Population Change in the Kirtland's Warbler

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

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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 northern 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 Warbler 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 theorizing 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

METHODS

Data are available from 12 censuses of singing male Kirtland's Warblers (Mayfield 1953, 1962, 1972a, 1973a, 1973b, 1975; Ryel 1976a, 1976b, 1979a, 1980a, 1980b; Burgoyne and Ryel 1978). Mayfield actively supervised and participated in all censuses from their inception in 1951 through 1974. His initiative and far-sightedness have provided us with over a quarter-century of population benchmarks. In addition, much published information from the literature as well as original data developed by the Kirtland's Warbler Recovery Team, was utilized in this paper.

RESULTS

Recent population trends. — Since 1971, the annual census results have been 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 available 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 range.

Winter range. — Mayfield (1960) felt that the survival of both adults and fledglings was high on the breeding grounds, which leads one to suspect that most 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 to 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 to late April. Recently there have also been two curious sightings of Kirtland's Warblers in Mexico. Lane (1975) observed one (perhaps two) birds south of Veracruz on 11 November 1974 and there is a report of three birds 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 species 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	1980
Michigan Counties												
Crawford	142	52	101	101	114	88	90	95	78	74	75	93
Oscoda	103	152	48	48	47	41	35	44	59	62	71	58
Iosco	74	30	1							2	1	3
Montmorency	43	61	1									
Presque Isle	34	34										
Roscommon	4	13				1	4	2	7	2	2	4
Alcona	4											
Kalkaska	28	32					3	7	11	16	21	38
Ogemaw		114	47	49	51	35	46	51	62	40	40	46
Otsego		14	3									
Wexford				2	4	2	1	1	1			
Michigan Total	432	502	201	200	216	167	179	200	218	196	210	242
Wisconsin Counties												
Jackson										2	1	1
Ontario Counties												
Renfrew									1	1		
Quebec Counties												
Gatineau										1		
NORTH AMERICAN TOTAL	432	502	201	200	216	167	179	200	219	200	211	243

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

In the winters of 1972 and 1973, Radabaugh (1974) spent a total of 800 hours in surveying habitat and searching for Kirtland's Warblers on 11 different islands. He found only one Kirtland's Warbler, a male, which he observed on 3 different days in March, 1973 on Crooked Island. One objective of Radabaugh's studies was to evaluate the idea that worsening habitat conditions in the winter range might be responsible for the decline of the warbler population between 1961 and 1971. He noted the most profound habitat change in and just prior to the decade of interest was the lumbering of Caribbean pines (*Pinus caribeae*) successively on Grand Bahama, Abaco, and Andros islands from 1956 to 1974. In all, some 1,690 km² were logged. He suggested this activity may have contributed to the population decline. Mayfield (1975), however, counters that in most logged over pine stands reforestation progressed rapidly and substantial tracts of pine were left uncut on each of the islands. Furthermore, Caribbean pine occurs on only four of the northernmost islands. Mayfield (1972b, 1975) also notes most annotated observations have placed the birds in young or stunted broadleaved scrub, even when associated with pines or the pine like exotic Australian "pine" (*Casuarina equisetifolia*).

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

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

Bulmer (1975) has devised a statistical test for density dependence which is based on the random walk model. In a density dependent population, the ratio $R = \frac{V}{U}$ will be "small" where:

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

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

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

For the Kirtland's Warbler, if we assume the spring breeding population is twice the number of singing males counted, then R = .727. The test is $R \leq R_L$. The critical value of R_L = .543 at the α = .05 level for N = 10. Therefore this analysis suggests the population, at least at current levels, is not strongly density dependent; but 10 years of data is not a very long period from which to draw conclusions.

Hurricanes and other storms. — Milton Trautman (1979) has long believed that hurricanes during the fall migration period were responsible for decimating Kirtland's Warbler populations. He feels that a series of devastating hurricanes during the late 1920's and early 1930's were responsible for a decline in Kirtland's Warblers which he is convinced occurred during this period.

Various species of birds encountering hurricanes during migration flights have been observed to experience much displacement and considerable mortality (Cruickshank 1939; Hill 1945). Sutton (1945), however, reports that when birds were caught while feeding or resting, they were able to adjust quickly to the storm's conditions. Following passage of an October hurricane in Orlando, Florida, he found only one dead bird, a Palm Warbler

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

There were 19 such storms (Table 2) which occurred from 1951 to 1979 during the fall migration period (August 15 to October 15) in the vicinity of the Bahama Islands. Data through 1977 were from Neumann et al. (1978), while John Hope of the National Hurricane Center, Coral Gables, Florida, 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 these storms, singing male census results for 1961 were 502, some 16% above the 1951 count (432). The population did not show any increasing trends from 1971 to 1979 when only one storm occurred (1979). The decade when the warblers declined (1961 to 1971) had five storms.

