

On the Population Dynamics of Kirtland's Warbler

New colonies in good habitat grow rapidly because they attract yearlings hatched in other colonies.

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Early work with Kirtland's Warbler (*Dendroica kirtlandii*) suggested that so-called "colonies" of birds both built up and declined rather slowly (Mayfield 1960) but much of this research was carried on well before annual censuses were begun in 1971. Actually when Mayfield's monograph on the species was published in 1960, only the 1951 census (Mayfield 1953) had been completed. Research concentrated mostly on a small number of colonies and workers had only limited knowledge of population levels elsewhere. In recent years, data on population trends have been collected not only for individual colonies, but the entire species as well. I was fortunate to have observed a colony in Ogemaw County, Michigan, a number of times from initial establishment to subsequent demise. In this paper I have used the term "colony" in the traditional way (Mayfield 1960, Berger and Radabaugh 1968).

The objectives of this paper are fourfold: (1) document the history of a large Kirtland's Warbler colony, (2) hypothesize about the mechanisms which result in rapid population increases, (3) hypothesize on the effect of variable sex ratios on population dynamics and (4) stimulate thought and provide an incentive for future research.

METHODS

"Complete" censuses of singing male Kirtland's Warblers were carried out in 1951, 1961, and 1971 to 1978 (Mayfield 1953, 1962, 1972, 1973a, 1973b, 1975; Ryel 1976a, 1976b, 1978; and Burges and Ryel 1978). Mayfield (1960) has detailed the rationale for using singing male counts as a census technique in Kirtland's Warbler. Briefly, the entire historical breeding range (and beyond, in some cases) of the species in northern Lower Michigan was divided into convenient blocks and assigned to various crews who scanned it for suitable habitat. Likely-looking areas were spot-checked for singing males; where any were found, an actual census was conducted.

Since 1961, all Roscommon and Ogemaw county censuses have been conducted using a mapping technique in which the location of singing males is spotted on 4-inches-to-the-mile sketch maps using compass lines and pacing. This mapping technique is similar to Emlen's (1961)

C method, except that in most cases merely a single search of an area is made. Hence, only locations of males at that time are noted on maps. No attempt is made to determine the territory size.

Published literature on the species has been used to supply information on survival, movement and sex ratios.

POPULATION CHANGES IN THE HORSESHOE LAKE COLONY

While Mayfield (1960) indicates there were some early records of Kirtland's Warbler for 2 townships in northeastern Ogemaw County, the late Vern Dockham told me that there had been none present in the county for a number of years prior to the 1951 census.

I first discovered a lone singing male in Sec. 17, T24N, R1E, Ogemaw County, on 29 June 1955 (Table 1). This was a portion of the area of the Horseshoe Lake forest fire of 1946. I made a fairly thorough search in suitable habitat of the burn without finding other birds. This male remained until at least 21 July and apparently was unmated. In 1956 and 1957 a single male was again present at this location. In 1957 I found a second male in Sec. 34 of the same township. In 1957 the State Conservation Commission selected sections 21, 22, 27, and 28, T24N, R1E as one of 3 Kirtland's Warbler management areas on state land (Mayfield 1963). I did not return to the Horseshoe Lake area until the 1961 decennial census when our 4-man crew found the astounding total of 114 males here on 5 sections (Mayfield 1962). In the next decade, I made several visits to the management area as did a number of other observers. Dr. Nicholas Cuthbert, Central Michigan University, used part of this area for a study of cowbird control methods. As far as I know, however, no new censuses were taken until the 1971 decennial census. That year our 3-man crew found only 44 singing males in 2 sections. In fact, a decline of birds in all areas was the rule. Overall the number of birds declined 60 percent from the 1961 census (Mayfield 1972). This prompted concerned individuals to form an ad hoc Kirtland's Warbler Advisory Committee which instituted immediate measures to try to save the species. Among the actions taken was the establishment of annual censuses. Hence there are 8 consecutive years of data for the Ogemaw Management Area and environs, 1971-1978. During this period the population remained at about the 1971 level for 2 more years and then steadily declined until only 5 birds were found in 2 sections in 1978.

MECHANISMS OF GROWTH AND DECLINE OF COLONIES

The magnitude of the population increase from 1957 to 1961 (2 to 114) was very surprising, although there are other examples of rapid build-ups. For example, Walkinshaw and Faust (1975) report an increase of 4 males in 1961 to about 100 in 1966 in a Crawford County area. How these increases happened will never be known, but I will speculate about some of the possibilities for the Ogemaw birds.

TABLE 1. Counts of singing male Kirtland's Warblers, Ogemaw County management area and adjacent sections.

