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Reply to: 1630 Publications
(2670)

Date: December 7, 1983

Subject: Research Paper on Kirtland's Warbler
(NCFES - Dr. John R. Probst)

To: District Ranger, Mio, Tawas, and Harrisville R.D.

Enclosed is a preliminary copy of the first of four papers that John is writing on his KW habitat studies.

Although there is to be a more definitive paper to be written on habitat suitability, this paper does cover several factors on suitability that are germane to habitat management. First, it appears that there would be significantly fewer nesting KW's in marginal habitats (i.e. stands with <1200 stems of jack pine per acre). There would be virtually no use where jack pine stems are <1000 per acre. Thus, it appears that we must develop stands with >1200 stems of jack pine per acre to provide optional KW nesting habitat. This would be true whether the jack pine is regenerated naturally or by planting on sites prepared by prescribed burns, mechanical treatments or on wildfire areas. The marginal habitats (<1200 stems per acre) would not only have a lower KW population densities, but would probably have a slower population buildup and reduced nesting success. Planting density should be made at a rate that exceeds 1200 stems per acre for the planted area. Where stocking is under the 1200 rate after first or third year stocking surveys, fillin planting should be done.

The second factor of habitat suitability covered by John that has management implications is the amount of hardwoods (chiefly oak but may include aspen, cherry and June berries) that would make habitat unsuitable. It appears that the KW will use habitat with a relative high amount of deciduous species. As stated by John, Elaine Smith found KW's nesting in stands with as much as 20% oak cover (crown cover). However, jack pine was still the dominant tree species ranging from 55% to 95% by stem counts while oak accounted for 2% to 28% of the stems on her study areas. Mayfield stated,"If any of these deciduous trees or shrubs begin to approach the jack pine in numbers, the area is not used by the Kirtland's Warbler." The criterion established for type composition of KW habitat recognized the "Areas may contain a limited hardwood (oak) component." A definite amount was not stated but we tried to identify only those stands where the oak component did not exceed 25% of a moderate to well stocked jack pine stand. In the interest of habitat dispersion some stands were identified as KW habitat where the oak component was higher. It was recognized that oak control would be necessary in some cases. Where a potential for oak problems have been recognized, we have advised summer burns. There are a couple of examples where this may have cut back the oak sprouting. There are other areas that have been treated, especially spring burns, where the new stand has regenerated to a stocking of more than 25% oak. We have cut the oak sprouts to favor jack pine seedlings. In some very limited tests we have used herbicides on oak also. Early indications are that this does suppress the oak and create better KW habitat.

We do not (cannot) dispute John's statement, "It seems likely that the species is adapted to moderate amounts of oak." The question is, what is moderate? It still seems that we should still try to keep the oak stocking below 26% either by stand selection, summer burns or oak sprout treatments.

We have been finding more instances of KW's using jack pine stands that have regenerated without a recent fire history. If the density and configuration of jack pine cover is a major habitat factor and fire does not have a major influence on ground cover composition as suggested in John's paper, recent changes in methods of harvesting jack pine or post sale treatments could explain why these birds are using "unburned habitats." It opens up the possibility of developing nesting habitats in areas where prescribed burning may not be feasible.

But why are KW's occupying some unburned areas and not others where soils, etc. are seemingly the same? One thing that seems to be common to the areas that have been occupied has been the removal or reduction of slash. Without the shade of the slash, this could have a significant effect on the succession of the ground vegetation. Perhaps this should be investigated. .

If you have any comments on this paper I'm sure John would be interested in hearing them. We will send you copies of his other papers as they are received. I'm sure they will give us a better basis for our management directions.

HHL

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Enclosure

cc; Nels Johnson, DNR, Roscommon
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GWIrvine:ckg

Radtke

JRP

September 1983

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POPULATION LIMITATION OF THE KIRTLAND'S WARBLER ON THE BREEDING GROUNDS

John R. Probst

Bill — as per call Bob Radtke

Bob — This is the first of four KW papers I hope to get to journals by the end of 1984, incl. our major paper on habitat suitability. (Our Station editors have ~~edited~~ added some minor editorial corrections to the present draft which will not affect the general content)

JRP

ABSTRACT

Current speculation about Kirtland's Warbler population limitation has centered about nesting success and winter mortality. It is suggested that population regulation may also operate through habitat maturation, pairing success, fledgling mortality and dispersal of yearlings. Kirtland's Warblers are concentrated into a few large breeding areas, each of which provides suitable habitat for only 10-14 years. It is possible to relate the growth and decline of these "colonies" to the annual population count. As few as 80% of male KWs may pair successfully, though this is offset by polygamy to some unknown degree. An estimate of fledgling mortality (30%) is provided from a literature review, and it is suggested that many yearlings may be lost to dispersal outside the breeding range.

The primary habitat requirements are dense pine growth (>400 stems/ha) in large stands (>40-80 ha.) in conjunction with most ground covers found on the poorer phases of the Grayling sand soil type. A habitat management program strives for a goal of 10,400 ha of suitable habitat at any given time. For the short term, regenerating habitat may not be sufficient to replace currently occupied maturing stands and a habitat shortfall is predicted for 1986-87.

Keywords: habitat, dispersal, mating system, natality, mortality

INTRODUCTION

The known nesting range of the Kirtland's Warbler is restricted to an area about 80 by 100 miles in northern Lower Michigan. All nests have been found within 13 counties. 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 to the east (Tilghman 1979). In 1951, Harold Mayfield organized the first census of the entire population of the species (Mayfield 1953). This count totaled 432 males. The second decennial census discovered 502 male Kirtland's Warblers (Mayfield 1962). However, the third count taken in 1971 showed a 60 percent decrease to 201 males (Mayfield, 1972). The principal reason for this decline appears to have been nest parasitism by the Brown-headed Cowbird. The rate of parasitism was estimated to be 55 percent (Mayfield 1960) and 69 percent (Walkinshaw and Faust 1974) and the number fledged per nest was less than one. The quantity of suitable breeding habitat available to the Kirtland's Warbler has also decreased in recent decades (Ryel 1981b).

Typically, the species occupies dense jack pine (Pinus banksiana) stands of wildfire origin that are about 5-16 ft. in height. Populations in burn areas generally build for 3-5 years after first occupancy, level off for 5-7 years and decline rapidly within 3-5 years. Plantations are also used (including a few red pine [P. resinosa] stands) but logged, unburned jack pine stands stocked by natural regeneration from non-serotinous cones usually lack sufficient tree density for breeding warblers.

In response to the dramatic population decline from 1961 to 1971, the Kirtland's Warbler Recovery Team instituted; a) annual censusing of the population, b) cowbird control, c) closure of breeding areas during the nesting season, and d) a habitat management program. I will address six major topics in this paper: 1) the present concentration of Kirtland's Warblers into only a few breeding areas, and the buildup and decline of such colonies; 2) an interpretation of the annual census data which postulates lower reproductive potential, and higher rates of breeding dispersal and fledgling mortality than has been assumed previously; 3) speculation about the relationship between habitat quantity, decline of individual nesting areas and the annual census results; 4) a description of the habitat limits for Kirtland's Warblers; 5) an overview of habitat management; and 6) an assessment of future prospects for Kirtland's Warblers and their habitat based on the first five topics.