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

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

TABLE 2. Hurricanes and tropical storms in the Bahama Islands, August 15 to October 15, 1951 to 1979.

Year	Number	Year	Number
1952	1 H*	1960	1 H, 2 T
1953	1 T**	1963	1 H
1954	2 H, 1 T	1964	2 H
1956	2 T	1965	1 H
1958	1 H, 1 T	1966	1 H
1959	1 H	1979	1 H

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

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

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

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

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

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

Winter is normally the dry season in the Bahamas, but some years are much drier than others. The November to April period for the 10 years from 1951 to 1960 averaged 328.2 mm. of rain. The following decade, when the warbler population declined, was decidedly drier, averaging 200.5 mm. or 40% less per year. The past nine winters have been intermediate, averaging 302.7 mm.

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

the university's AMDAHL/v8 computer), we constructed a simple model based on the number of singing males in Michigan in year t (X_1), the estimated number of fledglings produced in year t (X_2), and the sum of the Nassau rainfall in mm from November to April for years t and t + 1 (X_3) to predict the number of singing males in Michigan in year t + 1 ($\hat{Y}$). The estimated number of fledglings (X_2) was calculated by multiplying the number of males by the average number of fledglings produced per pair from field studies. In some years the average number of fledglings per pair was in turn estimated from the number of fledglings per nest.

The resultant prediction equation is: $\hat{Y} = -.05752\ X_1 + .03976\ X_2 + .09389\ X_3 + 163.89$. The significance level is .09 and the R^2 value is .6979. The actual and predicted values for 1972-1980 are shown in Figure 1. This equation is the best fit for this particular set of data, but I do not mean to imply this is a general model. Clearly it is not applicable for populations at 1951 or 1961 levels.

The partial regression coefficient for the Nassau rainfall variable (X_3) is significant at the $\alpha = .05$ level, while neither of the other two coefficients approach significance. The simple correlation matrix which was used to develop the regression equation is shown in Table 3. Nassau rainfall from November to April is significantly correlated with the number of singing

FIGURE 1
SINGING MALE KIRTLAND'S WARBLERS
ACTUAL VS. MODEL

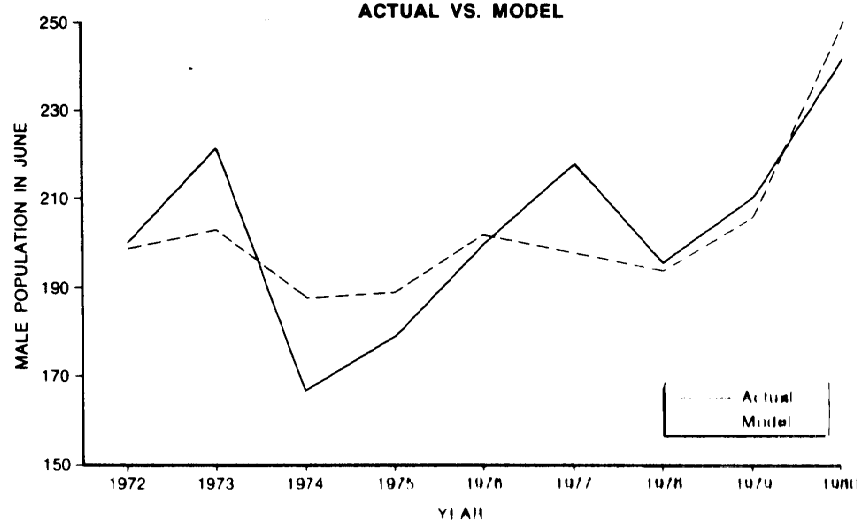

TABLE 3. Simple correlation matrix of variables used in population model.

Variable		Males year t (X_1)	Fledglings year t (X_2)	Nassau rain Nov.-Apr. (X_3)	Males year t + 1 (Y)
		Variables			
Males year t	(X_1)	1.0000			
Fledglings year t	(X_2)	-.0255	1.0000		
Nassau rain Nov.-Apr.	(X_3)	.2690	-.1813	1.0000	
Males year t + 1	(Y)	.1749	.1734	.7712*	1.0000

Significance levels:
.01 = .7977 **
.01 .05 = .6664 *

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

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

Competition. - At higher population levels, competition might well become a significant factor. Fretwell (1976, 1977, 1978) hypothesized that competition for food, both from other warbler species, particularly the Palm Warbler and Prairie Warbler (*Dendroica discolor*), as well as intraspecific competition, influenced the number of Kirtland's Warblers that survived the winter. He felt that the population was strongly density dependent and that the more birds that attempted to winter, the higher the relative mortality. Subsequent population changes did not completely support his predictions, nor did the test described above reveal density dependence at current population levels. In addition, simple correlations (Table 3) between fledglings in year t and males in year t+1, as well as males 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 ¾ 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)*.