Township	Range	Section	1951	1955	1956	1957	1961	1971	1972	1973	1974	1975	1976	1977	1978
24N	1E	15	0	0	0	0	0	0	4	3	2	3	4	3	0
24N	1E	22	0	0	0	0	0	14	24	32	23	14	13	4	4
24N	1E	23	0	0	0	0	1	0	0	0	0	2	1	0	1
24N	1E	26	0	0	0	0	26	0	0	0	0	0	0	0	0
24N	1E	27	0	1	1	1	30	30	19	15	6	2	1	1	0
24N	1E	28	0	0	0	0	28	0	0	0	0	0	0	0	0
24N	1E	34	0	0	0	1	29	0	0	0	0	0	0	0	0
TOTAL			0	1	1	2	114	44	47	50	31	21	19	8	5

The first hypothesis is that there were really more birds present here in the mid-1950's than the 1 or 2 males found. I discount this. In 1954 the jack-pine reproduction resulting from the Horseshoe Lake burn area was just then developing into proper habitat for Kirtland's Warblers. As Mayfield (1960) states: "Typically, the warblers first appear when the tallest trees of the young growth are about as tall as a man (Christmas tree size), with trunks 1 to 2 in. in diameter at the base." Furthermore, I spent considerable time scouting for potential warbler management areas in Ogemaw and Roscommon counties; consequently, it seems unlikely that I would have missed any large colonies.

A second possibility was that a large colony was located nearby which shifted to this location; however, no other colonies were present in Ogemaw County. During this period, the closest area with birds was in northeastern Roscommon County, about 4 miles (6.4 km) away. Nine birds were tallied here in the 1951 census (Mayfield 1953). I made no regular censuses, but my impression was that these birds peaked about 1954 when I made a casual tally of 25 males. On the 1961 census we found 13 males there. The occupied habitat burned in 1964 and birds were not present there again until 1974. At best, only a small portion of the 1961 birds in Ogemaw County could have come from Roscommon County.

A third possibility was that the population present in 1961 was simply the normal increase of the 2 pairs which were present in 1957, assuming these males really had mates. Would it be possible to produce 114 pairs from 2 pairs in 4 breeding seasons? One can easily calculate the required rate for exponential growth from the usual equation $N_t = N_0 e^{rt}$ where N_t is the ending number of pairs (114), N_0 the initial number of pairs (2), t is the number of breeding seasons (4), and r is the geometric rate of increase. Solving this equation provides an estimate of 1.01 per year for r . This is equivalent to an interest rate of 101% compounded annually. Put another way, for every pair present 1 year, 2.75 pairs (5.50 birds) would be present the following year.

Under thoroughly favorable conditions, a species having 2 broods totaling 9 eggs can achieve an annual rate of increase per head of 1.01 (Brewer and Swander 1977); however, the Ogemaw Kirtland's Warbler population probably failed on several grounds to satisfy the requirements for a rate this high. Although it is now known (e.g., Berger and Radabaugh 1968) that double broods occur in the Kirtland's Warbler it seems unlikely (see Walkinshaw and Faust 1974, Orr 1975) that every pair attempts a second brood. While unparasitized nests may show a mortality rate from laying to fledging as low as the 23% assumed in Brewer's model (1977) (e.g., Orr 1975), it seems probable that the Ogemaw area from 1957 to 1961 had a high level of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) like that reported by Mayfield (1960) of 55% and Walkinshaw and Faust (1974) of 69%. For such nests a mortality rate of around 80% from laying to fledging seems likely (Anderson and Storer 1976). The cowbird control program was not instituted until 1972 (Shake and Mattsson 1975). Furthermore, the model's assumed mortality rates for yearlings (40% per annum) and adults (35% per annum) are probably both underestimates (although

the latter may be close; see beyond). In sum, it seems unlikely that Kirtland's Warbler could achieve an r of 1.01 except under the most favorable conditions, including the absence of cowbird parasitism and extremely high survival of young on the wintering grounds. I conclude that the population of 1961 did not arise solely from the natural increase of the birds present in 1957.

A fourth hypothesis involves augmentation by birds from other areas. To my mind, this is the only logical explanation. Recoveries of banded birds (Berger and Radabaugh 1968, Walkinshaw and Faust 1974, and Walkinshaw 1976) indicate the following:

(1) Most adult (2 years old and older) males return to the same territory, or very close to the same territory, year after year as long as they live. For example, Berger and Radabaugh (1968) reported on the returns of 28 males, 82% of which returned to the same territory at least once in subsequent years (not necessarily the original territory), another 14% returned to the same colony but different territories, while only 1 male (4%) was found in a different colony.

(2) Adult females also tend to return to the same colony year after year, but are less likely to return to the same territory. Data from Berger and Radabaugh (1968) show that for the returns of 34 females banded as adults, 97% returned to the same colony at least once. Forty-one % of these also returned to the same territory at least once. Only 1 (3%) was found in another colony.