METHODS

The annual census results for the whole and individual areas (Mayfield 1953, 1962, 1972, 1973a and b, 1975; Ryel 1976a, 1976b, 1979, 1980a, 1980b, 1981a, Burgoyne and Ryel 1978) were used in several of the analyses that follow. Kirtland's Warbler density estimates were made by estimating stand area from the stand maps used for the annual census. Vegetation measurements for percent tree cover were made using the line transect method (Lindsay 1955) combining some adaptions of that technique as done by Buech (1980) and Probst (1976).

RESULTS

Historical Trends

Within the past century the Kirtland's Warbler probably reached peak abundance during the logging of the virgin pine forests of Michigan (Mayfield, 1960), although J. Weinrich (pers. comm.) has suggested they may have been more numerous during disturbances related to the formation of the Great Lakes pine forests about 500 years ago. Historically the extent of wildfire varied greatly over time in northern Lower Michigan. Because the reproductive potential of most birds is inadequate to take advantage of a temporary abundance of habitat or food resources, it seems likely that the Kirtland's Warbler population has usually lagged behind the quantity of habitat available. Temporary shortages in suitable wildfire habitat probably resulted in population decline, because excess birds were forced into marginal habitat where reproductive success could suffer. This situation probably existed prior to the pine logging era, when extensive areas were over-mature.

The Brown-headed Cowbird was not common in Michigan until forests were cleared by early human colonists (Mayfield 1960, 1975). When this occurred, the frequency of cowbird nest parasitism increased. Control of forest fires has reduced the availability of wildfire acreage throughout the last half century, and the rate of cowbird parasitism increased from 40 percent before 1955 (Mayfield, 1960) to as much as 69-75% by the late 1960's (Walkinshaw, 1972). As a result, the population declined about 60 percent from 1951 to 1971. Because the cowbird-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 have problems off the breeding grounds. Trautman (1979) suggested that hurricanes in the Bahamas may have decimated birds during early in this century. Winter survival may also be influenced by amount of rainfall on the wintering grounds (Ryel 1981b).

Although numerous specimens and sight records of the Kirtland's Warbler exist for the Great Lakes region, there are no nesting records outside of northern lower Michigan. 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 has a broad dispersal effort, because it occupies habitat that is only temporarily suitable. It is possible that the Kirtland's Warbler could have formed successful colonies in areas outside of the known nesting range during the recent past. However, these populations probably could not be sustained because areas outside Michigan were not large enough to maintain enough suitably-aged jack pine habitat.

Figure 1 shows the townships in Michigan that have had nesting Kirtland's Warblers since 1951, with the 1981 breeding distribution shown with darker shading. Although the most peripheral areas are currently unoccupied, this is probably related to the current distribution of habitat rather than to their population biology. For example, Mayfield (1953) reported that Kirtland's Warblers were in Montmorency County to the north and absent in Ogemaw County to the

south. By 1961 the Canada Creek wildfire in Montmorency County had matured and new burns had occurred in Ogemaw County (Mayfield, 1962). Presently, Kirtland's Warblers are still numerous in Ogemaw County, and a few have appeared to the east in Iosco County. Two were found in Montmorency County and may increase substantially there in the 1990's when a 1981 wildfire and managed habitat become old enough.

Recent Trends

In the 1971 decennial census the number of singing Kirtland's Warbler males fell to 201. This decline stimulated corrective action. Cowbird trapping methods developed by Nick Cuthbert and Bruce Radabaugh were begun at several breeding areas in 1972 and expanded to all Kirtland's Warbler areas in 1973 under the administration of the U. S. Fish and Wildlife Service. As a result, cowbird nest parasitism dropped to less than 5 percent during 1972-74 (Walkinshaw and Faust 1975), and has averaged 3.4% from 1972-1981. The number of fledglings produced per nest increased from .81 to 2.76 (Kelly and DeCapita 1982). The production per pair is now estimated to be 3.3 to 4.0 (Ryel 1981b). Predation on about one-third of the nests (Cuthbert 1982) is the only major cause of nest failure that remains.

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, Ryel 1977, Mayfield 1978). However, it may be unreasonable to expect a 3-fold increase in reproduction to lead to dramatic population growth for reasons discussed below (see "Annual Trends"). Indeed, the population as measured by the annual census has declined in some years. However, the average for the years 1976-82 (219) is 13% higher than that from 1971-76 (194) and the 1981

decennial census of 232 male Kirtland's Warblers represents a gain over the 1971 count of 201. Although the Kirtland's Warbler population continued to decline after the start of cowbird control, 1974 may represent the low point from previous decades of cowbird pressure. If so, the 1981-82 census would represent a 33 percent increase from this low.

In the past decade, most Kirtland's Warblers have aggregated in a few discrete locations or clusters, which have been termed "colonies". Ryel (1978) noted that three-fourths of the population was in the five largest colonies. This distribution was a slight improvement over 1971 (Fig. 2) when one-half were in just two colonies, and over 90 percent were in only seven areas. Such concentration is undesirable because the population is then vulnerable to a serious decline from events occurring in any single major nesting areas.

Population trends within individual breeding areas indicate that colonies build for 3-5 years, level off for 5-7 years, and decline rapidly in 3-5 years (Fig. 3). Thus, the useful life of a stand for Kirtland's Warblers is about 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, Walkinshaw in press). Yearlings are less likely to return to their natal colony, especially in mature habitat, so the decline in a single colony could be related to a failure to replace older birds with new recruits (Ryel 1979b, Walkinshaw pers. comm.). 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.

This pattern of population buildup and decline in single colonies suggests the annual censuses 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 reflects the difference between the amount of declining and the amount of developing, or optimal habitat (Probst 1980).

For a first approximation, I combined the census results of contiguous areas with a similar date of origin. The annual number of singing males in some of these discrete locations or colonies is shown in Fig. 3. The annual population changes of these separate breeding areas were totaled for all areas showing gains and for all those showing losses (Fig. 4). This confirms that there are partially compensating trends among individual colonies, and that annual population changes are not reflected in every breeding area. Most losses occurred in old, declining habitat and almost all gains were in young habitat. Thus age synchrony among breeding areas is an important factor to understanding Kirtland's Warbler population dynamics (Fig. 5). 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. Conversely, the general increase in population during the period 1975-80 coincided with the buildup of five major colonies that are now supporting three-fourths of the birds and will so into the near future. This suggests that the stationary warbler population over the last decade may be a result of

a rough balance between old habitat being abandoned and new habitat being colonized, despite successful cowbird control and excellent nesting success.

Below, I suggest that the reproductive potential of the Kirtland's Warbler may be lower than previously assumed (Mayfield 1975, 1978; Walkinshaw and Faust 1974, 1975; Ryel 1981b), and I re-assess the fate of birds leaving the nesting grounds in late summer.

Reproductive Potential and Recruitment

Several factors could result in overestimates of Kirtland's Warbler reproduction or underestimates of males on the annual census. Non-singing, non-breeding "floater" males have been observed for the Kirtland's Warbler (pers. obs., Orr pers. comm.) including males presumed to be floaters on territories in colonies where most birds were colormarked (Walkinshaw, pers. comm.). If the floater population were sizable, the presence of uncounted birds would help explain their stationary population.

