptions, including random mating. Through the use of existing management programs [GENES, Lacy], based on pedigree analysis, it may be possible to optimize mating strategies to produce more genetically valuable animals than expected with a random system. Conversely, unexpectedly poor breeding by some animals could lead to more rapid losses of genetic diversity than projected by the simulations.

Based on these simulations, initial management plans would consist of: (1) continued maintenance of a small demographically stable captive population; (2) collection of sperm from 20-30 genetically valuable males present in the captive population; (3) initiation of cryopreservation of sperm from individuals in wild populations; and (4) interactive management of the living herds and the sperm banks.

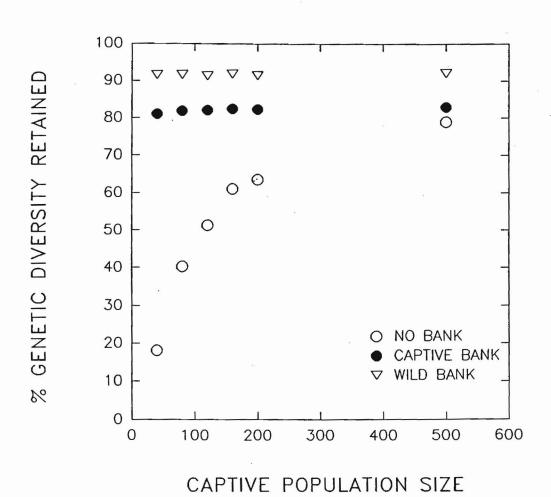
Although these simulations focused on the captive population, wild populations are facing the same threats. Eventually this type of management strategy may be required to sustain healthy wild populations. It is apparent that there is a wide range of possible strategies, and refined modelling of options is important as a part of adaptive program management. Although this is a simple model, in any genetic management scheme it is important to analyze the expected consequences of the program and determine whether it will achieve its desired goals before the program is implemented. Properly utilized, sperm banks can be very effective tools for preserving genetic diversity in a living population, and for introducing gene diversity from additional subpopulations.

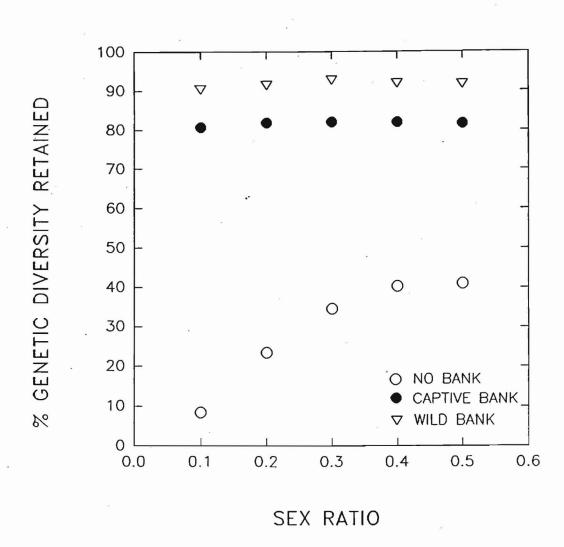
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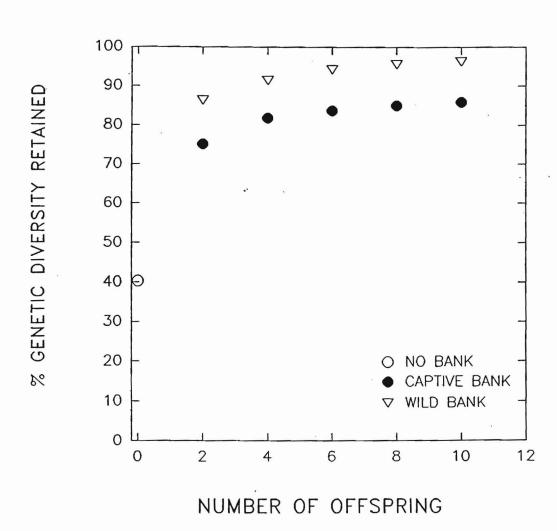
The authors wish to thank Jon Ballou for stimulating discussions on the concepts of cryopreservation banks.

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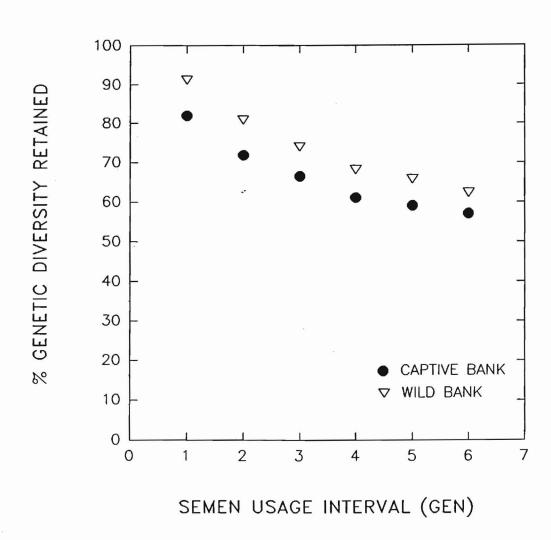
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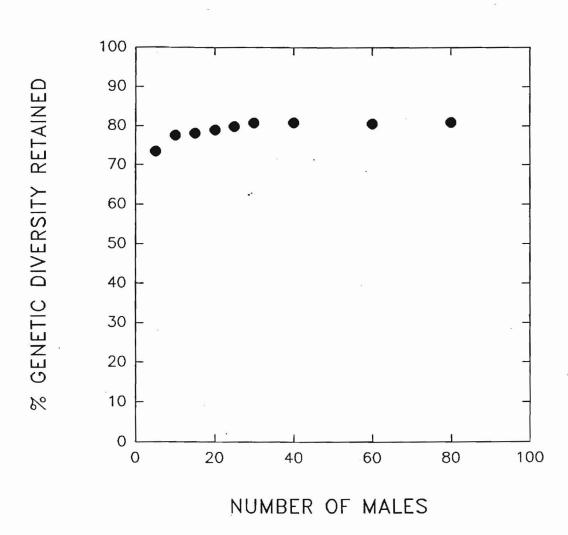


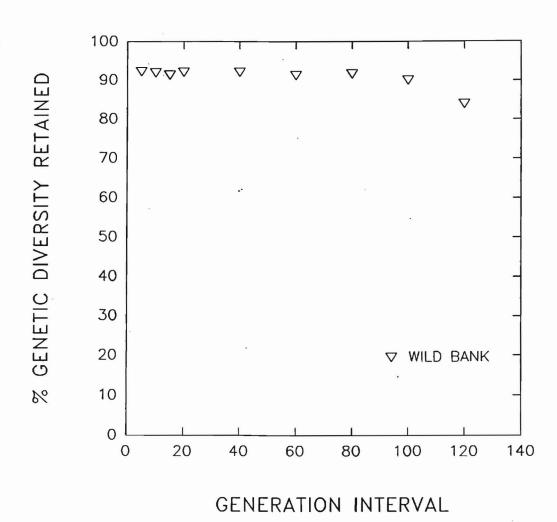




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POPULATION BIOLOGY GUIDELINES FOR USE OF GENOME BANKING AS A MANAGEMENT TOOL FOR CONSERVATION OF WILD CATTLE POPULATIONS

Omaha Zoo, 13-16 June 1991

INTRODUCTION

Genome banking offers the opportunity to expand the scope, time span, scale, security, and economy of programs for conservation of species and of within species genetic diversity. As populations of wild cattle species are fragmented in distribution and reduced in numbers, genetic diversity is lost and the populations become increasingly vulnerable to extinction. Some of the species are vulnerable to hybridization with domestic cattle or domesticated stock of the wild species. Cryopreservation of representative samples of genomic materials from the wild populations will allow indefinite preservation of presently available diversity and protect against extinction. These materials also may be used for the genetic management of living wild and captive populations now and in the future.

Formulation of goals and objectives for a genome banking program are necessary for development of sampling and utilization strategies to guide: (1) selection of an optimal representation of the genetic diversity, (2) collection and storage of an adequate amount of material, and (3) distribution and use of the appropriate materials. These materials may then be used to assist restoration of extinct wild populations, genetically supplement small living wild populations, assist in the exchange of genetic material between previously connected wild populations, and support smaller captive populations with indefinite retention of presently available genetic diversity.

The utilization of genome banks as part of an integrated program for management of living wild and captive populations may allow retention of a larger fraction of the present genetic diversity in the wild populations with smaller living captive populations. It also may be possible to distribute embryos to other sites without removing animals from threatened populations. These might then be transferred to surrogate hosts to produce living populations

as a basis for further expansion of the genome bank, introductions to other sites, or supplementation of the wild population. The living population could receive periodic infusions from the genome bank to replace diversity lost by drift or to maintain a closer correspondence to the genetic composition of the wild population. The cryopreserved materials will allow indefinite (thousands of years) retention of the present day genetic diversity which will significantly modify current goals for captive conservation programs based upon 90% retention of genetic diversity for 100 or 200 years in the captive populations.

This capability to retain more diversity with smaller living captive populations should allow a dramatic (4-10 fold) expansion of the number of species or evolutionary significant units that might be supported with living captive populations and genome banks. This expansion in the number of species to be managed will greatly increase our need for systematic data collection, analysis, and distribution and for simpler development of species management plans. The addition of another mode for protection of species against loss should further secure them from extinction from catastrophic events and the impacts of continuing loss of habitat quantity and quality.

GOALS

- 1. Long term conservation of species, of genetically distinct populations, and genetic diversity within species.
- 2. Provide a resource for enhancement and development of agricultural breeds.
- 3. Transfer of cryopreservation, reproductive, and molecular genetic technology to collaborators in the range country of each species from which specimens are collected. One intent of this program would be to support genome banking of these species in the countries of origin.

OBJECTIVES

- 1. Develop models for optimal sampling of the wild and captive populations across space and time to meet program goals for genetic representation and for use over the proposed time span of the program.
- 2. Develop models for optimal use of the banked materials to preserve the genetic diversity of the wild and captive populations, to support the living wild and captive populations, and as a resource for reintroductions to replace extinct populations.
- 3. Develop models for the amounts of materials to collect and store from

individual animals in the captive populations and from animals in the wild populations.