(3) Yearling males (1 year old), by contrast, often go to colonies other than the one where they were fledged. The evidence here is more circumstantial. Berger and Radabaugh (1968) examined virtually all of the Kirtland's Warbler banding data from 1932 to 1966. Nearly 2/3 of the birds banded (296 of 457) were nestlings or recently fledged young. Of these only 8 (2.7%) were ever seen again as adults, and only 1 was a male. This was found virtually by accident in another colony. In addition, Walkinshaw and Faust (1974) report on the returns of 9 other males banded as young-of-the-year between 1967 and 1972. Four of the 9 were subsequently found in the same colony where they were banded. Walkinshaw (1976) reported on 3 more males, 1 of which returned to the same colony. Mayfield (1960) and Berger and Radabaugh (1968) concluded the survival rate of Kirtland's Warblers 1 year old and older is about 60%, based on banding data. Hence, for a stable population we would expect about 40 of every 100 breeding birds to be 1 year olds. For example, Walkinshaw (1977) has calculated a total production of 544 young fledged in 1972 by expanding the results from his study area to the entire population. If we assume a 60% survival of the 400 adults present, then about 240 were present in 1976 along with 192 1 year olds (both sexes) from the previous year to make up the 1973 estimated breeding population of 432 birds. Hence, the survival of fledglings must have been on the order of 35% ($192 \div 544$). This is much higher than the apparent survival of about 8% based on 7 returns of 88 nestlings banded by Walkinshaw in 1972 (Walkinshaw and Faust 1974). When studies are restricted to only a few colonies, the chances are slim of recovering young which move to other colonies.

(4) Yearling females (1 year old) also often go to colonies other than the one where they were fledged, but perhaps a higher proportion return to their birthplace than do males. As mentioned above, Berger and Radabaugh (1968) provided data for 7 female nestlings. Four of the 7 returned as adults to colonies other than where they were reared. Note that the text (page 167) is in error here. Table 7 is correct. Walkinshaw and Faust (1974) have detailed records for 5 more females, 3 of which returned to the same colony. The same comments on overall survival apply to yearling females as well as yearling males.

This evidence may indicate that in order for a colony to maintain or increase its population, it must "recruit" year-old birds, primarily those produced in other colonies. If it does not attract the 40% or so needed annually to maintain its numbers, it declines. Even though a colony no longer attracts new birds, the older birds keep returning as long as they live. The decline of the singing males tallied in Sec. 27, T24N, R1E, can be approximated quite well by assuming a constant 62% annual survival and no recruitment (Table 2).

It appears that most, if not all, multi-year nesting studies of Kirtland's Warblers have been carried out in declining colonies (Mayfield 1960, Walkinshaw and Faust 1974). If this is true, then it is possible that most yearlings actually recruited to these colonies were produced there. However, because of the small numbers involved, the derived recovery rates would imply poor survival, which they do. The remainder of the surviving yearlings would go elsewhere. For increasing colonies, however, most surviving young birds may return to the colonies where they were fledged along with varying numbers of recruits from declining colonies. Obviously, further research is needed.

Many ornithologists who have worked with the species have commented that there seem to be suitable areas that are never occupied (Wood 1904, Mayfield 1960). One might speculate that initial colonization occurs essentially at random with the subsequent development of a colony determined by its ability to attract yearling birds.

TABLE 2. Comparison of counts of singing male Kirtland's Warblers with a constant survival rate, Sec. 27, T24N, R1E, Ogemaw County.

YEAR	ACTUAL NUMBER OF SINGING MALES	EXPECTED NUMBER BASED ON A 62% ANNUAL SURVIVAL RATE
1971	30	30.0
1972	19	18.6
1973	15	11.5
1974	6	7.1
1975	2	4.4
1976	1	2.7
1977	1	1.7
1978	0	1.1

POSSIBLE EFFECTS OF VARIATIONS IN SEX RATIOS

In general, a 1:1 sex ratio appears to be the best evolutionary strategy for a species since it provides for maximum genetic variability and maximizes the probability of male-female encounters (Lerner 1968). Maximal productivity would presumably result if the maximum possible number of pairs were formed each spring. Ideally, then, the 2 sexes should be able to find each other and approximately equal numbers of males and females should be present in the breeding population.

One wonders how it is possible for each singing male to find or attract a mate, considering the apparent constraints on the movements of adults, as discussed above, coupled with the discontinuous distribution of colonies. Van Tyne (1953) reported that Dockham felt pairs were formed prior to arrival on the breeding grounds. One can envision definite advantages to such a system, since it would save valuable time on the breeding grounds. Mayfield (1960), however, discounted such early pairing based on field observations of early arrivals on the breeding grounds and pointed out that Dockham later changed his mind. In addition, wintering birds would seem to have considerable problems forming pairs and migrating together after pairing. So far as is known, Kirtland's Warblers winter only in the Bahama Islands, which consist of around 700 islands and 2,400 cays spread over 750 lineal miles (Mayfield 1960). Little is known about the actual distribution of wintering birds since they are now virtually impossible to find (Radabaugh 1974), but since 1879 birds have been collected or seen on at least 15 islands and cays (Mayfield 1960, Radabaugh 1974). No staging areas have been reported for the species.