In a study of the Prairie Warbler, Nolan (1979) found no evidence of a floating surplus of males, but did find that territorial males could undertake extensive explorations into surrounding habitat. Such behavior could be an attempt to establish additional pair bonds (secure additional mates) because Prairie Warblers (and Kirtland's Warblers) are known to be polygynous. However, widespread polygamy implies a large number of unmated males which probably search for mates in more than one area--and could become floaters in occupied habitat.

Similarly, some unpaired singing males are almost certainly present, though one can never be 100 percent sure that a female is not on their territory. However, by recording the time it takes to determine a mated pair (N. Cuthbert 1982), it should be possible to establish a time limit during which pairing can be confirmed for a given percentage of the males. Because many males in less suitable habitat wander extensively, I propose that the pairing percentage could be lower in (a) declining habitat, b) young habitat, c) marginal habitat, and d) peripheral habitat. Although Cuthbert suggested that the pairing rate is quite high, if about 10 percent of males in optimal habitat were unpaired, and one-third to one-half of males in the smaller or less suitable colonies were also unmated, the fledgling production rate could be about three-fourths of previous assumptions. On the other hand, this factor could be offset somewhat by polygynous matings (Berger and Radabaugh 1968 and Radabaugh 1972b) and instances of double broods (Radabaugh 1972a).

Post-fledging mortality reduces the number of young birds surviving until fall migration. Estimates of such losses for other species are about 20-65% (Brewer 1981, Nolan 1979, Scott and Ankney 1980). For the Kirtland's Warbler, Walkinshaw and Faust (1974) were able to find only 60 percent of the young they had recorded as having fledged. The combined effect of reduced pairing success (about 80%) and post-fledging mortality (about 30%) could reduce the number of young available for fall migration to 450-600 from the 800 assumed in the past. On this basis a stationary population could be explained by annual survivorship of 70% of the 400 adults, and by assuming that 40% of the immatures from the previous fall return to the nesting grounds each year.

Dispersal and Mortality

The major loss of both adult and young birds probably occurs during migration and on the wintering grounds. Although a long term trend of winter habitat degredation could be occurring, Mayfield (1975) presented evidence that winter habitat has not been significantly altered. Ryel (1981b) developed a model that strongly suggests recent population fluctuations may be related to rainfall levels in the Bahamas.

There should also be numbers of Kirtland's Warblers unaccounted for because of dispersal to areas outside the traditional nesting grounds, including areas outside Lower Michigan. This view is supported by more intensive censuses that have revealed single birds or groups in marginal habitat, often many miles from the nearest colony. In addition, from 1977-82 eight males were found during the breeding season in Wisconsin (4), Ontario (2), Quebec (1) (Ryel 1981a) and the Michigan Upper Peninsula (1) (Probst unpubl.). In the past, specimens were also taken outside the presumed migration route in Ontario (2), Illinois (3), Missouri (1), Minnesota (1) and Virginia (1) (Mayfield 1960). 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 in 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 a very high proportion of birds dispersing to remote locations, because isolated males may sing weakly or not at all, and the chance of discovering birds over a large area is poor. Similarly, females would not likely be discovered unless paired with a singing male. These vagrants seldom contribute to the annual census and would only rarely pair with a female. These extra-limital birds could have formed colonies in the past, but their populations probably did not persist due to insufficient habitat of the proper age.

Because little habitat was generated in the 1950's, there was little overlap between the decline of older colonies in the early '70s and the buildup of new colonies at four wildfire areas and two management areas in the mid 1970's (Fig. 5). There may have been a further population lag due to reduced pairing rates in these new, small colonies in their early years of use. One reasonable speculation is that yearlings were unable to find sufficient suitable, young habitat in the late 1960's and were forced into marginal habitat where they were missed by the less intensive census effort at that time. However, I suspect that cowbird parasitism had kept the population below carrying capacity before 1971.

Habitat Suitability

At present, Kirtland's Warblers are located on forest stands that comprise about (3000-3200 ha), out of a total of around (6,400 ha) in the 8-20 year age range generally selected by the species (D. Sorenson and J. Weinrich, pers. comm.). In the 1980-82 censuses, three-fourths of the population (about 180 birds) were located in 5 or 6 major breeding areas that totaled about (1440 ha). At the other

extreme, an aggregate area of over (1200 ha) supported only about 25 birds. 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 (usually unburned). Alternatively, the very low Kirtland's Warbler densities in marginal habitat could be viewed as evidence that habitat is not limiting at current population levels (see below).

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 model of habitat utilization that postulates a distribution of birds among habitats that results in near-equal nesting success. For example, Dickcissels in less preferred habitat had lower nesting density, but similar nest success compared to birds in more preferred habitats (Zimmerman 1982).

Although there is no evidence to support lower fledging rates in Kirtland's Warbler marginal habitat, very few nest studies have been conducted in such areas. I suggest above that the main disadvantage of marginal habitat might be reduced pairing success, and 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 poorer reproduction as well as lower densities in marginal habitat.

Habitat Limitation

Determining the degree of habitat saturation for bird species is difficult because it is unusual for a species to use all available space--even for abundant species in uniform, optimal habitat. There

may be annual shifts in spatial use, (Wiens and Dyer 1975), and/or local clumping due to social organization as with Least Flycatchers and Henslow's Sparrows (pers. obs.). At high densities, Kirtland's Warbler patterns of spatial utilization are similar to those of other species but the scale for home range size and space between territories is expanded by about ten times presumably because of the low net productivity of the jack pine habitat.

The population density in habitat that originates from wildfire or management averages about 5 males per 100 acres (Probst 1979). Although some sub-areas may support over 30 males/100 acres for a year or two, optimal habitat usually supports 10-20 males per 100 acres. This density is similar to that of other songbirds. In 39 breeding-bird censuses in forests, clearcuts and old fields, only 18 out of 57 species were ever able to attain more than 20 males per 100 acres in any of the habitats included in the study (Probst 1976), so local distributions of the Kirtland's Warbler does not appear more fragmented than that of other species.

In past decades, habitat was apparently more abundant than at present, and Kirtland's Warblers were in smaller, more numerous colonies (Mayfield 1960). The best conclusion I can draw from the present evidence is that optimal habitat is more saturated than in the past, but it is difficult to approach habitat as a limiting factor using density figures or patterns of spatial utilization alone.

Primary Habitat Factors

There is considerable evidence that points to tree density as the primary factor controlling habitat suitability for Kirtland's Warblers (Probst 1981). In typical habitat that results from wildfires, areas

with dense regeneration are occupied first, and areas lacking minimal tree stocking are never used. Stands of intermediate tree density are older when first used, than dense stands (Buech 1980) and usually carry fewer birds. There is a tendency for territory sizes to be larger in the more open areas of a stand (Smith 1979, Mayfield 1960, and pers. obs.).