- 4. Delineate the species distribution and population structure based upon concordance of geographic distribution, molecular genetics, and morphology.
- 5. Define a sampling strategy for collection of genetic materials (semen, ova, embryos) from the wild populations of the species to provide representation of 98% of the presently available species genetic diversity.
- 6. Determine if there has been introgression of genes from domestic cattle into the present wild populations of each of the species of wild cattle. If so, then determine on a case by case basis what strategy will be employed to sample these populations.
- 7. Evaluate whether there have been human caused movements of genetic materials between wild populations of each wild cattle species. If so, then determine on a case by case basis what strategy will be employed to sample these populations.
- 8. Conduct a workshop: a) to review the distribution, numbers, and threatened status (according to the Mace-Lande criteria; Appendix I) of all populations of wild cattle; b) to recommend conservation actions for each population in terms of protection and management needs, need for a Population Viability Analysis, need for establishment of a captive population, and need for establishment of a genome banking program.
- 9. Develop procedures and resources for transfer of the cryopreservation, reproductive, and molecular genetic technologies to specialists in each of the range countries of the wild cattle species.
- 10. Initiate a process to identify interested collaborators to explore the potential usefulness of these materials for enhancement and development of domestic breeds of cattle for use in the range countries and elsewhere.

SELECTION STRATEGY FROM SOURCE POPULATIONS

Wild populations.

Identify populations for genome banking based on:

- 1. Level of threat (Mace-Lande criteria)
- 2. Availability of collaborators, resources, and animals

3. Cooperation and interest of range country wildlife officials

Animals from populations living in nature are especially valuable gamete/embryo donors for three primary reasons:

- 1. They can be objectively selected from all parts of the species range and collectively represent the existing (remaining allelic) diversity for that species as a whole. In each case, care must be taken in the sampling strategy to avoid artifacts (i.e. artificial movement of individuals by humans)
- 2. It can be argued that the genetic makeup of adult animals from healthy populations in nature is, by definition, the current ideal. Perpetual reproductive access to these genomes provides the antidote to genetic drift (i.e. reduced "fitness") both in skewed gene frequencies and in absolute loss for both multi-generation captive populations and bottle-necked wild populations.
- 3. It is not always sufficient to only utilize captive animals since: 1) founder populations are frequently small and an inadequate sample; 2) we rarely have access to many of the founders, access only to descendants means an immediate loss of genetic diversity; 3) founders are commonly of unknown province (i.e. are they representative of the geographic range and range of diversity; are they litter mates)

It is recommended that appropriate sampling methods be developed for selecting the number and location of wild donors for continuing collections in future generations. It is also recommended that:

- 1. Wild donors be permanently identified (e.g., tagged, transponder implant etc.)
- 2. Blood and other tissue samples be stored from each donor for comparative (multi-generational) genetic studies as well as for epidemiological work both present and future.

Captive Populations.

Founder animals: It is recommended that the degree of relatedness between living founders (i.e., wild caught animals) be assessed with modern molecular genetic techniques. Founder animals are automatically given highest priority for gamete/embryo banking for many of the same reasons wild specimens are valued (see above), and

Captive-born animals: Careful analyses of the pedigrees of the current population are necessary to select gamete/embryo donors of captive-born origin for banking. Two criteria

for selection have been initially identified:

- 1. Mean Kinship calculated from the gene drop analysis (Lacy, 1991) using studbook data. The Mean Kinship is the average relatedness of each individual to every other animal in the population, and is calculated based on the kinship coefficient, using the additive matrix and pedigree data. Priority is positively correlated with mean kinship coefficient. Mean kinship will always rank parents higher than offspring.
- 2. The need to identify relationships among individuals listed in the high priority category to avoid over-representation of family lineages (i.e. siblings)

Additional scenarios may need to be examined for adequate assessment on a case by case basis.

Sample Sizes.

The number of selected donors will generally range between ten and twenty-five individuals. Collectively, the individual donors will represent a "percent of the genetic diversity retained" figure that is greater or equal to that of the current captive population as a whole. A model needs to be developed to evaluate and identify: 1) additional individuals for collection and 2) utilization of offspring produced by the frozen germ plasm.

MATERIALS TO BE BANKED

- 1. Reproductive management
 - a. Semen
 - b. Ova (as technology advances)
 - c. Embryos
- 2. Genetic and disease management
 - a. Fibroblasts in cell culture
 - b. Serum

Until such time that ova can be reliably cryopreserved it is recommended that oocytes/ova be in vitro matured/fertilized and resulting embryos frozen.

AMOUNT OF SEMEN TO BANK

- 1. Quantity of semen stored should be sufficient to:
- a. Provide duplicate samples for storage in geographically separate banks for security reasons, each bank providing sufficient insemination and/or embryo transfer opportunities to allow:
 - 1) achievement of genome resource bank utilization goals,
 - 2) protection against catastrophes,
 - 3) establishment of genome resource bank in range country, and
 - 4) full restoration of the original genetic diversity of the donor population in living form at least three times (generally meaning the potential of producing 30-50 living offspring x3).
- 2. Development of a formula for calculating the number of insemination opportunities (i.e., minimum sperm for conception per straw) and/or embryos will require values for the following variables:
 - a. Post-thaw viability.
 - b. Range of ejaculate quality (viable sperm per ml).
 - c. Samples required for testing.
 - d. Degradation through time (e.g., background radiation).
 - e. Female conception and birth rates using cryopreserved gene plasm.
 - f. Neonatal mortality.

STRATEGIES FOR COLLECTING MATERIALS:

Methodical/deliberate: Species specific programs need to be established in order to effectively collect the required genetic material from specified individuals or populations for the genome bank within the next year. This program would identify the logistics encountered for collecting semen, and nonsurgical collections of ova and embryos. Ova collected will be identified for either: 1) cryopreservation or 2) IVF and resulting embryos frozen.

Rescue/salvage: In order to protect against the loss of valuable genetic material a program needs to be developed for opportunistic gamete recovery from individuals. Circumstances under which material can be collected will include: 1) ovariohysterectomies, euthanasia, natural deaths (captive populations) and 2) human induced mortalities of

individuals in the wild (i.e. road kills, regulated hunting).

DEVELOPMENT OF COMPUTER SIMULATION MODELS

Projects:

- 1. Sampling strategies for wild and captive populations through time.
- 2. Designing explicit program goals, i.e. defining program length and levels of genetic diversity to be maintained.
- 3. Sperm/ova banks.
- 4. Embryo banks.
- 5. Interactive management between wild and captive populations including banks.

Computer simulations are designed to provide a basis for making decisions about the genetic management of both wild and captive populations. Simulations are intended to be used to explore and define the effects that different utilization and management strategies will have on the genetic composition of a population.

Studies have been initiated in designing simulation models that begin addressing the issue of how to utilize the genetic material in sperm banks and the impact of different utilization schemes on the management of the living captive and wild populations (Appendix II). Conceptually, ova banks can be modelled as sperm banks with the knowledge that genetic material from individual females will be more limited. To-date, little effort has been directed to evaluate quantitatively the role of embryo banks in the genetic management of captive and wild populations. The use of embryo banks will influence the utilization of the bank, since the embryo genome bank will represent a diploid versus a haploid population.

As part of the metapopulation genetic management of populations it is necessary not only for living captive and wild populations to interact but also for interaction with respect to genome banks. Simulation programs provide an infinite source of options to evaluate and allow for refine modelling of such interactions. Suitable models need to be developed within the next 1-2 years to guide programs. These models will be dynamic and continually evolving as additional new information becomes available.

Prepared by: Leslie Johnston, Ulie Seal, Dan Wharton, and Jean Brennan with contributions from Jon Ballou and Bob Lacy.

KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 13 TRANSLOCATION Reprint Series 4 August 1989, Volume 245, pp. 477–480 **Science**

Translocation as a Species Conservation Tool: Status and Strategy

Brad Griffith, J. Michael Scott, James W. Carpenter, and Christine Reed

Translocation as a Species Conservation Tool: Status and Strategy

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Surveys of recent (1973 to 1986) intentional releases of native birds and mammals to the wild in Australia, Canada, Hawaii, New Zealand, and the United States were conducted to document current activities, identify factors associated with success, and suggest guidelines for enhancing future work. Nearly 700 translocations were conducted each year. Native game species constituted 90 percent of translocations and were more successful (86 percent) than were translocations of threatened, endangered, or sensitive species (46 percent). Knowledge of habitat quality, location of release area within the species range, number of animals released, program length, and reproductive traits allowed correct classification of 81 percent of observed translocations as successful or not.

TRANSLOCATION IS THE INTENTIONAL RELEASE OF ANImals to the wild in an attempt to establish, reestablish, or augment a population (1) and may consist of more than one release. To date, translocations have been used to establish populations of nonnative species and restore native species extirpated by hunting. An increasing perception of the value of biological diversity has focused attention on translocations of rare native species. These latter translocations are expensive (2, 3) and are subject to intense public scrutiny (4). They have varied goals (3) that include bolstering genetic heterogeneity of small populations (5–7), establishing satellite populations to reduce the risk of species loss due to catastrophes (8, 9), and speeding recovery of species after their habitats have been restored or recovered from the negative effects of environmental toxicants (2) or other limiting factors.

In the face of increasing species extinction rates (10–12) and impending reduction in overall biological diversity (12), translocation of rare species may become an increasingly important conservation technique. If current patterns of habitat loss continue, natural communities may become restricted to disjunct habitat fragments and intervening development may disrupt dispersal and interchange mechanisms (2). Increased rates of extinction may be expected in small fragmented habitats (13) and translocation may be required to maintain community composition, especially for species with limited dispersal abilities.

The immediacy of reduction in biodiversity (14) demands a rigorous analysis of translocation methodology, results, and strategy. We need to know how well it works, what factors are associated with success, and what strategies suggest greatest potential success.

We conducted three surveys of contemporary (1973 to 1986) translocations of native birds and mammals in Australia, Canada, Hawaii, New Zealand, and the United States (15). In the first

survey, we obtained general information on the number of programs completed by various organizations. In the later surveys, we sought detailed information on translocations of (i) threatened, endangered, or sensitive species and (ii) native game birds and mammals.

Current Status

At least 93 species of native birds and mammals were translocated between 1973, the year the Endangered Species Act became law, and 1986. Most (90%) translocations were of game species; threatened, endangered, or sensitive species accounted for 7%. Ungulates (39%), gallinaceous birds (43%), and waterfowl (12%) dominated translocations of game species; raptors (28%) and marsupials (22%) dominated threatened, endangered, or sensitive species translocations.

A typical translocation consisted of six releases over the course of 3 years. Many (46%) released 30 or fewer animals and most (72%) released 75 or fewer animals.

The average number of translocations per reporting organization doubled from 1974 (5.5) to 1981 (10.6) suggesting contemporary totals of 700 translocations per year. Most (98%) of these were conducted in the United States and Canada. Effort was not uniformly distributed; 21% of North American agencies conducted 71% of North American translocations. Only 27% of reporting organizations had protocols that specified the types of information to be recorded during translocation programs.

