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

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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 I present a review and synthesis of published and unpublished reports on Kirtland's warbler demography which suggests that this species may also be regulated by habitat maturation and fragmentation, pairing success,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.

INTRODUCTION

The known nesting range of the Kirtland's warbler (*Dendroica kirtlandii*) is restricted to an area ca. 120 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.

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-
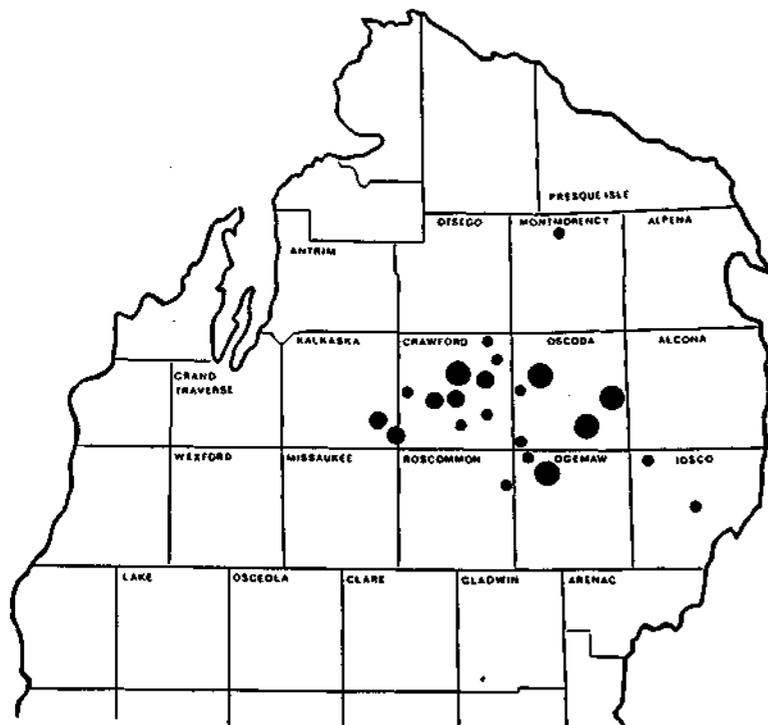

Fig. 1. — 1983 Distribution of Kirtland's warbler breeding areas in three population size classes: • <6 Kirtland's warbler males; ● = 6-18 Kirtland's warbler males; ● >18 Kirtland's warbler males

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.
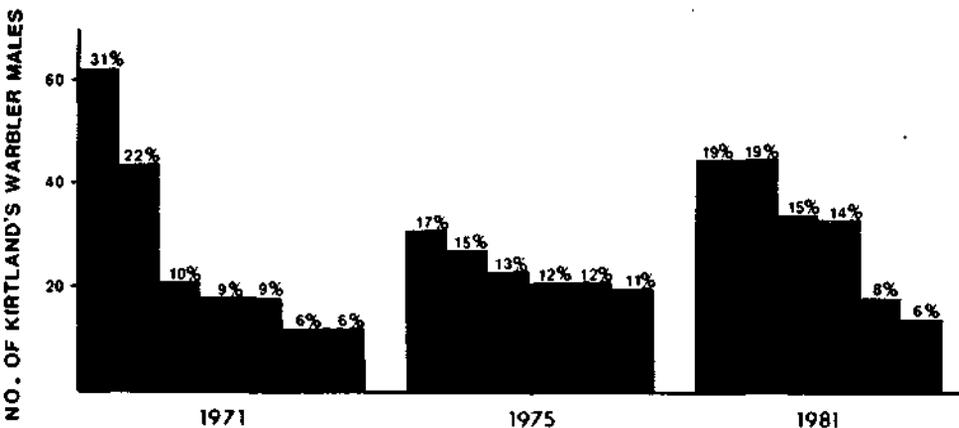

Fig. 2.—Concentration of Kirtland's warblers into major breeding colonies for 1971, 1975 and 1981. Each bar represents a discrete colony, and the percentage of the total population is above each bar