Unburned jack pine stands are characterized by less dense natural regeneration and are seldom occupied by Kirtland's Warblers. This is because tree stocking in unburned stands rarely achieves the 20 percent tree cover threshold critical for the species. When unburned stands do achieve this stocking they are older than stands regenerated by wildfire. At this threshold, unburned stands average about 10 feet in height. Unburned areas that have been planted can produce suitable tree cover at the usual 6-8' height and can support optimal Kirtland's Warbler populations. Similarly, a Red Pine plantation at Mack Lake that received optimal use in the 1970s was characterized by denser-than-normal tree spacing (5'x7'). Consequently, the limits to habitat suitability can be expressed as an ordination of tree height versus percent cover (Probst 1979). The composition and height of ground cover should also become important outside the bounds of poor sites determined to be critical habitat for the species under the Endangered Species Act of 1973.

Percent tree cover is more useful for evaluating habitat than stocking frequency or stem density because it integrates the stocking, spacing, and height factors. It appears that 30-60 percent tree cover is optimal (Probst, unpublished). Fire-regenerated stands generally have stem densities in excess of 7500 per ha. Because trees are

evenly distributed in plantations, optimal habitat can be produced with a lower tree density. However, stands with less than 2500 stems/ha will probably not be used appreciably, and those with less than 3000/ha are questionable, especially in naturally regenerated areas. In any stand, the stocking should be equivalent to at least 20-25 percent tree cover to have a good chance of occupancy. Warbler habitat declines when average tree height reaches 4.3-5 m (5.0-5.7 m in plantations) and lower tree foliage is dead up to about 1.0-1.3 m in height (At this stage, percent tree cover ranges between 65-85%).

Previous explanations of Kirtland's Warbler habitat suitability have centered about the bird's nesting biology, and the Recovery Team has emphasized the importance of ground cover to nest site selection (Byelich, et al. 1976). However, it is unlikely that a ground-nesting bird should be limited by nest sites, therefore I have emphasized habitat factors important to the warbler's foraging ecology. The threshold for initial occupancy may be related to minimal foliage volume necessary for foraging. The decline of habitat could be related to a lack of live lower branches for fledgling cover and for the foraging of female Kirtland's Warblers.

Secondary Habitat Factors

Ground Cover. Within the range of very poor sites that characterize Kirtland's Warbler critical habitat, ground cover does not appear to be limiting to Kirtland's Warblers because it almost always consists of a low, light cover of shrubs and/or grass-sedge interspersed with moss, lichen, and bare ground. The overwhelming site character influencing this vegetation is moisture stress as determined by soil structure. In addition, almost all ground plants can sprout from

underground roots, so fire probably does not have a major influence on ground cover composition, though it may enhance the vigor of the subsequent regrowth. The major determinants of ground cover composition are site quality and historical factors--especially shade. Buech (1980) has shown that there can be more grass-sedge and lichen-moss in open areas, and more bare ground in heavy shade. The individual shrub species showed conflicting trends in their shade affinities, but I believe that the shrub group as a whole does better in intermediate shade.

There are differences in the species composition of burned and unburned stands on Grayling Sand, but these are often obscured by site and historical factors (Abrams and Dickman, 1982). In addition, data from the latter study suggest a convergence in ground cover composition as succession progresses toward the 6-8 year minimum age for Kirtland's Warbler occupancy.

Other Factors. Since the Kirtland's Warbler has so frequently been found in nearly pure jack pine stands, it has been assumed that sprout-growth from hardwoods (chiefly oak) would make the habitat unsuitable. However, before the logging period of 1880-1900, fires were almost certainly less frequent but more extensive and there should have been a larger oak component to Kirtland's Warbler habitat in the past (J. Weinrich pers. comm.). It seems likely that the species is adapted to moderate amounts of oak. For example birds were found in an area with as much as 20 percent oak coverage (Smith 1979). Because hardwood coppice is actively used for foraging it should not be detrimental unless it is dense enough to crowd out the jack pine.

In marginally stocked jack pine stands sprout-growth may actually be beneficial by providing supplemental foliage volume for their foraging.

DISCUSSION

Habitat Management

In the early 1960's four areas (4676 ha) were set aside specifically for the preservation of the Kirtland's Warbler (Mayfield 1963), one in the Huron National Forest and three on state land. The state areas were to be planted, and the federal areas were to be regenerated by prescribed burning (Radtke and Byelich 1963). Since then, the area designated for Kirtland's Warbler management has been increased to 50,800 ha. The Recovery Plan calls for regenerating habitat through harvest followed by burning jack pine stands on state (31,200 ha.) and federal (22,000 ha.) lands, so that there will be about 10,800 ha. of suitably-aged habitat each year.

This habitat will be regenerated at the rate of about (1080 ha.) per year in 16 state forest management areas and 7 areas on U.S. Forest Service lands. These stands will be managed on a 50-year commercial timber rotation, with Kirtland's Warblers being the key resource objective. Because prescribed burning has failed to provide the dense tree stocking required by the Kirtland's Warbler, land managers have been seeking alternatives to expensive full planting without sacrificing any secondary habitat requirements.

Future Prospects for the Kirtland's Warbler

Habitat Decline

The success of the Cowbird control program may allow the Kirtland's Warbler to continue a slow population increase if there are

not severe losses off the nesting grounds. All of the six major Kirtland's Warbler breeding areas currently in use could decline significantly by 1984, when they will be 16-20 years old and will have received 8-12 years use by Kirtland's Warblers. We have not followed enough colonies through an entire period of occupancy to be able to predict the number of birds present at a given time, or the degree of utilization of young colonies. However, the data in Figure 3 gives me sufficient confidence to predict that none of the six major breeding areas will be major colonies (more than 15 males) beyond 1985. Several of these areas have some younger patches of habitat that could carry a reduced colony beyond the normal 10-12 year duration of use. Although a few of these colonies may support Kirtland's Warblers through the end of the decade, it is unlikely that their combined populations would exceed 40-50 birds by 1986 or 20-30 birds by 1987, when only one stand would still be under 20 years old. Figure 5 suggests that new colonies must be formed in adequate habitat to replace those that decline. However, predicting the presence of new colonies, and the populations they might support, is even more speculative than estimating the rate of decline of areas already known to hold Kirtland's Warblers.

Future Habitat Quantity

The quantity of suitable habitat has remained roughly constant since 1971, and would have declined to about 1/2 to 1/3 of the present area during the next decade (Sorenson and Weinrich, unpubl. report). However, on May 5, 1980 a prescribed burn went out of control and burned almost 10,000 ha. of forest, including 100 ha. of current warbler habitat. This Mack Lake Fire alone has the potential to

regenerate more habitat by 1990 than exists at the present time. The early indications are that Jack Pine regeneration on the Mack Lake Burn will be good enough to produce thousands of hectares of Kirtland's Warbler habitat.

However, only 120 ha. appears dense enough to support early occupancy in 1987-88 (G. W. Irvine, pers. comm.). Three other areas on the Huron National Forest have potential to support Kirtland's Warblers in 1986-87 (including two presently occupied). These areas might support a combined total of 30-50 birds. Three plantations on Michigan State Forest land total 750 acres and could support 50-80 pairs of Kirtland's Warblers. Two wildfire areas on state land could hold 15-30 Kirtland's Warblers, but the biggest unknown concerns the 1000 ha. Bald Hill Burn (1975) in Crawford County. This area could probably support anywhere between 50-100 birds depending on the degree of jack pine regeneration that develops. In any event, use will probably not peak until 1985-87. Despite all the unknowns (decline rates, habitat suitability of developing areas, degree of occupancy, and total Kirtland's Warbler numbers) it appears that there will be a habitat deficit equivalent to that required to carry 50-150 birds by 1987.