Theoretical Considerations

A translocation is a success if it results in a self-sustaining population; conversely, the founder group may become extinct. Theoretical considerations predict that population persistence is more likely when the number of founders is large, the rate of population increase is high, and the effect of competition is low (13). Low variance in rate of increase (16), presence of refugia (9), reduced environmental variation (16), herbivorous food habits (17), and high genetic diversity among founders (18) may also enhance persistence. Suitable, protected, and maintained habitat, control of limiting factors, and proper care and training of captive reared

B. Griffith was in the Department of Fisheries and Wildlife Resources, University of Idaho, Moscow, ID 83843, and is currently assistant leader, U.S. Fish and Wildlife Service (USFWS), Cooperative Fish and Wildlife Research Unit (CFWRU), University of Maine, Orono, ME 04469. J. M. Soott is leader, USFWS, CFWRU, University of Idaho, Moscow, ID 83843. J. W. Carpenter is a research veterinarian, USFWS, Patuxent Wildlife Research Center, Laurel, MD 20708. C. Reed is a Conservation Officer, Department of Conservation, Twizel, New Zealand.

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animals (3, 19) are also considered prerequisites of a successful translocation.

We found that several factors were associated with success of translocations (Table 1). Native game species were more likely to be successfully translocated than were threatened, endangered, or sensitive species. Increased habitat quality was associated with greater success. Translocations into the core of species historical ranges were more successful than were those on the periphery of or outside historical ranges. Herbivores were more likely to be successfully translocated than either carnivores or omnivores. Translocations into areas with potential competitors of similar life form were less successful than translocations into areas without competitors or areas with a congeneric potential competitor. Early breeders with large clutches were slightly more likely to be successfully translocated than were species that bred late and had small clutches.

Translocations of exclusively wild-caught animals were more likely to succeed than were those of exclusively captive-reared animals (Table 1). Among translocations of exclusively wild-caught animals, success depended ($P \le 0.10$) on whether the source population density was high (77% success, n = 109), medium (78%, n = 37), or low (37%, n = 8). Success of translocations of wild-caught animals was also associated ($P \le 0.10$) with whether the source population was increasing (83% success, n = 93), stable (63%, n = 49), or declining (44%, n = 9). Successful translocations released more animals than unsuccessful translocations (160 compared to 54, respectively; P = 0.024).

Our results are consistent with analyses of naturally invading or colonizing species that show (i) larger founder populations are more successful (20, 21), (ii) that habitat suitability is important (21), and (iii) increased number and size of clutches enhances successful invasion (22). Our data also support the hypothesis that herbivores

Table 1. Percentage success of intentional introductions or reintroductions (translocations) of native birds and mammals to the wild in Australia, Canada, Hawaii, New Zealand, and the United States between 1973 and 1986. Data were obtained from a survey conducted in 1987 (15). The data include 134 translocations of birds and 64 translocations of mammals. For all variables listed, χ^2 was statistically significant ($P \le 0.10$), implying true differences in the percentages of successful translocations among the categories. Animals that first give birth at age 2 or less with average clutch size of three or more are considered early breeders with large clutches; all others are late breeders with small clutches.

Variable	Trans- locations (n)	Success (%)
Threatened, endangered, or sensitive species	80	44
Native game	118	86
Release area habitat Excellent Good Fair or poor Location of release	63 98 32	84 69 38
Core of historic range	133	76
Periphery or outside	54	48
Wild-caught	163	75
Captive-reared	34	38
Adult food habit Carnivore Herbivore Omnivore	40 145 13	48 77 38
Early breeder, large clutch	102	75
Late breeder, small clutch	96	62
Potential competitors Congeneric Similar Neither	39 48 105	72 52 75

are more successful invaders than carnivores (17) and the conclusion that, for birds, morphologically similar species have a greater depressing effect on successful invasion than do congeneric species (23).

We found no consistent association of translocation success with number of releases, habitat improvement, whether the release was hard (no food and shelter provided on site) or soft, immediate or delayed release on site, or average physical condition of animals at release. We were unable to directly evaluate genetic heterogeneity, sex and age composition, or specific rearing and handling procedures for released animals because of inadequate response to survey questions.

Evaluating Alternative Strategies

Analyses of individual factors associated with translocation success do not adequately reflect the multivariate nature of actual translocations. To overcome this problem, we used stepwise logistic regression (24, 25) to develop preliminary predictive equations for estimating the success of translocations (Table 2). An expanded data set or independent sample would probably yield different regression coefficients and estimates of success than we report. As a result, extrapolation to conditions much different than those represented by our data and applications to individual species are discouraged.

The coefficients from Table 2 can be used to plot predicted success of different kinds of translocations as a function of continuous variables such as the number released. We present an example for a threatened, endangered, or sensitive bird (Fig. 1).

This exercise (Fig. 1) illustrates that the increase in success associated with releasing larger numbers of organisms quickly becomes asymptotic. Releases larger than 80 to 120 birds do little to increase the chances that a translocation will be successful for this particular set of conditions. The asymptotic property is consistent across other classifications of the data but the inflection point varies. For large native game mammals the asymptote is reached at releases of 20 to 40 animals with a concurrently higher predicted success.

The asymptotic property of the association of translocation success and number released (Fig. 1) is consistent with theoretical predictions (13) and analytical treatments (26) that suggest a threshold population size below which extinction is likely, primarily due to chance events affecting birth and death of individuals. The existence of the inflection (Fig. 1) is also consistent with the prediction of a threshold density below which population social interactions and mating success are disrupted (27), again leading to diminished population viability.

The coefficients from Table 2 and relationships presented in Fig. 1 can be used to assess alternative strategies. Suppose 300 threatened and endangered birds are available for a translocation program and they must be released during a 3-year time frame. Further suppose that two potential translocation areas are available within the core of the species historical range. If the goal of the translocation is to establish at least one geographically disjunct population to reduce the risk of catastrophic loss of the species, how should the birds be distributed between the two potential translocation areas to minimize the probability that both translocations will fail?

If both release areas have excellent habitat quality, and the areas are independent, the answer is obvious. The birds should be divided between the areas. The coefficients from Table 2 allow us to estimate the probability that a single release of 300 birds will fail (1.0 minus probability of success) is 0.257. Two releases of 150 birds each have individual probabilities of failure of 0.312. The probability that both will fail is $0.312 \times 0.312 = 0.097$; substantial gain is achieved by splitting the birds between areas.

If we complicate the picture and say that one potential area has excellent habitat quality and the other has only good habitat quality; we see that it remains slightly advantageous to split the birds between areas. Predicted probabilities of failure are 0.312 for excellent and 0.698 for good habitat, respectively. The probability that both translocations will fail is $0.312 \times 0.698 = 0.218$ compared to 0.257 for putting all birds in a single excellent habitat quality area. In this example, slight advantage to splitting the translocated birds between areas is maintained down to a total release of 40 birds. However, with so few birds released the probability that both translocations will fail is increased to about 0.42.

The model coefficients in Table 2 may be used to evaluate other scenarios. For example, given two alternatives, should a given number of birds be released in good habitat quality in the core of the historical species range or in excellent habitat quality on the periphery or outside the historical range? Good habitat quality in the core of the range is the better choice regardless of the number of birds released. This suggests that the physiological amplitude of a species may influence local population viability.

Enhancing the Chances of Success

Without high habitat quality, translocations have low chances of success regardless of how many organisms are released or how well they are prepared for the release. Active management is required. Limiting factors must be identified and controlled and assurances of maintenance of habitat quality obtained prior to translocation.

Identification and retention of adequate habitat will require a combined species and ecosystem approach. Ecological information will be necessary to identify critical life history traits, factors determining habitat quality, species interactions, and minimum

Table 2. Stepwise logistic regression (24) model coefficients for predicting probability $[P=1/(1+e^{-x})]$ of success of intentional introductions or reintroductions (translocations) of native birds and mammals in Australia, Canada, Hawaii, New Zealand, and the United States between 1973 and 1986; x is the sum of applicable coefficients for categorical variables plus the applicable coefficient times the value of continuous variables. The model is based on 155 translocations; 100 were of birds and 55 were of mammals. Data were obtained from a survey conducted in 1987 (15). The stepwise procedure was run at the $\alpha=0.10$ level for entry of terms and the $\alpha=0.15$ level for removal of terms. Probability of larger test statistics for the model were χ^2 , P=0.90 (24); Hosmer-Lemeshow χ^2 , P=0.121 (24); Brown's χ^2 , P=0.537 (24). The model correctly classified 81.3% of observed translocations based on a cutpoint of 0.50 in predicted probability of success.

Variable	Coefficient (SE)
Threatened, endangered, or sensitive species Native game	-1.418 (0.738) -0.972 (0.253)[1]* 0.972 (0.253)[1]
Birds Mammals	-0.919 (0.374)[6] 0.919 (0.374)[6]
Release area habitat Excellent Good Fair or poor	1.681 (0.438)[2] 0.053 (0.314)[2] -1.734 (0.450)[2]
Release area Core of historic range Periphery or outside	1.028 (0.267)[3] -1.028 (0.267)[3]
Early breeder, large clutch Late breeder, large clutch	1.080 (0.355)[5] -1.080 (0.355)[5]
Log(number released) Program length (years)	0.887 (0.405)[7] 0.181 (0.074)[4]

^{*}Numbers in brackets represent order of entry.

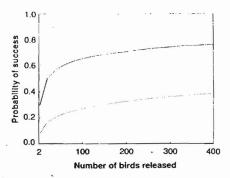


Fig. 1. Predicted probability of successful translocation as a function of the number of animals released during a 3-year period in the core of the historic species range in either excellent (solid line) or good (dashed line) habitat quality for a threatened, endangered, or sensitive bird species that first breeds at 2 years of age or more with average clutch size

of three or less. Probabilities are based on stepwise logistic regression model coefficients (Table 2).

habitat fragment size (28). Regional approaches to maintaining diversity (29) will be essential to ensure that existing species and habitat assemblages are identified, their interactions are understood, and remnant habitats are protected. The latter approach may ultimately reduce the number of species that require translocation if it enhances understanding of the effects of habitat fragmentation on persistence of multiple disjunct populations.

We may reduce the need for and increase the success of translocations if we can improve our ability to identify potentially tenuous situations and act before we are faced with a rescue. Simulation modeling (28, 32) of the behavior of small populations of species or of groups of species with similar reproductive strategies can provide guidance for establishing minimum population and vital rate goals. Simulations will be most productive if set in a regional context that addresses the interaction among metapopulations and the spatial relation among reserves or potential release sites (28).

The asymptotic nature of the relation between translocation success and number of animals released emphasizes the point that releasing large numbers of animals does little to increase the success of translocations. Lack of demonstrated success after translocating large numbers of animals is cause for reevaluating other variables associated with success.

The asymptotic levels do suggest that there is a minimum number of animals that should be released. Because longer translocation programs are more successful (Table 2), the minimum number may be released over several years if insufficient animals are available for a single release. Captive rearing programs that are focused on translocation should have the goal of establishing multiple self-sustaining populations so they can provide sufficient animals over a number of years and increase the success of these expensive (2, 3) programs.