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
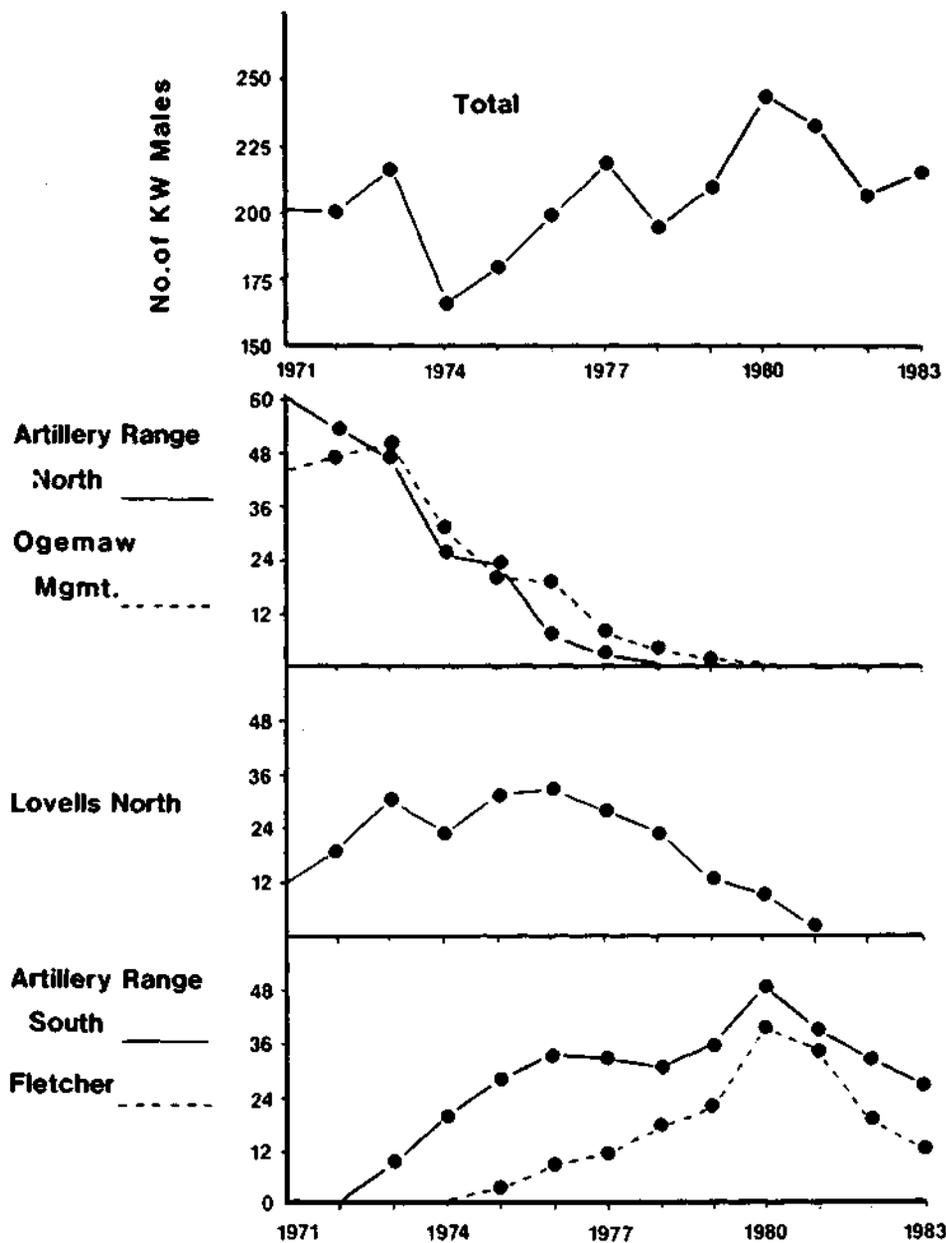

Fig. 3. — Annual census trends for total population of Kirtland's warbler (KW) males (top) and for five selected major breeding areas

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
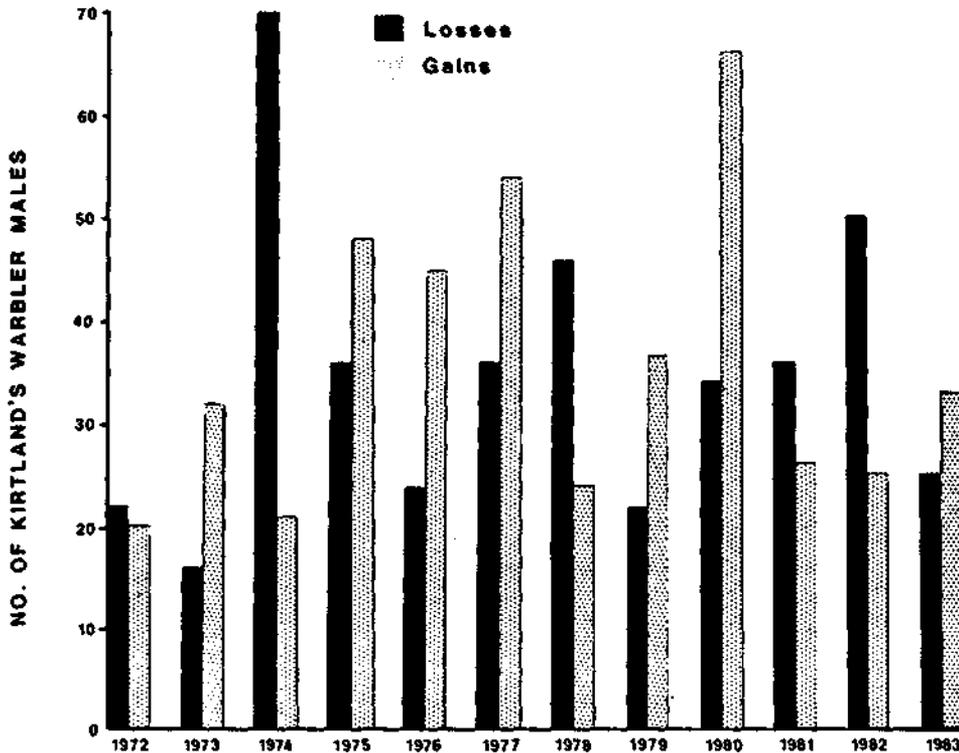