Population Projections

We might speculate on the fate of the "extra" birds for which we project insufficient habitat. It seems least likely that they would move into the declining areas, especially if the decline of such colonies is due to attrition of older birds with minimal replacement by new colonists. Yearlings might move into developing or other marginal habitat sooner or in greater numbers than might be

anticipated from the pattern of occupancy suggested by Figure 3. It is most likely that surplus birds will disperse to marginal habitat where their pairing success would probably be lower. The resulting depression in overall reproductive potential could prevent maximal utilization of the Mack Lake fire during the peak years of 1990-2000. Because almost all State and Federal Kirtland's Warbler habitat planted before 1980 would require 10 years to attract Kirtland's Warblers, and recent dense plantings would not be suitable before 8 years (1988), the only opportunity to increase the supply of high quality habitat before 1988 would be to interplant existing plantations by hand to achieve adequate tree density and canopy volume to attract Kirtland's Warblers by 1986-87. Because jack pine plantations from 1977-79 are .7-1.3 tall, some were interplanted in spring 1982 which could produce a dense stand of trees 1.3-2.3 m tall by 1986. The moderate tree age diversity that would result is similar to that found in natural stands, and should not be an obstacle to Kirtland's Warbler occupancy.

If habitat regenerated by wildfire or Kirtland's Warbler management is of sufficient quality to hold 5 males per 40 ha. then about 2000 ha. would be required to maintain the current population of about 240 males. When the goal of 10,800 ha. of suitable habitat is reached, and if two-thirds of the stands are occupied at an average density of 3-5 males per 40 ha., it would yield habitat for 550-900 Kirtland's Warbler males (this is somewhat less than the goal of 1000 established in the Recovery Plan). If all stands were occupied at the same approximate densities they could support 810-1350 Kirtland's Warbler males and achieve the goals of the Recovery Plan.

Acknowledgments

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FIGURE LEGENDS

FIGURE 1: Dark squares show locations of townships in which Kirtland's Warblers were found in the 1981 census. Light squares indicate additional townships where KWs were found in previous censuses since 1951 (after Mayfield 1960).

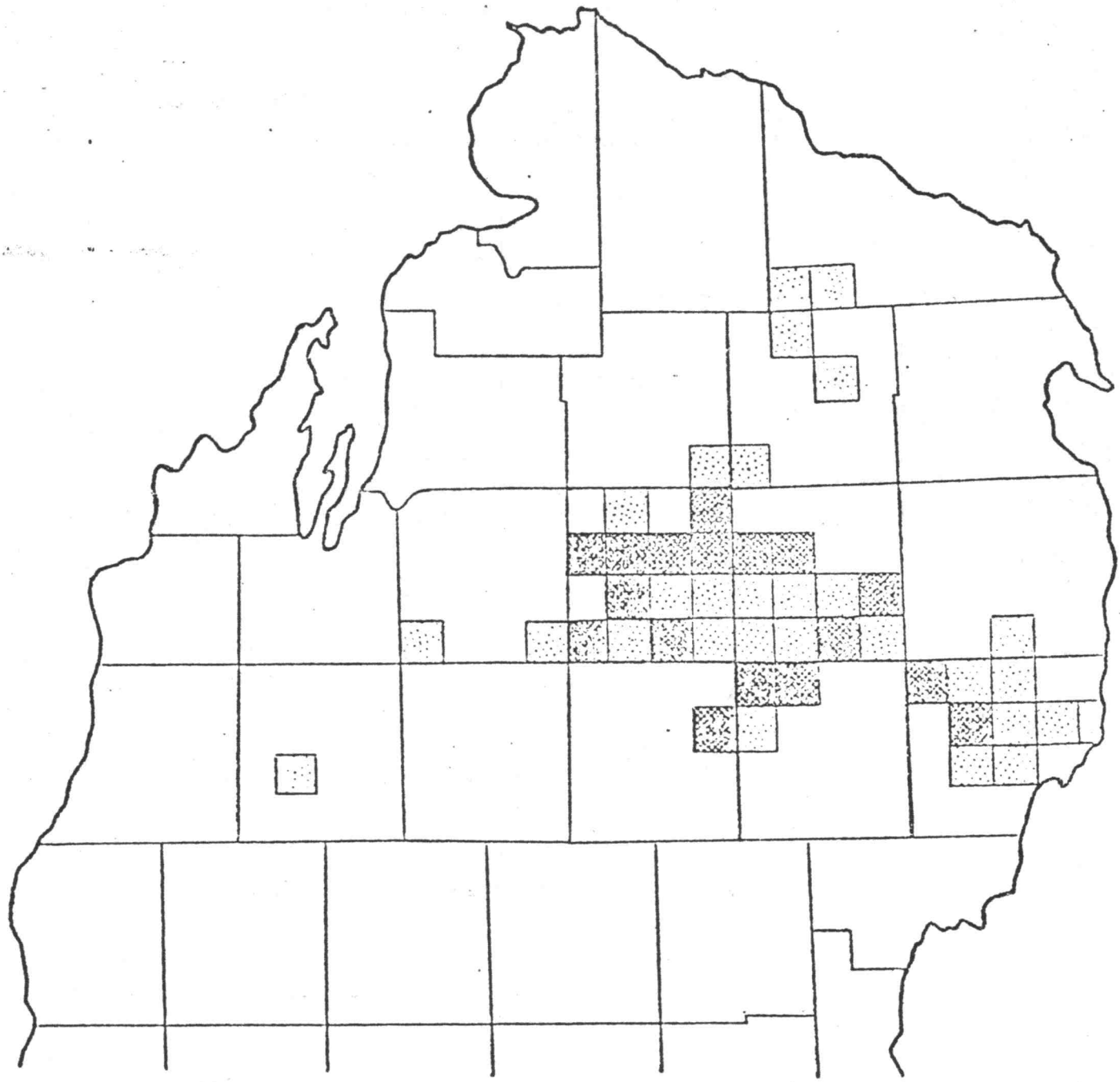
FIGURE 2: Concentration of Kirtland's Warblers into major breeding colonies for 1971, 1975 and 1981. Each bar represents a discrete colony. The areas are in rank order and the percentage of the total population is above each bar.

FIGURE 3: Annual census trends for some major Kirtland's Warbler breeding areas, in chronological order from 1971 to 1981.

FIGURE 4: Aggregate changes in population for all Kirtland's Warbler breeding areas showing gains (right bar) and losses (left bar) in a given year relative to the previous year. The annual census change for a particular year is equal to the difference between the two bars (see text).

FIGURE 5: Overlap and synchrony among major breeding areas. Increases and decreases in total population are related to buildup and decline of individual colonies, especially when major colonies are synchronous.