Those planning translocations should adopt rigorous data recording procedures (19, 30). Details of translocation attempts should be assembled in a database. It is critical that both failures and successes be adequately documented. Permit-granting agencies may need to assume the role of ensuring that adequate records are kept so the database can be increased and predictability of success enhanced.

Because of the low success of translocations of small numbers of endangered, threatened, or sensitive species, even in excellent habitat quality, it is clear that translocation must be considered long before it becomes a last resort for these species—before density has become low and populations are in decline. Both these traits are associated with low chances of successful translocation. In addition, obtaining sufficient numbers of animals to achieve reasonable chances of success may be impossible. The greatest potential for establishing satellite populations may occur when a candidate population is expanding and numbers are moderate to high. These conditions are the ones that tend to make endangered species biologists relax; our analysis suggests that these conditions may point out the time for action.

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 We used standard procedures (31). The general survey covered 3 years selected randomly (1974, 1979, 1981) and asked for the total number of translocations by group (such as game hirds). It was sent to the heads of wildlife group (such as game birds or nongame birds). It was sent to the heads of wildlife management in conservation organizations; 93% of 81 distributed questionnaires were usable. The two detailed surveys asked 52 questions about specific translocations. These were sent to conservation organizations and to curators of zoos. The threatened, endangered, and sensitive species survey was intended to census all . work between 1973 and 1986 and was sent to 350 people; 85% replied. The native game survey obtained a random sample of translocations conducted in 1983 and 1984 and was sent to 65 organizations in North America; 94% replied. In both cases, some respondents reported that no translocations were conducted. A total of 240 detailed surveys describing 72 threatened, endangered, or sensitive species and 176 surveys on 18 native game species were received. Of these, 198 were classed as successful (self-sustaining population established) or not (translocated animals

declined and disappeared or declined but were still present) by respondents and could be used in contingency table analyses; 155 were useable for multivariate

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25. Potential species bias in results of analyses was evaluated by deleting the dominant (30% of observations) species (wild turkey, Meleagris gallopavo) and reanalyzing. Only 1 of 11 univariate analyses (reproductive traits) changed because of the deletion. For multivariate analyses, the model without turkeys included the exact same set of variables as the all species case, the sign of coefficients remained the same, and the magnitude of coefficients was comparable.

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KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 14 DISEASE

DISEASE AND CONSERVATION OF THREATENED SPECIES

Report of A Working Group Meeting

28-29 May 1991

National Zoo, Washington, D.C.

Arranged by CBSG/SSC/IUCN in collaboration with AAZPA, AAZV and VSG.

Supported, in part, by a grant from AAZPA

8 October 1991

Introduction

There has arisen, in the captive breeding and the conservation communities, a concern about the risk of diseases acquired in captivity being introduced into wild populations with the release or reintroduction of captive held, and captive-bred wild animals. There is also concern that diseases endemic in wild populations may adversely affect released animals, jeopardizing the entire effort. Disease risks need to be addressed in the planning of any captive breeding release/translocation program so that appropriate pre- and post-release health monitoring procedures can be developed, thereby reducing the potential on the released and native populations.

Disease, whether induced by viruses, procaryotes, or eucaryotes has long been recognized as an important selective factor in the evolution of all organisms. Mechanisms for recognition and defense against invasion by foreign organisms and mechanisms for the repair of damage are prominent in vertebrates and present in all eucaryotes. The challenges of disease may sometimes be the most powerful evolutionary selection forces acting on all life forms.

A general lack of data or information on (1) the incidence, distribution and risks of disease in captive populations, (2) the distribution and incidence of disease in wild populations, (3) effective quarantine requirements, and (4) detection and monitoring of disease, has resulted in a lack of a working database for informed risk assessment.

In an attempt to clarify the scope of the problem, a disease working group was formed, comprised of representatives from the following affiliations or institutions: American Association of Zoo Veterinarians, Association of Avian Veterinarians, American College of Zoological Medicine, American Association of Zoological Parks and Aquariums, Captive Breeding Specialist Group SSC/IUCN, Center for Reproduction of Endangered Species, Desert Tortoise Recovery Team, IUCN Veterinary Specialist Group, Pathologists, USFWS National Wildlife Health Research Center, University of Washington Veterinary College, Wildlife Disease Association, Zoological Society of London.

This working group meeting defined the following issues and recommended that:

- A. Events be defined that may lead to potential situations for disease spread and instances described where disease transmission has occurred between populations. There is a need to fund a short-term project to assemble the literature and anecdotal information on such events
- B. Information on disease processes in captive collections needs to be collected in a central location. There is an immediate need to fund the further development of MEDARKS for use by zoos as a standard record system and for a central database
- C. Information on disease processes in wild populations needs to be collected on a current basis, assessed and monitored, and maintained in a central location. An agency and mechanisms to accomplish this task need to be identified.

- D. Disease diagnosis has a central role in monitoring and assessment. Needs, limitations, current capabilities and future directions of disease diagnosis were outlined. Specific research and development needs were identified to utilize current technology to enhance our diagnostic capabilities
- E. Effective quarantine procedures to prevent the spread of diseases between populations is essential. Protocols will need to be developed on a taxon, project, and geographic basis
- F. Research resources available to further study disease processes and transmission in exotic species are limited. More resources are needed for targeted research to enhance our knowledge
- G. The working group recommended that an international symposium be held to further discuss and explore the issues at hand and to begin drafting preliminary guidelines for the recognition, assessment and long-term monitoring of infectious disease processes and their impact on the conservation of captive and wild populations.

A. Disease Event Categories, Potential Problems, and Examples

- 1. Zoo to zoo animal movements (local and global) and zoo to private sector and private sector to zoo animal movements
 - a. Regulatory inconsistencies of diagnostic screening (e.g. tuberculosis in non-domestic hoofstock)
 - b. Lack of uniformity of preshipment procedures and quarantine (e.g. screening for chlamydia, salmonella, parasites; vaccinations and other preventative procedures, etc.)
 - c. Lack of adequate transfer of medical records with animal movements (e.g., health certificate and medical history do not always accompany animal)
 - d. Disease exposure during transportation (e.g., canids contracting viral diseases during transport; potential exposure during off-loading or zoonotic exposure)
 - e. Lack of recognition of specific transmissible diseases in a collection prior to designated SSP moves (e.g., Herpes in many species, FIP, TB, etc.)
 - f. Permanent identification of each animal (tattoos, bands or transponders)
 - g. Lack of awareness and routine screening for potential hereditary defects and diseases

2. Translocations

- a. Contamination of naive population by infected animals and vice versus. (e.g., Leptospirosis in black rhino)
- b. Lack of recognition of specific transmissible diseases in the old and new environment prior to designated moves (e.g., parasites, canine distemper in black footed ferrets)

- c. Appropriate long term monitoring of the health status of both populations
- d. See 1a, 1b, 1d, 1f, 1g
- 3. Supplementation of Wild Populations by translocation of individual animals.
 - a. 1f, 1g, 2a, 2b, 2c, 2d.
- 4. Supplementation of wild populations by utilizing artificial breeding techniques to enhance genetic diversity
 - a. Determine health status of gamete donors and recipient
 - b. Determine possible diseases transferred by genetic material (e.g., FMD, Brucella, viruses.)
 - c. 1f, 1g, 2d
- 5. Supplementation of wild populations with captive animals
 - Prior to release, determine health status of the captive animals and the receiving population, and other species (including domestic animals and humans) in the ecosystem (e.g., TB, Pasteurella, lung worms in Arabian Oryx)
 - b. 1a, 1d, 1f, 1g, 2a, 2d.
- 6. Supplementation of captive population with wild populations by utilizing artificial breeding techniques and/or through individual animals
 - a. 1f, 1g, 4a, 4b, 5a, 5b, 2d.
- 7. Introducing captive animals into suitable ecosystems
 - a. Predict the disease impact of the animal on the existing resident species (including domestic and humans) and the reverse
 - b. 1a, 1b, 1d, 1f, 1g, 2d.
- 8. Introduction of captive animals to repopulate an historic ecosystem
 - a. Prior to release, determine health status of the captive animals and the receiving population, and other species (including domestic animals and humans) in the ecosystem (e.g., meningeal worm in cervids)
 - b. 1a, 1b, 1d, 1e, 1f, 1g, 2a, 2c, 2d,
- 9. Rehabilitation of wild and confiscated individuals with return to the wild habitat, be it at or distant from the original collection point. (Pancake Tortoises, Monk Seals)
 - a. 1a, 1b, 1d, 1f, 2a, 5a (e.g. confiscated Pancake Tortoises, Monk Seals)

- 10. Private sector and agency animal release programs and/or escapes, (including native and non-native species) in their home range or an appropriate or inappropriate ecosystem, (e.g., Desert Tortoises)
 - a. acknowledgment of our inability to always control and monitor the impact of these events.

11. Research Resources

a. Identify key personnel who have expertise with particular species and/or disease problems.

b. Obtain overviews of research resources from other organizations(e.g. AAZV, ACZM, WDA, AAV, etc.)

B. Lack of Biomedical Data Collection Across Captive Collections

Problem: Critical medical information affecting decisions that concern the movement of animals is currently limited.

- There are no universally used standardized programs of biomedical data collection (clinical and pathology records) in captive collections. Existing Programs: a. medARKS;
 b. Individual zoo computerized record keeping system; c. Individual zoo handwritten record keeping systems; d. No medical records or scanty medical records
- 2. Within existing programs there is limited centralized processing of collected data between institutions. Existing Programs: a. ISIS (clinical pathology, pathology codes); b. Studbooks, SSPs and TAGs; c. AAZV (infectious disease committee.); d. Surveys performed by an individual with a particular disease or species interest
- 3. Priorities: a. Identification and incidence of infectious diseases that are affecting the living collection; b. Identification and incidence of infectious diseases that are causing mortality in captive collections; c. Standardization of data collection between institutions; d. Centralization of collected data; e. Methods of data availability

4. Recommendations

- a. SSPs and TAGs should have veterinary advisors (medical, pathology)
- b. Gathering of biomedical information should begin with species that have studbooks, SSPs or TAGs
- c. Develop a task force comprised of veterinary advisors, ISIS and medARKS representatives, other knowledgeable groups and individuals to develop a standardized format for data collection, centralization and distribution. This task force should be sanctioned and given high priority and funding by AAZPA in concert with other groups.