Fig. 4.—Aggregate population changes in a given year relative to the previous year combined for all breeding areas showing losses (left bar) and gains (right bar). The total annual population change for a particular year is equal to the difference between the two bars in a pair (*see* text)

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

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-
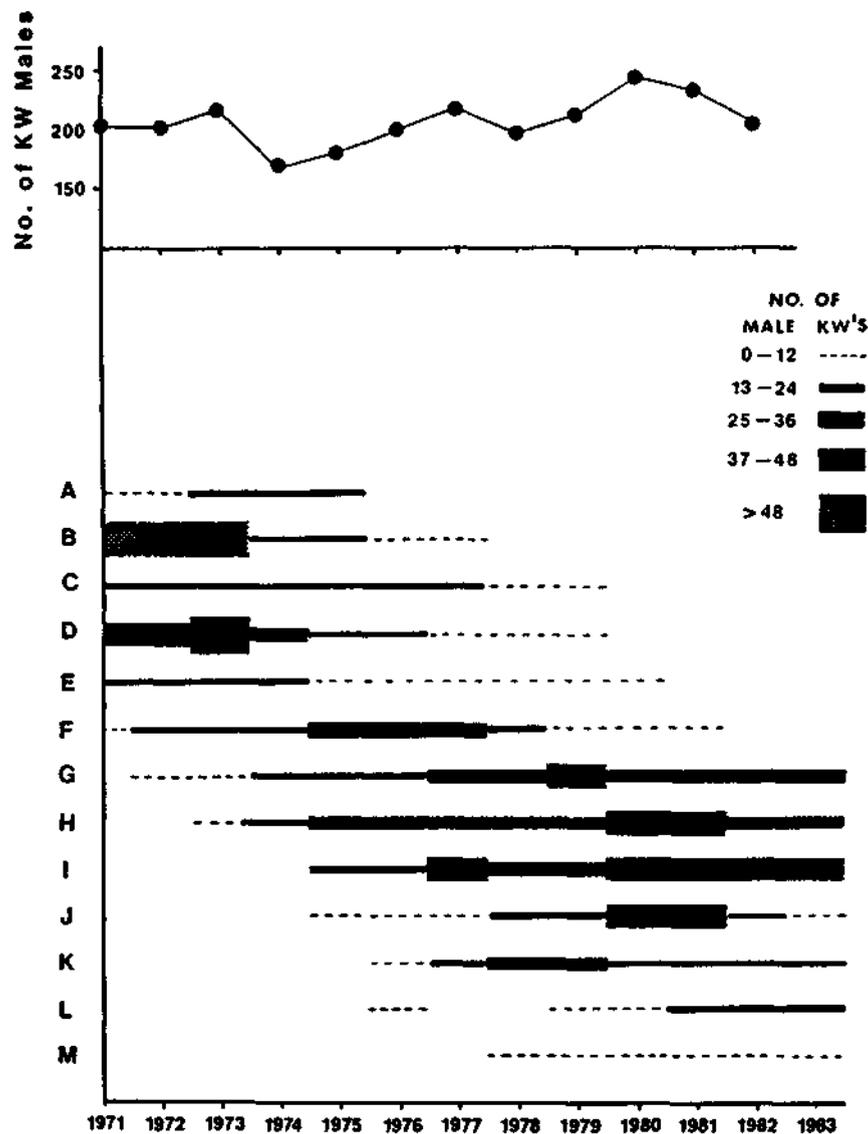

Fig. 5. — Overlap and synchrony among major breeding areas. Increases and decreases in total population (top) are related to buildup and declines of individual colonies, especially when major colonies are synchronous.

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

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

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 off 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 survivorship	Autumn immatures		Spring return rate		Adults (422)		Spring return rate		Breeding population	Number males
Previous	211[a]	x	3.1[b]	x	1.0	= (654	x	0.23[c])	+	(422	x	0.65[c])		= 423 ÷ 2	= 212
Current	180[d]	x	3.1	x	0.70[e]	= (391	x	0.28[f])	+	(422	x	0.75[g])		= 426 ÷ 2	= 213

[a] 1982 + 1983 average
[b] 3.1 per pair (Walkinshaw, 1983)
[c] 0.65 adults (Mayfield, 1983), 23% inferred rate for yearlings (Mayfield, 1960, 1978)
[d] 85% pairing success
[e] 0.70 fledgling survivorship until independence (modified from Walkinshaw and Faust, 1975)
[f] Calculated from other demographic data and an assumption of a static population (*see* text)
[g] Estimates 15% relocations of adults (previously assumed to have died)

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 ⅔ 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*

Year	Area* (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* (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

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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