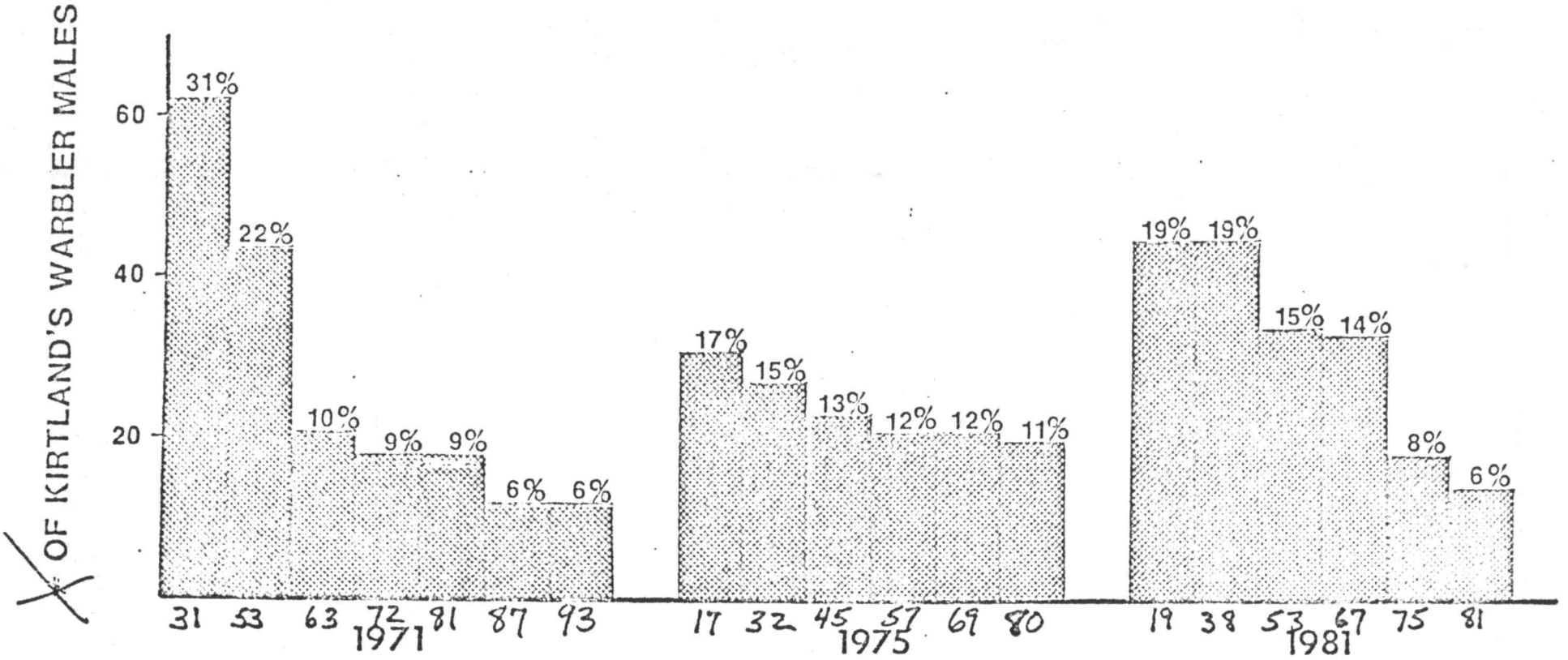
KIRTLAND'S WARBLER NESTING RANGE



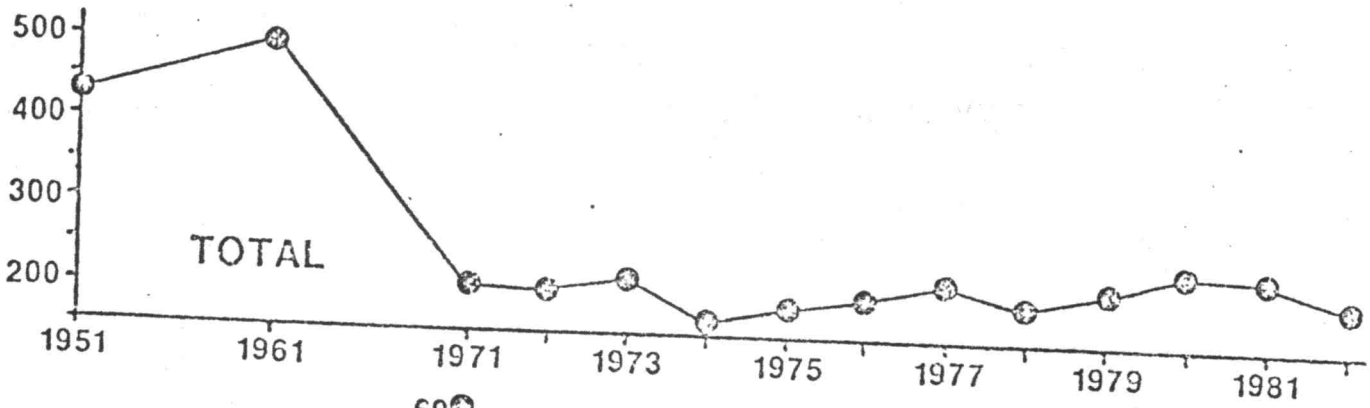
TOWNSHIPS WHERE KIRTLAND'S WARBLERS WERE KNOWN TO NEST IN 1981

TOWNSHIPS WHERE KIRTLAND'S WARBLERS WERE KNOWN TO NEST IN SINCE 1951

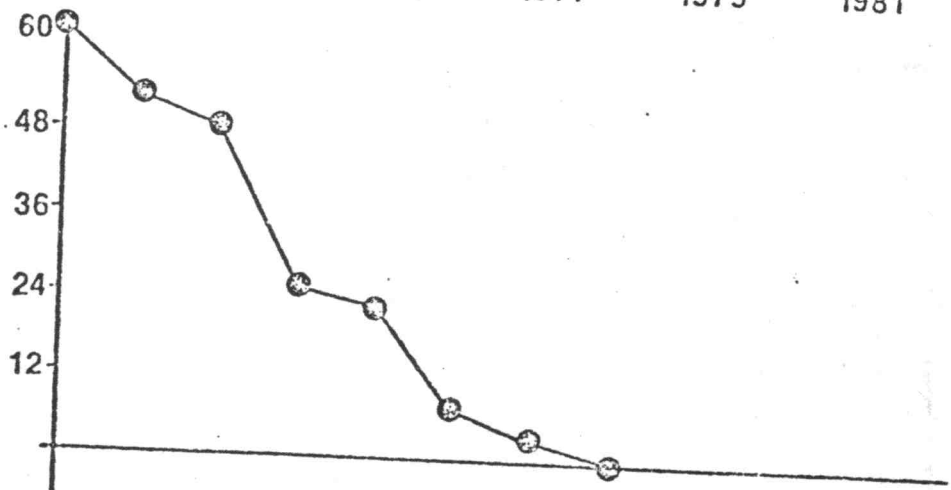
LOCAL DISTRIBUTION OF KIRTLAND'S WARBLERS



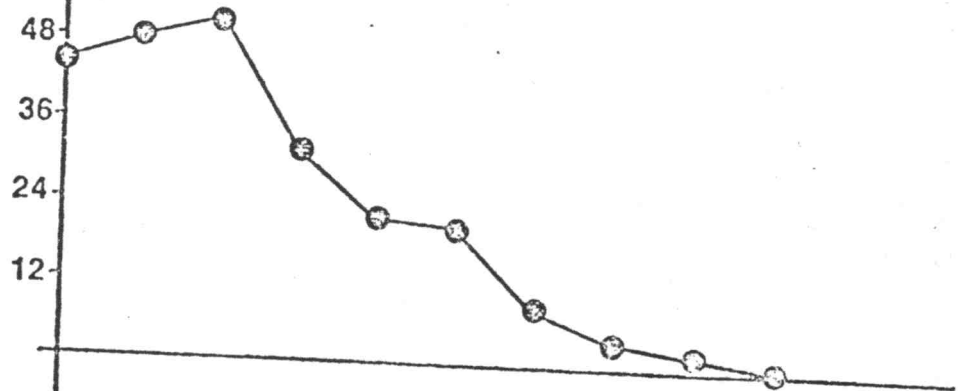