C. Collection of Information on the Health of Captive Species

For most endangered species, a centralized medical comparative data base does not exist. Developing an epidemiological data base is the foundation for comparison of disease risks in captive and wild populations, and translocations between and within each. Within the captive community, generation of such a data base should be given top priority and instituted via the following steps:

- 1. A veterinary advisor should be appointed to each regional captive management plan (e.g., SSPs, EEPs, etc.,). Such advisors should review all mortalities annually, evaluate the incidence of disease in the living population, and make recommendations regarding anesthesia, the prevention and monitoring of disease. Data collection should be standardized. An advisor should identify areas that require further research and assist in the identification of interested researchers and centralized facilities. Cooperation of regional management program veterinary advisors should take place through the auspices of the CBSG, including the distribution of annual regional reports for each species.
 - a. CBSG should petition SSP through this report and other means to effect the addition of veterinary advisors to all SSP Committees.
 - b. AAZV should also effect a similar petition and assist in the identification of interested veterinarians.
- 2. For each species, the Veterinary Advisor should supervise the establishment of centralized biomaterial (sera/tissue) banks to aid present and future research. These banks should be established in cooperation with ongoing projects.
 - a. Letters of support from CBSG and AAZV as above.
 - b. Identification of central funding resources.
 - c. Commitment of directors of SSP institutions to make not only funding commitments (e.g., shipment costs of materials to the central banks), but also the manpower commitments for increased participation in such programs on the individual and supervisory levels (e.g., time for veterinarians to coordinate these activities and attend related meetings).
- 3. Centralized data banks, such as MedARKS should be encouraged, and further effort should be made to design appropriate software for these programs (such as was done with the orangutan medical management survey similar studies with black lemurs and elephants are in progress).
 - Encourage more rapid development of MedARKS, in particular, rapid development of the text medical record keeping system that would allow for the evaluation of medical problems in the living population.
 - b. request that all medical data be submitted to the regional program Veterinary Advisor in MedARKS format, if not in the program itself.

- 4. Regional program veterinary coordinators should be included in any review evaluating disease risks in the reintroduction of captive species.
- 5. Additional contact and cooperation with the private community holding endangered species should be encouraged by:
 - a. Identifying private holders that are listed in studbooks.
 - b. Veterinary contact with holders of key species.
 - c. Contact with private interest groups.
 - d. Dissemination of information through lay publications.

D. Wild Population Concerns

All "translocation" activities have the potential to adversely impact wild populations. Generally, there is a paucity of information pertaining to the existence of diseases in a habitat, and if the data does exist it is difficult to assemble. Therefore, before any translocations occur, the following should be considered:

- 1. There are no universally used standardized programs of biomedical data collection (clinical and pathology records) for wild populations. Existing Programs: a. USFWS National Health Wildlife Laboratory; b. Individual national record keeping system; c. Individual regional, state and local record keeping systems; d. No international databases or systems except for diseases of domestic animals (FAO).
- 2. Translocation guidelines should apply to all species as resources are available.
- 3. Governments should identify or assign and agency or individual to serve as a central information source and central repository for disease related information. This office should be responsible for promoting public awareness and distribution of the guidelines.
- 4. During the planning of a translocation project, all interested parties should be assembled to discuss disease concerns, in relation to the entire project.
- 5. Disease related questions (handout) should be answered with regard to the prevalence of agents of concern in a habitat and potential impact on endemic species. a. This should be done after review of pertinent literature and diagnostic databases; b. Consideration should be given to undertaking significant specific surveys or monitoring efforts to address unanswered questions.
- 6. The benefits to the species should be considered with respect to the potential uncontrollable disease risks: a. An individual or agency should be designated to make the final decision.

7. If a decision is made for a translocation, consideration should be given to establish a monitoring program for both the introduced animals, the endemic population and other ecosystem components.

E. Quarantine Considerations for Reintroduction Programs as a Component of an Overall Health Screening Procedure

There is a recognized need and obligation to develop a Model Procedures Manual/Guidebook to address infectious disease-related issues in the release of captive wildlife. This document should include advice on a number of basic procedures including general standards for quarantine and diagnostic test which will probably be applicable at the taxon level, such a document has been started by the AAZPA (attached). It is understood that quarantine is one of several components of an overall health screening procedure to prevent the transfer of infectious diseases to various animals in the ecosystem where the reintroduced animals are released. It should be also recognized that the type and length of a quarantine is dependant upon: 1- species 2- disease concerns 3- facilities available. There are documented situations where a quarantine had a negative effect on the animals (e.g. introduction of Gould's Wild Turkey from Mexico to Arizona where the USDA required quarantine resulted in self-destruction of the bird).

For an effective quarantine the medical advisors must be aware of the infectious diseases of concern for this species and /or diseases that the animals may have been exposed to while in captivity. This information must be derived from a systematic gathering and review of medical and pathology data generated on the species while in captivity. The regulatory and unofficial concerns of the country receiving the animals must also be known and addressed.

The quarantine period will serve as a time to collect and process the necessary samples from these animal to assure their health status and hopefully detect animals who may be incubating or carriers of infectious diseases of concern. The reliability of the testing procedures is a concern of medical advisors and has been addressed elsewhere.

The quarantine process will occur on several levels and may have varied functions at each level. The first level of quarantine occurs at the captive animal's home institution. It may also be necessary to collect the animal at a central location prior to shipment to their final destination and it will be necessary to continue and possibly augment the quarantine procedure. The final area of quarantine will occur in the area of reintroduction where appropriate testing will also occur.

The standards of the quarantine should be guided by the following concepts:

- 1. Decisions should be made on pre-entry vs post-entry quarantines. Usually both are needed.
- 2. Quarantines by definition should be all-in/all-out.
- Quarantines by definition should isolate the animals from known routes of exposure for the primary diseases and parasites of concern, and/or treatments of animals in quarantine should be conducted to remove diseases or parasites.
- 4. Quarantines must be both general and specific. During the quarantine period, any abnormal health condition must be investigated and documented. In addition, specific testing required to document freedom of disease or parasites in question should be conducted (serology, culture, blood smears, fecals, ectoparasite infections, etc.)
- 5. Whenever possible, length of pre-entry and post-entry quarantine should be longer than incubation periods of any of the acute infectious diseases or parasites in question.
- 6. Freedom from a specific disease or parasites in the source population, when adequately documented, should be considered as an acceptable alternative to testing of animals in quarantine when such testing may be overly harmful to the animal or if no testing methods are available.
- 7. Quarantine standards for translocation of wild species should be formulated with consideration of current standards for the same potential disease problems in domestic animals so that wildlife restoration programs are not burdened with unreasonable restriction.
- 8. Prior to initiating a quarantine, a decision must be reached regarding the disposition of animals that test positive. In particular, whether entire groups of animals will be disqualified if one animal is positive.

F. Diagnostic Capabilities

- Summary of the Problem
 Limited resources available to evaluate samples and interpretation of the data.
 - a. Limited facilities;

- b. Lack of a priority list of high risk, low risk and undefined diseases. Define list of realistic goals in terms of disease diagnosis and captive management.
- c. Limited diagnostic reagents available for making disease diagnosis.
- d. Lack of quality assurance programs at the laboratory level.

2. Solutions

- a. For limited facilities
 - 1) List of currently available labs to do wildlife diagnosis
 - 2) Support the development of wildlife disease centers with specialty areas.
 - a) Reptiles Florida
 - b) Avian Wisconsin
 - c) Cooperation between universities and zoological parks and aquariums San Diego and Washington State University
 - 3) Support quality control programs
- b. Prepare a priority list through the various SSP groups
- c. Improve the quality of diagnostic reagents via biotechnology
- d. Standardized list of sample selection via handouts and workshops.
- e. Increase the validity of laboratory interpretation by increasing sensitivity and specificity. This increased validity will increase compliance of veterinarians and biologists working with SSP groups.

3. Implementation and Interactions with Other Working Groups

- a. Prepare directory of currently available diagnostic laboratories.
- b. Recommend use of a letter to be sent to Colleges of Veterinary Medicine inquiring about interest in developing centers for wildlife disease management. Letter also to biotechnology centers stating our needs. Request listing of contact individuals within each institution interested in wildlife disease. Also need to send letter to AVMA.
- c. Request the top 5 diseases from each SSP group. Request a report on causes of mortality and morbidity from each SSP group.
- d. Bring together individuals involved in wildlife disease/conservation with researchers in biotechnology. This would be best achieved through a meeting.
- e. Need to identify a person or persons within each SSP group to develop a handout for collection and handling of biologic specimens for evaluation. This should de done in consultation with a contact person in the lab receiving the samples.

Essentially there would be a brochure for each of the SSP programs developed.

- f. Put together a list of papers in the literature that are relevant to the diseases of concern to the SSP groups. Need to keep this file up to date. Needs to be a centralized repository possibly Minnesota. Needs to be an active computerized file. This file would center on diagnostic tests and infectious diseases.
- g. Quality assurance routine test checks between various laboratories. Need to establish serum and tissue banks for various specimens.
- h. Need to send out letter to universities inquiring about existence of various tissue/serum banks.

G. International Symposium

The working group recommended that an International Symposium be held to assemble current and state-of-the-art information on the past, present and future impact of infectious diseases as they relate to the captive management, introduction, reintroduction and supplementation of populations of captive and free-roaming species. There has not been a symposium on these topics for 10 years. One goal of the symposium is to generate guidelines to be used by captive and free ranging wildlife managers in an attempt to minimize the spread of human and captivity induced disease events.

Title: Implications of Infectious Diseases for Captive Propagation and Reintroduction Programs of Threatened Species.

Outline of Sessions

- 0. Introduction to Problem
- 1. Review of translocations: rationale and types; reintroductions; translocations
- Historical survey of disease problems associated with releases; Sections on mammals, birds, reptiles, amphibians, freshwater fish, marine vertebrates (fish, reptiles, mammals).
- 3. Investigation, monitoring and surveillance of disease in captive animals
- 4. Investigation, monitoring and surveillance of disease in free-ranging animals
- 5. Interspecies transmission of infectious agents
- 6. Emerging infectious diseases
- 7. Future thrusts in diagnostic technology
- 8. Information and data collection systems
- 9. Impact of infectious disease on population dynamics

- 10. Predisposing factors to infectious diseases: genetic, immunologic, nutritional
- 11. Economic considerations of monitoring and screening programs
- 12. Vaccination and prevention
- 13. Government and international interactions
- 14. Planning and risk assessment for release programs

We have suggestions for session leaders (chair persons). Each session would include a few papers and a discussion period. There would be poster displays and workshops (e.g., informatics, diagnostics).

The suggested symposium sessions originated from the issues identified during the working group. Sessions will expand on these issues by drawing on international experts in a particular field. Proceedings from the symposium will be published in such a manner so that they are universally available to those most in need of the information. This will be accomplished by publishing the proceedings in an internationally recognized journal.