	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 Iosco 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. Comparable data from Walkinshaw (1981) for the years 1931 through 1955 show a 25% nest parasitism and a fledgling production of 1.64 per nest. From 1957 to 1971, however, he found 75% of the nests were parasitized and an overall fledgling rate of less than one (Table 5).

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

Fledgling survival is much more difficult to evaluate. Most yearling Kirtland's Warblers apparently do not return to the colony where they were fledged (Ryel 1979a), hence, estimation of survival from banding returns is very difficult. Nolan (1978) estimated that the survival of Prairie Warbler fledglings to the following breeding season was about 32%. Roberts (1971) concluded that the first-year survival of fledglings for some "less successful" species of warblers (including Kirtland's) had to be on the order of 45% for a stable population. In most species of wildlife, the survival of young of the year is much more variable from year to year than that of adults.

As Mayfield (1960) points out, at the fledgling rates he observed in his 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 the 60% he calculated for adults.

TABLE 5. Kirtland's Warbler nesting success.

Year	Number of pairs	Number of nests	Number of Nestlings fledged per pair	per nest	Source	
1944–1957		206	1.35	.90	Mayfield	(1975)
1931–1955		28		1.64	Walkinshaw	(1972)
1957–1968		25		.64	Walkinshaw	(1972)
1969–1971		38		.92	Walkinshaw	(1972)
1972	26	32	3.35	2.72	Walkinshaw	(1981)
1973	31	34	2.97	2.71	Walkinshaw	(1981)
1974	54	63	3.35	2.87	Walkinshaw	(1981)
					Orr	(1975)
1975	32	37	3.19	2.76	Walkinshaw	(1981)
1976	30	33	2.97	2.70	Walkinshaw	(1981)
1977	29	31	2.21	2.06	Walkinshaw	(1981)

Further trials of the same sort of deterministic simulations also convinced me that either fledgling production was underestimated and/or that fledgling survival was extremely high (Table 6). The former, at least, turns out to be partially true. Early workers felt Kirtland's Warbler was single brooded (Mayfield 1960). Radabaugh (1972), however, found that if the first brood is fledged by the end of June, about 40% of these pairs may nest again. Overall, however, not many pairs attempt to rear two broods. Walkinshaw (1981) found only about 5% of the pairs he studied from 1972 to 1977 tried, while Orr (1975) in a 1974 study found 17% did. Per pair and per nest data from these studies are shown in Table 5. Of course, as with most bird species, if the first nest is destroyed, many will renest. Mayfield's (1960) data in Table 5 take this into account. Determining the true production for a given pair requires following them closely through the entire breeding season. Associated errors all tend to depress fledgling rates. Hence, actual fledgling rates per pair for early years were probably somewhat higher than studies indicated. If I had to pick a simulation which best fits the available data, it would be similar to number 5 in Table 6 which uses a 65% adult survival, a 35% fledgling survival, and 1.50 fledglings produced per pair. This results in a 60% population decline in 10 years. It is obvious that parasitism could easily have caused the observed decline.

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

TABLE 6. Effects of various survival and production rates.

Simulation	Assumptions: Annual adult survival	Assumptions: Fledgling survival to spring	Needed fledglings produced per pair to achieve: Stable population	Needed fledglings produced per pair to achieve: 60 percent decline in 10 years
1	.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

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. Rainfall 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 rainfall 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 fledgling rates too low to maintain stable population levels. Since 1971, a cowbird trapping program has essentially eliminated the cowbird as a factor, 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 over-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 birds during migration and on the wintering grounds. Winter habitat in the Bahamas 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 amounts of breeding habitat in the 1990's and beyond.

ACKNOWLEDGMENTS

This report is a contribution of Federal Aid in Wildlife Restoration, Michigan Projects W-124-R and E-1. Harold Mayfield offered many valuable suggestions and was most helpful in alerting me to pertinent reference material. Conversations with Stephen Fretwell about Kirtland's Warbler population dynamics were most enlightening and stimulating. My colleague, George E. Burgoyne, Jr., carried out the multiple regression analyses.

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