Mayfield (1960) feels the actual searching and pairing activities are relegated to the breeding grounds. There is much casual evidence that at least some males may do considerable moving in the spring to find mates, and Mayfield believes these are yearling birds. Similar movements of yearling females, if they occur, would be difficult to notice.

Very little is known about sex ratios in Kirtland's Warbler nestlings. There are 27 recoveries from some 400 banded nestlings reported in the literature (Berger and Radabaugh 1968, Walkinshaw and Faust 1974, Walkinshaw 1976). Of these, 13 were males and 14 were females. In birds, the sex ratio is normally about equal at hatching (Lack 1954: Chapter 10). In a rare species such as Kirtland's Warbler, chance alone might cause some rather important fluctuations in sex ratios. For example, Walkinshaw (1977) calculates a total of 654 nestlings fledged in 1976 by extrapolating his study area results over the total number of singing males. Normally, one would assume about 327 males and 327 females; however, if say 54% were males, then we would have 352 males and 302 females, a difference of 50. Using a χ^2 goodness of fit test, this is the largest deviation in either direction which would not be significantly different from a 1:1 sex ratio at the $\alpha = .05$ level for this population size. By chance alone, varying proportions of males and females in both adults and fledglings could survive to the following season from the various colonies. Since something on the order of 40% of a given year's breeding population are year-old birds, an unbal-

anced sex ratio in 1 year's crop could have a rather drastic effect on the production in the following years. One would expect that a surplus of either sex would result in lowered production.

Simple counts of singing males, of course, do not reveal sex ratios. Sex ratio observations are made difficult by the fact that territorial males sing repeatedly from exposed perches and, hence, are very conspicuous, whereas females are silent and skulk about near the ground. In fact, it is often difficult to determine whether a given male has a mate. Since annual Kirtland's Warbler censuses are really counts of singing males, the usual convention has been to double the count to arrive at a "breeding population." Attempts to assess accurate population trends or predict future levels through use of this method would be confounded by unbalanced sex ratios.

Most studies of individual colonies seem to suggest approximately equal numbers of males and females on the breeding grounds. Both Mayfield (1960) and Walkinshaw and Faust (1974), however, present evidence for a slight surplus of males. There are no instances reported where a female was attended by 2 males. On the other hand, there are colonies with apparent surpluses of females. Mayfield (1960), Berger and Radabaugh (1968), and Radabaugh (1972) all report instances of polygyny. In fact, Radabaugh (1972) calculated that perhaps about 1/3 of the adults in an Oscoda County colony he was studying were involved in polygynous matings, and about 1/3 of the nests resulted from these matings. He also noted apparently the only record of a female changing mates within a single season. While we would expect unbalanced sex ratios to result in reduced nesting, there appears to be some compensatory activities by females to overcome shortages of males where they occur.

SUMMARY

Surveys of singing male Kirtland's Warblers in a northwestern Ogemaw County colony showed a spectacular increase from 2 in 1957 to 114 in 1961. Subsequently, the 1971 census indicated a decline to 44 and thence to 5 in 1978. For 1 square mile, annual counts approximated an average annual survival rate of 62%, assuming no recruitment.

A review of the literature suggests birds 2 years old and older tend to return to the same colony as long as they live, while 1-year-old birds tend to go to other colonies. Increases in colony size appear to be largely the result of attracting 1-year-old birds which were fledged in other colonies.

The literature suggests pairing is a breeding ground activity, with yearling males being the most active in searching for mates. Various studies indicate sex ratios may be unbalanced in either direction. A surplus of females may result in polygyny.

ACKNOWLEDGMENTS

I have learned much from two long-time investigators of Kirtland's Warbler biology and management, Harold Mayfield and John Byelich. Any worthwhile ideas presented here probably developed from discussions with them. I'll accept the blame for the poor ones.

I am grateful to Richard Brewer and Van Nolan, Jr., for straightening out my fuzzy thinking and pointing out errors in the first draft.

I would like to acknowledge the help of various members of our Roscommon-Ogemaw census crews over the years, particularly Jerome Weinrich, Victor Janson, Elsworth Harger, and George Burgoyne, Jr.

The first draft of this paper was developed while the author was visiting professor in Wildlife

Science at Utah State University.

This paper is a contribution, in part, of Federal Aid in Fisheries and Wildlife Restoration, Michigan Project FW-3-R.

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