Disease Working Group Meeting Participant List

Mitch Bush Dept of Animal Health, National Zoo Washington, D.C. 20008 Ph=202-673-4793; Fax=202-673-4733

Joshua Dein USFWS National Wildlife Health Research Center 6006 Schroeder Road Madison, WI 53571 Ph=608-271-4640; FTS=364-5418; Fax=same

Scott Derrickson NZP Conservation and Research CTR Front Royal, VA 22630 Ph=703-635-6510; Fax=703-635-6551 Jim Evermann
Dept Vet Clinical Med/Surg
College of Vet Med
Washington State Univ
Pullman, WA 99164
Ph=509-335-9696; Fax=509-335-7424

Elliott Jacobson J-126,HSC, College of Veterinary Medicine University of Florida Gainesville, FL. 32610 Ph=904-392-22; 392-4751; Fax=071-392-3766

James K. Kirkwood
Department of Veterinary Science
Institute of Zoology
Zoological Society of London
Regent's Park, London NW1 4RY
Ph=071-722-3333 ex 870; Fax=071-483-4436

Eric Miller
St. Louis Zoological Park
1 Government Drive
Forest Park
St. Louis, MO 63110
Ph=314-781-0900 ext. 277; Fax=314-647-7969

Dick Montali, Dept of Pathology, National Zoo Washington, D.C. 20008 Ph=202-673-4869; Fax=673-4660

Victor Nettles SCWDS, College Vet. Med Univ. of Georgia Athens, GA 30602 Ph=404-542-1741; Fax=404-542-5743 Ulie Seal CBSG 12101 Johnny Cake Road Apple Valley, MN 55124 Ph=612-431-9325; Fax=612-432-2757

Michael Worley CRES, San Diego Zoo PO Box 551 San Diego, CA 92112 Ph=619-231-1515 ex.14448; Fax=619-557-3959

Susan K. Wells Audubon Park Zoo 6500 Magazine St New Orleans LA 70118 Ph=504-861-5109; Fax=504-866-0819

Peregrine L. Wolff
Minnesota Zoo
13000 Zoo Blvd
Apple Valley, MN 55124
Ph=612-431-9361; Fax=612-432-2757

KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 15 TRANSPONDERS



Captive Breeding Specialist Group

Species Survival Commission
IUCN - The World Conservation Union
U. S. Seal, CBSG Chairman

TRANSPONDERS

C.B.S.G. Working Group on Permanent Animal Identification

Report on Transponder System Testing and Product Recommendation: A Global Standard for Zoo and Aquarium Specimens.

BACKGROUND

Transponders offer a technology for unobtrusive permanent individual animal identification applicable across nearly all vertebrates and some invertebrates. Registration of this number with ISIS provides the world's zoos with an important technique for following individual animals throughout their life span which is essential for scientific management of animal populations in captivity. These and other needs prompted the formation of an international working group, at the CBSG meeting 25-26 August 1989 in San Antonio, to assemble and evaluate information on available technologies.

This group reported back to the CBSG meeting in Copenhagen and indicated that there were several products available with apparently different capabilities, availability, and costs. A copy of the report and recommendations from the meeting was distributed in the report from the meeting and summaries were provided in the CBSG Newsletter (Vol. 1, Numbers 2 and 3). These products appeared to have different capabilities and to be incompatible requiring their own readers. The assembled participants (140 people from zoos in 24 countries) agreed that it was desirable to choose one for recommended use by the entire international zoo and aquarium community. The following recommendations were adopted and transmitted to the international zoo and aquarium community (1) that all zoos and aquariums agree to use the same type of transponder, (2) that the final choice be delayed until the working group made its final report, and (3) that the international working group compare and test the different devices and recommend a preferred choice by the end of January 1991. This recommendation and the report, presented here, would then be printed in the regional zoo Newsletters and the first 1991 issue of the CBSG Newsletter.

REPORT

Introduction

At the CBSG meeting in Copenhagen, Denmark (15-16 September 1990), a report was presented on the applications and standardization of transponders for permanent identification of non-domestic vertebrates including mammals, birds, reptiles, amphibians and aquatic species. Previous reports had addressed issues such as central registration, medical concerns, costs, and limited read-ranges. However, indications of a changing technology, uncertainty concerning international availability, differences in standards, and a lack of consistent information available to the Working Group at the time did not allow a recommendation as to which system should be selected for use by the international zoo and aquarium community.

As a result of this report the CBSG, at the Copenhagen meeting, then recommended and urged all concerned parties to postpone their selection of a specific transponder system until the competing systems could be independently evaluated. This evaluation was to be completed and a report provided by the end of January 1991. This side-by-side evaluation, conducted by members of the Working Group, has been completed and a recommendation can now be made.

Criteria and Methods

The criteria used for evaluating the systems were:

- 1) Product performance (read range) under a standard set of conditions.
- 2) International commercial availability by January 1, 1991.
- 3) International distribution and availability for the tests.
- 4) Costs including acquisition and preparation of the transponders for use and cost of the readers.

In addition to the findings listed above, several other factors were considered by the Working Group:

- 5) The vast majority of specimens to receive transponder implants will be of a size in which medium (3 x 18mm) and large (3.5 x 29mm) implants would not be acceptable. Therefore, product choice should be based on the performance and price of the small size (approximately 2 x 11mm) transponders.
- 6) Most previous experience with transponders has been based on bulk-packed implants which were sterilized by the user, and required re-use of the implanter needle. The availability of pre-packaged, sterile transponders packaged in needles will result in easier and less traumatic use of these systems.

Product performance was evaluated by reading implants against a measured grid background. All systems were tested ten (10) times each and an average reading distance was calculated. In each instance, the transponders were placed flat on a table top oriented parallel to the reader. Although this orientation produced the shortest read-range for all systems, it most closely approximates the actual orientation of the transponder in most implanted specimens. System testing was recorded on videotape and copies are available upon request. The "original" transponder systems, manufactured by Destron/I.D.I. and distributed previously by Euro I.D., Biosonics, Biomedics, A.V.I.D., etc. have been included in the testing to demonstrate and document the improvements made in the development of the current systems.

Results

Table 1. Results of Transponder System Tests

<u>Manufacturer</u>	Manufacturer's Suggested Read-Range	Actual Read-Range
		Mean+S.E. #
	cm	cm
"Original"	_	
Destron/I.D.I.	5	2.6 ± .13
A.V.I.D.	5.8	5.2 <u>+</u> .14
Destron/I.D.I.		
small	11.4	5.6 ± .61**
medium	29.2	12.9 <u>+</u> .24
large	38.1	$16.4 \pm .38**$
Trovan/A.E.G.	15	10.7 <u>+</u> .38

^{**} Actual Read-Range calculated from only 5 readings due to battery problems in the reader.

[#] Statistical analysis (Repeated measures ANOVA) of the read distances for the 4 products of similar size yielded an "F"=91.3 with P<.0001. The Trovan product had a significantly greater (p<.01) read distance than the small Destron/I.D.I and the A.V.I.D. products.

Table 2. Costs of the systems.

Reader		Transponder		Availability	
Manufacturer		Plain	Sterile	Commercial	International
A.V.I.D.	\$1,250.00	8.50	N/A*	Yes	No
Destron	\$ 815.00++			No++	Yes
S		5.50	11.25	Yes	Yes
M		7.75	N/A	Yes	Yes
L		8.25	N/A	Yes	Yes
Trovan/A.E.G.	\$ 837.00	N/A	5.85	Yes	Yes

⁺⁺ New Dual Coil Reader, which was used for this test. Other, shorter distance reading readers are available. * N/A = Not available.

Recommendations

Based upon the listed criteria and the results of the testing, the CBSG Transponder Working Group has chosen the <u>Trovan/A.E.G. transponder system</u> as the recommended system for use by the world's zoos and aquariums.

Distribution of Report

These findings and recommendations are being provided through the CBSG Newsletter to national and regional zoo associations and to more than 1200 zoos and aquariums in 147 countries. It is also being provided to other regional and international agencies and organizations (S.S.C, I.U.C.N., C.I.T.E.S., E.E.C., Trade International, U.S.F.W.S., etc.) along with the recommendation that they consider adoption of similar standards.

Additional Tentative Recommendations

- 1. Registration of ID numbers of zoo and aquarium specimens needs to be done in regional central databases and in ISIS for zoos and aquariums. ARKS III allows entry of these numbers and numbers for implants from other systems.
- 2. Standardized locations of placement of the implants in different groups of animals have been suggested but need more discussion.

3. Choice of species and priorities have focused on endangered, studbook, regional management plan, and CITES listed species. Each institution will need to develop a systematic program for their installation as animals are handled for any purpose. The use of an injectable device should simplify this process. All animals shipped from one institution to another should have them installed and the ID number registered.

Availability:

The Trovan/A.E.G. system can be purchased from:

North America International Infopet Systems

31264 La Baya Drive, Suite A

Westlake Village, CA 91362, U.S.A.

Telephone:

(818) 707-9942; 800-463-6738

Telefax:

(818) 707-9947

Contact:

Lindy Harton

Europe

Euro I.D.

Grossbuellesheimer Str. 56

5350 Euskirchen 16

West Germany

Telephone:

(02251) 7 11 25

Telefax:

(02251) 7 34 88

Contact:

Joe Masin

Additional Regional distributors are being developed.

Additional Information

Copies of the previous reports and the Newsletter are available from the CBSG office.

Questions or requests for additional information should be sent to:

Dr. Evan S Blumer Fossil Rim Wildlife Center

Royal Zoological

P. O. Drawer 329

Society of Antwerp Koningin Astridplein 26

Paul van den Sande

Glen Rose, Texas 76043, U.S.A.

B-2018 Antwerpen, BELGIUM

Telephone:

Telephone:

Fax:

(817) 897-3147 (817) 897-3785

03-231-16-40

Fax:

03-231-00-18

KIRTLAND'S WARBLER

BRIEFING BOOK

SECTION 16 IUCN POLICY STATEMENTS

COLLABORATION BETWEEN SSC TAXA-BASED SPECIALIST GROUPS AND THE CAPTIVE BREEDING SPECIALIST GROUP

(Article to appear in SPECIES)

During the last five years, the degree of collaboration between the many taxa-based Specialist Groups within the SSC and the Captive Breeding Specialist Group (CBSG) has increased considerably. There are now two important ongoing programmes in operation that require close collaboration between CBSG and the other Specialist Groups:

- Conservation Assessment and Management Plan (CAMP) Workshops, a product of which are Global Captive Action Plans (CAP)
- 2) Population and Habitat Viability Assessment (PHVA) Workshops.

At its meeting in Gland on 23-24 November 1991, the SSC Steering Committee strongly endorsed the further development of both of these programmes. The Steering Committee also established some working procedures to assist Specialist Groups in their collaboration with each other. The purpose of this article is to explain the background to both programmes, since many SSC members are probably not yet informed of the various possibilities.

Conservation Assessment and Management Plans and Captive Action Plans:

As populations of many taxa are reduced and fragmented in the wild, more intensive management becomes necessary for their survival and recovery. This intensive management to an ever increasing extent includes, but is not limited to, captive breeding. Conservation Assessment and Management Plans are needed to provide strategic guidance for application of intensive management techniques to threatened taxa. CAMP's are conducted as collaborative ventures of the taxa-based Specialist Group and the CBSG.