ANNUAL CENSUS TRENDS



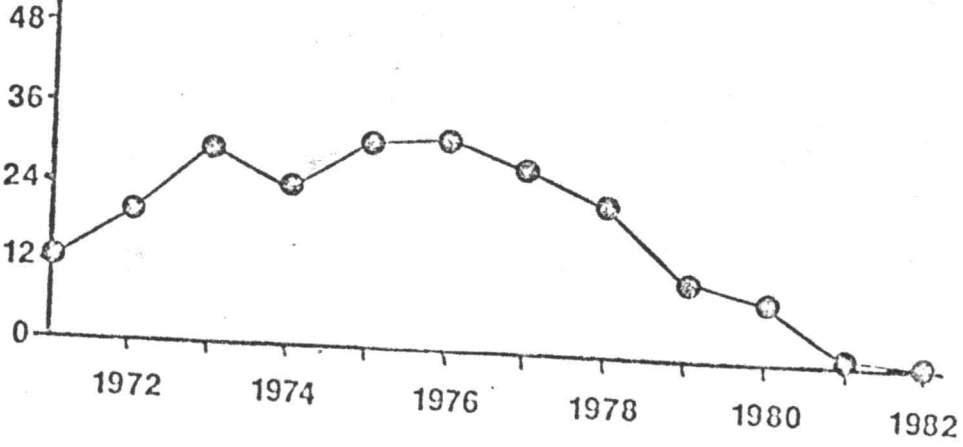
Old Military

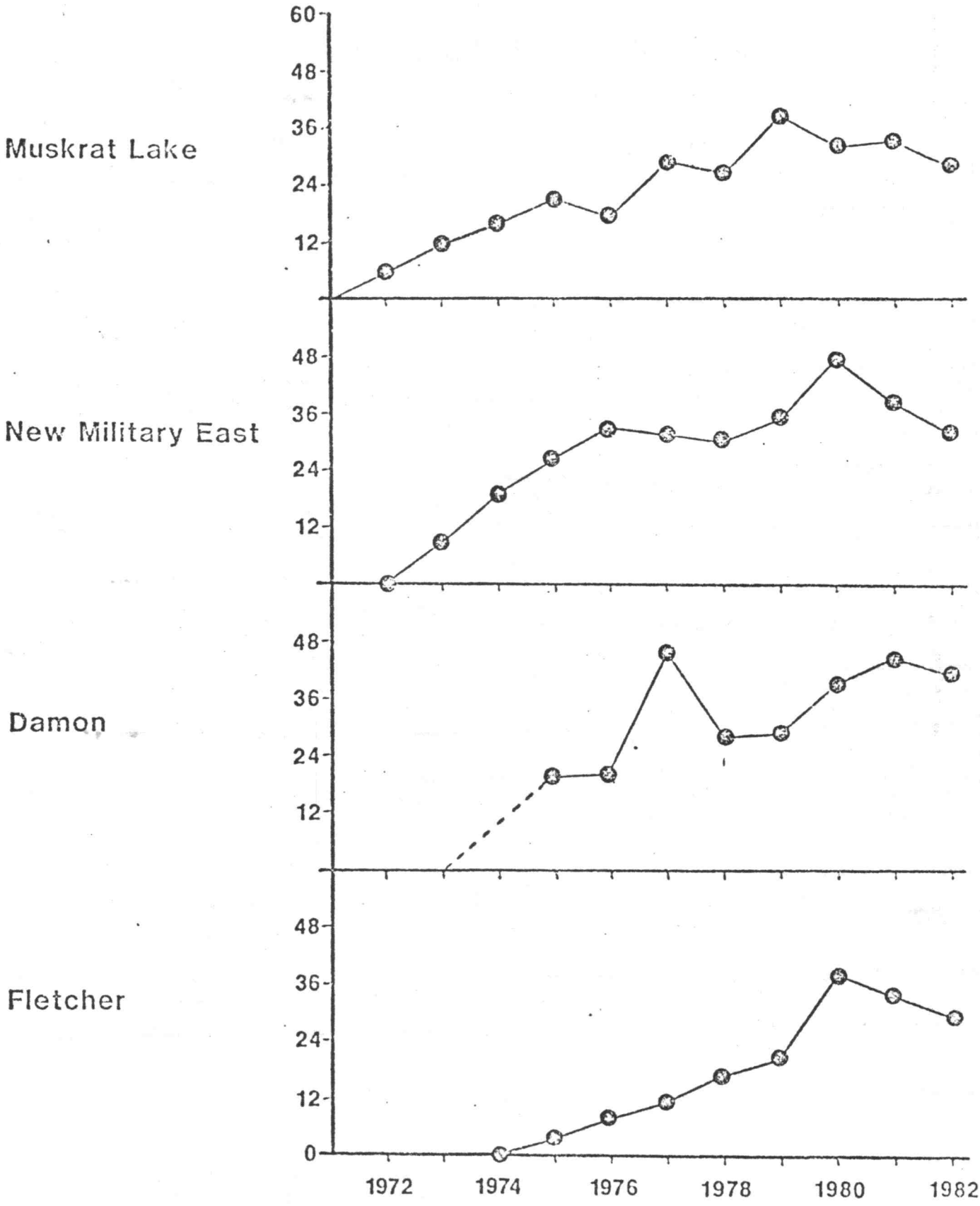


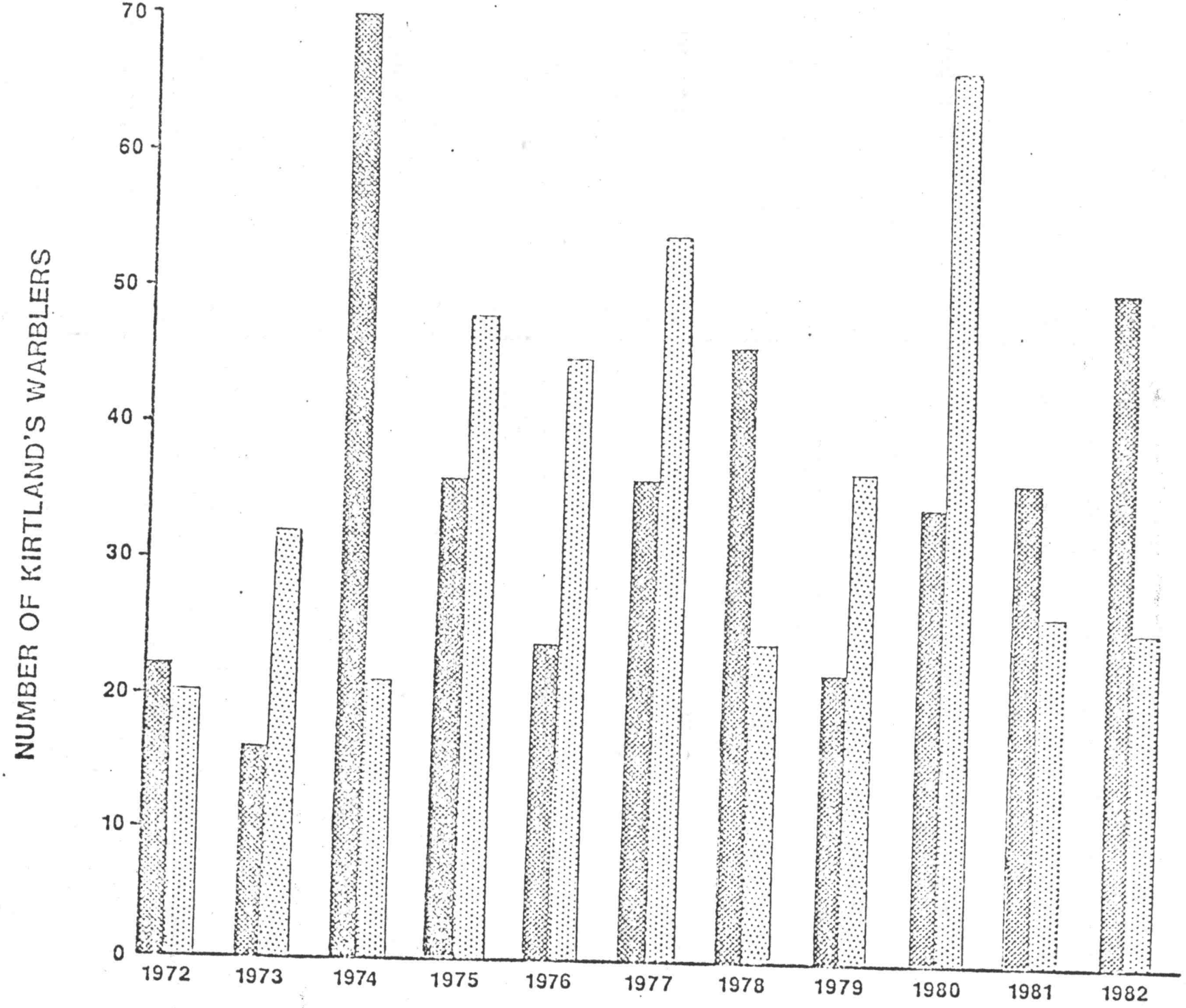
Ogemaw Mgmt.

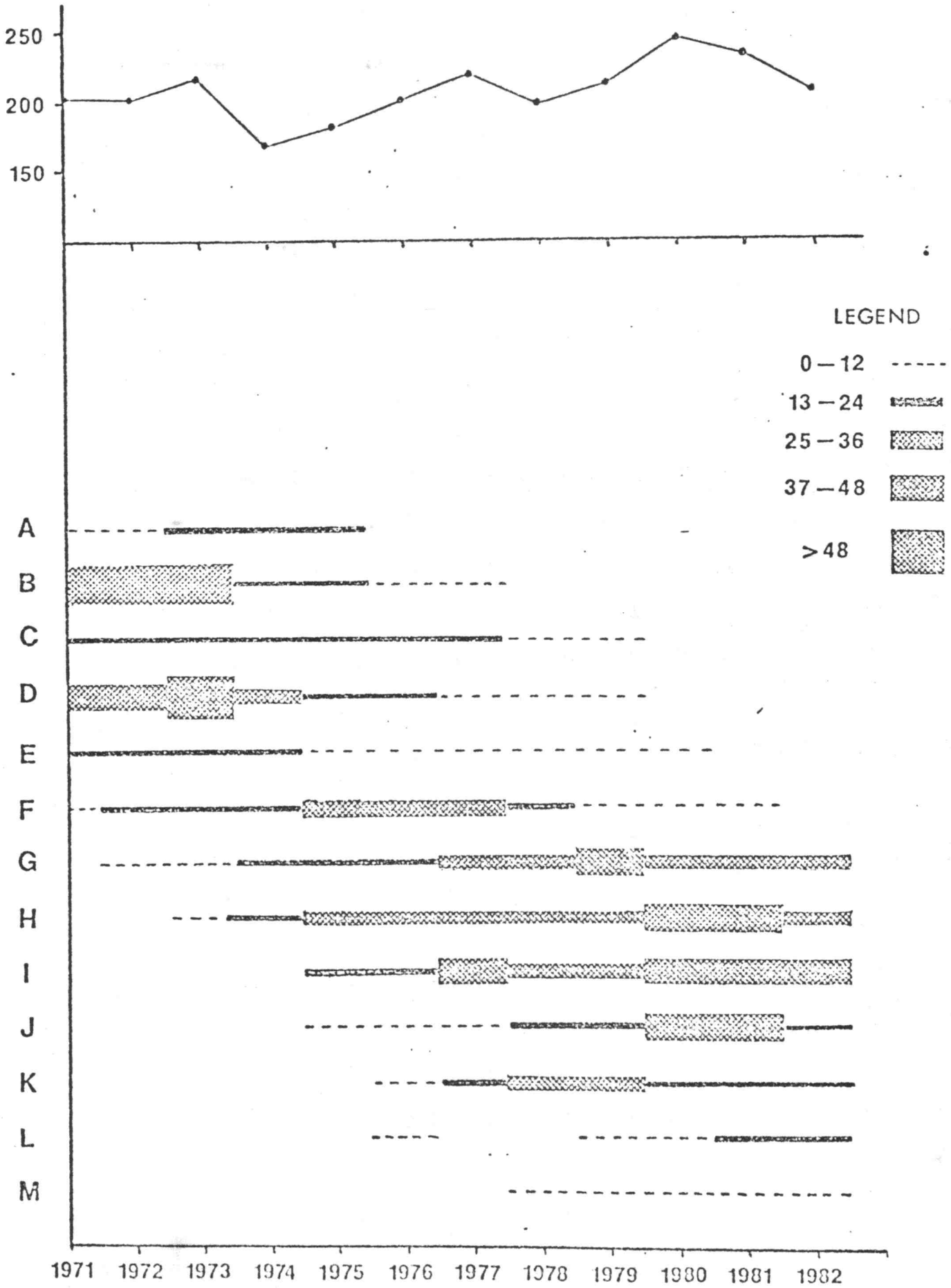


Lovells




Muskrat Lake
New Military East
Damon
Fletcher
60
48
36
24
12
0
1972
1974
1976
1978
1980
1982


NUMBER OF KIRTLAND'S WARBLERS
70
60
50
40
30
20
10
0
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982


250
200
150
LEGEND
0 — 12
13 — 24
25 — 36
37 — 48
>48
A
B
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G
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I
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K
L
M
1971
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982

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