The CAMP process reviews the wild and captive status of all taxa in the taxonomic group under consideration. For this purpose, the process utilizes information from SSC Action Plans that may already have been formulated by the taxa-based Specialist Groups. Where such Action Plans do not yet exist, the CAMP process produces the necessary assessment of status and prospects to permit formulation of Global Action Plans for both *in situ* and *ex situ* efforts.

Based on these assessments, the CAMP provides a set of recommendations about which taxa are in need of which kinds of intensive management attention. The kinds of attention include:

- (A) Population and Habitat Viability Assessment and Conservation Management Plan (PHVA/CMP) Workshops.
- (B) Intensive (captive-type) protection and management in the wild.
- (C) In situ and ex situ research where the captive community can reasonably assist: e.g., taxonomic clarification, some survey support.
- (D) Captive propagation programmes that sooner or later could be linked to interactions with wild populations.

The CAMP process has also provided an opportunity to test the applicability of the Mace/Lande Criteria (Conservation Biology) for assessment of threat. The Mace/Lande Criteria are the proposed new IUCN Categories of Threat and are still under active development. The Criteria provide an estimate of the risk of extinction of taxa based on information about size, distribution, trend of their population as well as conditions of their habitat.

An important product of the CAMP process is a Global Captive Action Plan (CAP) which attempts to provide a strategic overview and framework for effective and efficient application and allocation of captive resources to conservation of the broad group of taxa of concern, i.e. an order, family, etc. CAP provide strategic guidance for captive programs at both the Global and Regional level in terms of captive breeding and also possible other support (technical, financial) for *in situ* conservation.

More specifically, CAP's recommend what taxa are most in need of captive propagation and hence which taxa in captivity should remain there, which taxa not yet in captivity should be there, and which of those currently in captivity should no longer be maintained there. For the taxa recommended for captivity, the CAP suggests an appropriate level of captive programme required in terms of demographic and genetic goals and hence size of target population to be developed. Ultimately, the CAP will also recommend how responsibilities for captive programmes might best be distributed among organized Regions of the global captive community. While captive breeding programmes are emphasized in the CAP's, the Plans also attempt (1) to identify where and how the captive community can assist with transfer of intensive management information and technology (2) develop priorities for the limited financial support the captive community can provide for *in situ* conservation (e.g., adopt-a-sanctuary programmes).

It is the intention of the SSC Steering Committee that as far as possible, Captive Action Plans be incorporated into the overall Action Plans. The CAMP process obviously facilitates this objective. Action Plans already published that do not include a Captive Action Plan component will hopefully add them as part of the continuing process of development. CAMP and CAP workshops have already been conducted for parrots, Asian hornbills, primates, felids, cervids, antelopes. Others that will occur during the next year include penguins, cranes, Australian marsupials, and canids as well as a neotropical regional follow-up for primates.

In summary, the CAMP and CAP process assembles expertise on captive and wild management under review. It provides for a rational means of assessing priorities for intensive management including captive breeding within the context of the broader conservation needs of threatened taxa. SSC Members who would like copies of existing CAMP's and CAP's can obtain them from the CBSG Office, 12101 Johnny Cake Ridge Road, Apple Valley, MN 55124, U.S.A. They are available at US \$25.00 per copy, including surface postage. (SSC members who do not have access to convertible currency can request a free copy.)

Population and Habitat Viability Assessments

Population and habitat viability assessments (PHVA's) are the enhanced versions of population viability analyses (PVA's) that have evolved as the process has been applied by the CBSG. PHVA's use computer models

(1) to explore extinction processes that operate on small and often fragmented populations of threatened taxa

(2) to examine the probable consequences for the viability of the population of various management actions or inactions.

The models incorporate information on genetic and demographic characteristics of the population and on conditions in the environment to simulate probable fates (especially probability of extinction and loss of genetic variation) under these circumstances. The primary computer programme that has been used for the modelling to date is VORTEX, which has been developed by Dr. Robert C. Lacy of the Chicago Zoological Society and a member of the SSC. VORTEX allows workshop participants to model a range of scenarios for the populations under a variety of management (or non-management) regimes. As a result of the different scenarios modelled, it is possible to recommend management actions that maximize the probability of survival or recovery of the population. The management actions may include: establishment, enlargement, or more management of protected areas; poaching control; reintroduction or translocation; captive breeding; sustainable use programmes; education efforts. PHVA's thus provide an important resource for development of comprehensive conservation and recovery programmes for threatened taxa. Moreover, while the PHVA process commences with an initial workshop, the process normally continues as the results are reviewed and refined. The process frequently entails one or more follow-up workshops.

The PHVA process is still very much under development, partly because the VORTEX programme and the models on which it is based continue to be improved, and partly because the workshops themselves are learning and evolutionary experiences. In the past year, a major improvement has been the incorporation of more habitat information into the models (hence the term PHVA).

Because PHVA's are an important step in the development of an overall recovery programme for a threatened taxa, it has been SSC policy to conduct the workshops in a range state of the species in question and only at the invitation of the appropriate wildlife agencies with management responsibility and authority.

Among the PVA's and PHVA's conducted so far are: Florida panther, Puerto Rican parrot, Bali starling, Javan rhino, black rhino in Kenya, primates of the Tana River Reserve in Kenya, bald ibis, pink pigeons, Caribbean parrots, whooping crane, and the lion-tamarins of Brazil. Copies of the reports from these PHVA workshops can be obtained from the CBSG Office, 12101 Johnny Cake Ridge Road, Apple Valley, MN 55124, U.S.A. They are available at a cost of US\$25.00 per copy which includes surface postage. (SSC members who have no access to convertible currency can request a copy free of charge.)

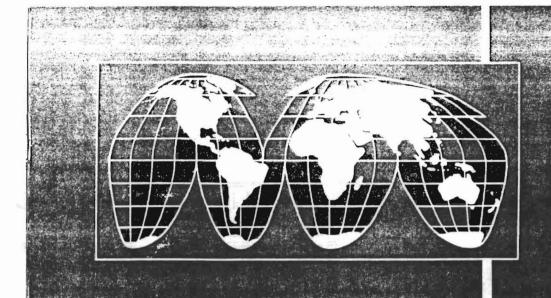
Working Procedures for the CAMP, CAP and PHVA Programmes:

- 1. Each workshop and process are conducted from the outset as a collaboration between CBSG and the appropriate taxa-based Specialist Group (and other SSC inter-disciplinary Specialist Group where appropriate).
- 2. The initiative for a CAMP and CAP can originate with either the CBSG or from the taxabased Groups, but each should involve the other before additional contacts occur.
- 3. The initiative for a PHVA workshop can originate with one or more range states, a taxabased Specialist Group, or occasionally the CBSG, but in all cases no real development

of the process occurs until or unless there is an official invitation to the SSC from the governmental wildlife agency(ies) in the range state(s).

- 4. The Specialist Groups (taxa-based, CBSG, other inter-disciplinary) and the governmental wildlife agencies should agree on the agenda, participants, location, dates, and finances for each workshop. The conduct of each workshop should also be a point of agreement, in particular there should be consensus on the chairs for the various sessions. Responsibility for each aspect of the workshop and process should be clearly assigned.
- 5. A briefing book should be prepared for each workshop. The Specialist Groups should agree on the contents of each briefing book and secure the resources for their production.
- 6. An overall editor should be appointed to prepare the report of each workshop. After each workshop, a draft report should be prepared for review. The draft report should be distributed for review to all workshop participants and to others agreed to by the parties associated with the workshop. The editor should revise the report based on feedback from this review. The final report should then be published and circulated. The Executive Office of CBSG and, where they exist, of the taxa-based Specialist Groups are available to serve as editors, advisers, and assistants for report production.

Finally, it should be re-emphasized that neither the CAMP/CAP or PHVA Workshops should be considered single events. Instead, they are part of a continuing and evolving process of developing conservation and recovery plans for the taxa involved. In nearly all cases, follow-up workshops will be required to consider particular issues in greater depth or on a regional basis. Moreover, some form of follow-up will always be necessary to monitor the implementation and effectiveness of the recommendation resulting from the workshop. In many cases a range of PHVA workshops will result from the CAMP/CAP Workshops.



Captive breeding



IUCN POLICY STATEMENT

4 September 1987

THE IUCN POLICY STATEMENT ON CAPTIVE BREEDING

Prepared by the SSC Captive Breeding Specialist Group

As approved by the 22nd Meeting of the IUCN Council Gland, Switzerland

4 September 1987

SUMMARY: Habitat protection alone is not sufficient if the expressed goal of the World Conservation Strategy, the maintenance of biotic diversity, is to be achieved. Establishment of self-sustaining captive populations and other supportive intervention will be needed to avoid the loss of many species, especially those at high risk in greatly reduced, highly fragmented, and disturbed habitats. Captive breeding programmes need to be established before species are reduced to critically low numbers, and thereafter need to be co-ordinated internationally according to sound biological principles, with a view to the maintaining or re-establishment of viable populations in the wild.

PROBLEM STATEMENT

IUCN data indicate that about 3 per cent of terrestrial Earth is gazetted for protection. Some of this and much of the other 97 per cent is becoming untenable for many species, and remaining populations are being greatly reduced and fragmented. From modern population biology one can predict that many species will be lost under these conditions. On average more than one mammal, bird, or reptile species has been lost in each year this century. Since extinctions of most taxa outside these groups are not recorded, the loss rate for all species is much higher.

Certain groups of species are at particularly high risk, especially forms with restricted distribution, those of large body size, those of high economic value, those at the top of food chains, and those which occur only in climax habitats. Species in these categories are likely to be lost first, but a wide range of other forms are also at risk. Conservation over the long term will require management to reduce risk, including *ex situ* populations which could support and interact demographically and genetically with wild populations.

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FEASIBILITY

Over 3,000 vertebrate species are being bred in zoos and other captive animal facilities. When a serious attempt is made, most species breed in captivity, and viable populations can be maintained over the long term. A wealth of experience is available in these institutions, including husbandry, veterinary medicine, reproductive biology, behaviour, and genetics. They offer space for supporting populations of many threatened taxa, using resources not competitive with those for *in situ* conservation. Such captive stocks have in the past provided critical support for some wild populations (e.g. American bison, *Bison bison*), and have been the sole escape from extinction for others which have since been re-introduced to the wild (e.g. Arabian oryx, *Oryx leucoryx*).

RECOMMENDATION

IUCN urges that those national and international organizations and those individual institutions concerned with maintaining wild animals in captivity commit themselves to a general policy of developing demographically self-sustaining captive populations of endangered species wherever necessary.

SUGGESTED PROTOCOL

WHAT: The specific problems of the species concerned need to be considered, and appropriate aims for a captive breeding programme made explicit.

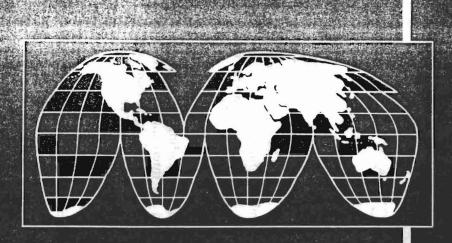
WHEN: The vulnerability of small populations has been consistently underestimated. This has erroneously shifted the timing of establishment of captive populations to the last moment, when the crisis is enormous and when extinction is probable. Therefore, timely recognition of such situations is critical, and is dependent on information on wild population status, particularly that provided by the IUCN/Conservation Monitoring Centre. Management to best reduce the risk of extinction requires the establishment of supporting captive populations much earlier, preferably when the wild population is still in the thousands. Vertebrate taxa with a current census below one thousand individuals in the wild require close and swift cooperation between field conservationists and captive breeding specialists, to make their efforts complementary and minimize the likelihood of the extinction of these taxa.

HOW: Captive populations need to be founded and managed according to sound scientific principles for the primary purpose of securing the survival of species through stable, self-sustaining captive populations. Stable captive populations preserve the options of reintroduction and/or supplementation of wild populations.

A framework of international cooperation and coordination between captive breeding institutions holding species at risk must be based upon agreement to cooperatively manage such species for demographic security and genetic diversity. The IUCN/SSC Captive Breeding Specialist Group is an approrpiate advisory body concerning captive breeding science and resources.

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Captive programmes involving species at risk should be conducted primarily for the benefit of the species and without commercial transactions. Acquisition of animals for such programmes should not encourage commercial ventures or trade. Whenever possible, captive programmes should be carried out in parallel with field studies and conservation efforts aimed at the species in its natural environment.



Research involving species at risk of extinction

La recherche en rapport avec des espèces menacées d'extinction

Investigaciones en que se usan especies en riesgo de extinción



IUCN POLICY STATEMENT DECLARATION DE PRINCIPE DE L'UICN **POSICION DE LA UICN** 14.6.89

Approved by the 27th Meeting of IUCN Council

Adoptée durant la 27e Session du Conseil de l'UICN

Aprobada durante la 27a. Reunión del Consejo de la UICN

IUCN POLICY STATEMENT ON RESEARCH INVOLVING SPECIES AT RISK OF EXTINCTION

PROLOGUE

IUCN holds that all research on or affecting a threatened species carries a moral responsibility for the preservation or enhancement of the survival of that species. Conservation of the research resource is clearly in the interest of the researchers.

IUCN recognizes that the taking and trading of specimens of threatened species are covered by international agreements and are normally included in national legislation which provides authorized exemptions for the purpose of scientific research.

Basic and applied research is critically needed on many aspects of the biology of animal and plant species at risk of extinction (e.g. those listed by IUCN as Vulnerable, Rare, Endangered, or Indeterminate) to provide knowledge vital to their conservation.

Other scientific interests may involve the use of threatened species in a wide variety of studies. Taking into account the importance of many kinds of research, as well as potential threats such species could be subject to in such activities, IUCN, after careful consideration, adopts the following statements as policy.

POLICY

IUCN encourages basic and applied research on threatened species that contributes to the likelihood of survival of those species.

When a choice is available among captive-bred or propagated, wild-caught or taken, or free-living stock for research not detrimental to the survival of a threatened species, IUCN recommends the option contributing most positively to sustaining wild populations of the species.

IUCN recommends that research programmes on threatened species that do not directly contribute to conservation of the species should acknowledge an obligation to the species by devoting monetary or other substantial resources to their conservation, preferably to sustaining populations in the natural environment.

Whether animals involved are captive-bred, wild-caught, or free living, or whether plants involved are propagated, taken from the wild, or in their natural habitat, IUCN opposes research that directly or indirectly impairs the survival of threatened species and urges that such research not be undertaken.

PROTOCOLS

In this context IUCN urges researchers to accept a personal obligation to satisfy themselves that the processes by which research specimens are acquired (including transportation) conform scrupulously to procedures and regulations adopted under international legal agreements. Further, researchers should adopt applicable professional standards for humane treatment of animal specimens, including their capture and use in research.

IUCN urges that any research on threatened species be conducted in conformity with all applicable laws, regulations and veterinary professional standards governing animal acquisition, health and welfare, and with all applicable agricultural and genetic resource laws and regulations governing acquisition, transport, and management of plants.

DECLARATION DE PRINCIPE DE L'UICN SUR LA RECHERCHE EN RAPPORT AVEC DES ESPECES MENACEES D'EXTINCTION

PROLOGUE

L'UICN estime que toute recherche sur une espèce menacée ou affectant cette espèce est moralement tenue de préserver cette espèce ou d'accroître ses chances de survie. Il est clairement de l'intérêt des chercheurs de conserver leur sujet de recherche.

L'UICN reconnaît que le prélèvement et le commerce de spécimens d'espèces menacées sont réglementés par des accords internationaux et, habituellement, couverts par la législation nationale qui prévoit des exceptions légales pour les besoins de la recherche scientifique.

La recherche fondamentale et appliquée, relative à de nombreux aspects de la biologie des espèces animales et végétales menacées d'extinction (celles auxquelles l'UICN attribue le statut Vulnérable, Rare, Menacé ou Indéterminé), est absolument indispensable et apporte des connaissances vitales pour leur conservation.

D'autres types de recherche scientifique peuvent impliquer l'utilisation d'espèces menacées pour les études les plus diverses. Tenant compte de l'importance de nombreuses formes de recherche, ainsi que des menaces potentielles que ces activités pourraient faire peser sur les espèces concernées, l'UICN, après mûre réflexion, adopte les déclarations suivantes comme ligne de conduite politique.

PRINCIPES

L'UICN encourage la recherche fondamentale et appliquée sur les espèces menacées, quand cette recherche augmente les chances de survie de ces espèces.

Lorsque, pour entreprendre des recherches ne compromettant pas la survie d'une espèce menacée, il est possible de faire un choix entre des spécimens élevés ou reproduits en captivité, capturés ou prélevés dans la nature ou vivant à l'état sauvage, l'UICN recommande l'option contribuant le plus possible au maintien de populations sauvages des espèces concernées.

L'UICN recommande que les programmes de recherche sur des espèces menacées qui ne contribuent pas directement à la conservation de ces espèces, se reconnaissant une obligation envers celles-ci, consacrent des ressources substantielles, notamment financières, à leur conservation et, de préférence, au maintien de populations dans leur milieu naturel.

Que les animaux concernés soient élevés en captivité, capturés dans la nature ou vivent libres, que les plantes concernées soient propagées, prélevées dans la nature ou se trouvent dans leur biotope naturel, l'UICN s'oppose à la recherche qui, directement ou indirectement, compromet la survie des espèces menacées et préconise de renoncer à entreprendre une telle recherche.

PROTOCOLES

Dans ce contexte, l'UICN demande instamment aux chercheurs de s'engager personnellement à s'assurer que le processus d'acquisition (y compris le transport) des spécimens destinés à la recherche, obéisse scrupuleusement aux procédures et réglementations adoptées en vertu d'accords juridiques internationaux. En outre, les chercheurs adopteront

des normes professionnelles applicables, afin que les spécimens animaux soient traités sans cruauté, notamment au moment de la capture et de l'utilisation pour la recherche.

L'UICN demande instamment que toute recherche sur des espèces menacées soit menée conformément à toutes les lois, réglementations et normes vétérinaires professionnelles applicables, régissant l'acquisition, la santé et le bien-être des animaux, et à toutes les lois et réglementations applicables, sur l'agriculture et les ressources génétiques, régissant l'acquisition, le transport et la gestion des espèces végétales.

POSICION DE LA UICN SOBRE LAS INVESTIGACIONES EN QUE SE USAN ESPECIES EN RIESGO DE EXTINCION

PROLOGO

La UICN mantiene que toda investigación sobre, o que afecta a, una especie amenazada, lleva consigo una responsabilidad moral con respecto a la preservación o mejoramiento de la supervivencia de dicha especie. La conservación de lo que es sujeto de investigación está claramente en favor del interés del investigador.

La UICN reconoce que la toma y comercialización de especímenes de la especie amenazada están contempladas en los acuerdos internacionales, y normalmente están incluídas en la legislación nacional, la que hace lugar a las exenciones requeridas cuando se trata de la investigación científica.

La investigación básica y aplicada es de una importancia crítica para muchos aspectos de la biología de las especies animales y vegetales en riesgo de extinción (como por ejemplo aquellas incluídas por la UICN en la lista de especies vulnerables, raras, en peligro, o en situación intermedia) a fin de obtener el conocimiento que es vital para su conservación.

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Pueden existir otros aspectos científicos que requieran el uso de especies amenazadas en una variedad de tipos de estudios. Teniendo en cuenta la importancia de las muchas clases de investigación, como así también las amenazas potenciales que pueden afectar a esas especies como sujetos de dichas actividades, la UICN, luego de un cuidadoso análisis, ha adoptado la siguiente posición.

POSICION

La UICN fomenta la investigación básica y aplicada sobre especies amenazadas que contibuye a la posibilidad de supervivencia de dichas especies.

Cuando se puede elegir entre ejemplares criados en cautividad o propagados, cazados o tomados de la naturaleza, o que viven en libertad, para su uso en la investigación que no vaya en detrimento de la supervivencia de una especie amenazada, la UICN recomienda la opción que contribuya de manera más positiva al mantenimiento de las poblaciones silvestres de la especie.

La UICN recomienda que los programas de investigación sobre especies amenazadas que no contribuyan de manera directa a la conservación de la especie acepten un compromiso con respecto a esa especie, destinando sustanciales recursos monetarios o de otro tipo para su conservación, preferiblemente en favor del mantenimiento de las poblaciones en el medio ambiente natural.

Ya sea que los animales utilizados sean criados en cautividad, cazados, o que vivan en libertad, o que las plantas que se utilicen hayan sido propagadas, tomadas del medio silvestre o de sus hábitat naturales, la UICN se opone a la investigación que directa o indirectamente perjudica la supervivencia de las especies amenazadas y urge a que las investigaciones de ese tipo no sean llevadas a cabo.

PROTOCOLOS

Dentro de este contexto, la UICN urge a los investigadores a aceptar la obligación personal de asegurarse que los procesos por los que se obtienen los especímenes para la investigación (incluyendo su transporte) respeten escrupulosamente los procedimientos y normas adoptados bajo los acuerdos internacionales de carácter legal. Además, los investigadores deben adoptar estándares profesionales que sean aplicables en cuanto al tratamiento compasivo de los ejemplares de especies animales, tanto en lo que hace a su captura como a su utilización en la investigación.

La UICN urge a que toda investigación sobre especies amenazadas sea llevada a cabo en conformidad con todas las leyes, normas y estándares de la profesión veterinaria que sean aplicables a la adquisición, salud y bienestar de los animales, y con todas las leyes y normas que en el campo de la agricultura y de los recursos genéticos sean aplicables a la adquisición, transporte y manejo de las plantas.

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