BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. XXXIX JULY, 1968 No. 3

RETURNS OF KIRTLAND'S WARBLERS TO THE BREEDING GROUNDS

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The Kirtland's Warbler (*Dendroica kirtlandii*) is unusual among the North American species of the American Wood-warblers (Parulidae) because of its restricted and ecologically well-defined nesting area in north-central Michigan (Van Tyne, 1951). Because of the warbler's specific habitat requirements, it has been possible (on two occasions, 1951, 1961) to conduct singing male censuses of the entire breeding population of this interesting species (Mayfield, 1953, 1962). Both censuses indicated that the total population was about 1,000 birds. The Kirtland's Warbler also has been one of the most intensively studied species of wood-warbler (Mayfield, 1960). Nevertheless, it seems to be true that many significant new data can be obtained by further studies of the breeding biology of even the most common species of birds.

The analysis we present is based on a total of 457 banded Kirtland's Warblers. Harold Mayfield generously supplied us with data from the master file on the Kirtland's Warbler, which spans the period of 1931-1957, inclusive. This, also, is the period covered by Mayfield's monograph, *The Kirtland's Warbler* (1960), but the banding data are not included in the monograph. Data obtained by us covers the period of 1958 through 1965 (returns of previously banded birds through 1966). A break-down of this banding by years and by sex or age is presented in Table 1.

It will be noted that approximately twice as many adult females (110) have been banded as adult males (51). This is largely due to the relative ease with which incubating or brooding females of this ground-nesting species may be caught at the nest with a bow-net or butterfly-net, or even with a shirt or a felt hat.

Dr. Lawrence H. Walkinshaw banded the first Kirtland's Warbler ever banded near Lovells (Crawford County) on 25 June 1932. When he was in Honolulu on 25 October 1965, Walkinshaw told Berger that this female was so tame that he simply reached out and picked the bird off a branch.

Walkinshaw informed Berger (letter 8 February 1963) that he photographed this same female Kirtland's Warbler near her nest two days before he banded her in 1932. Walkinshaw wrote: "I set my camera on a short tripod because the bird kept landing on me (my back, legs, head, etc.), tied a string to the shutter, and

TABLE 1. BANDING OF KIRTLAND'S WARBLERS BY SEX OR AGE AND BY YEAR

Year	Males	Females	Nestlings (or fledglings)	Total
1932	1	2	3	6
33	0	1	0	1
34	0	0	0	0
35	0	0	4	4
36	0	0	2	2
37	0	0	0	0
38	0	2	14	16
39	0	0	2	2
1940	1	0	5	6
41	2	2	7	11
42	2	3	3	8
43	1	1	3	5
44	2	2	4	8
45	2	4	4	10
46	5	5	19	29
47	3	4	10	17
48	0	9	37	46
49	0	1	0	1
1950	0	1	0	1
51	0	4	14	18
52	2	5	23	30
53	1	4	26	31
54	0	8	14	22
55	2	4	9	15
56	8	10	16	34
57	0	4	9	13
	32	76	228	336
1958	0	1	0	1
59	0	0	0	0
1960	0	0	0	0
61	2	4	0	6
62	0	2	0	2
63	2	7	15	23
64	9	13	17	39
65	6	7	37	50
	51	110	296	457

then took the picture of the bird on my own hand" (Fig. 1). This is the photograph that appears as Plate 5 in *The Kirtland's Warbler* (Mayfield, 1960).

Josselyn Van Tyne banded the second Kirtland's Warbler (a male) on 29 June 1932, in Oscoda County (9½ miles southwest of Luzerne). Neither Walkinshaw nor Van Tyne appear to have been aware of the banding activities of the other man.

The first banded Kirtland's Warbler to be found in a subsequent year was a male Van Tyne banded on 30 June 1932; it was captured by him at the same location on 21 May 1933. The second banded Kirtland's Warbler recaptured in a subsequent year was a female banded by Walkinshaw in 1938 and recaptured by him in 1940. (Other historical data can be found in the works by Mayfield, 1960, and Berger, 1965, 1966.)

Figure 1. First Kirtland's Warbler banded (a female). Photograph taken 23 June 1932 near Lovells, in Crawford County, by Lawrence H. Walkinshaw. (Courtesy of Lawrence H. Walkinshaw.)

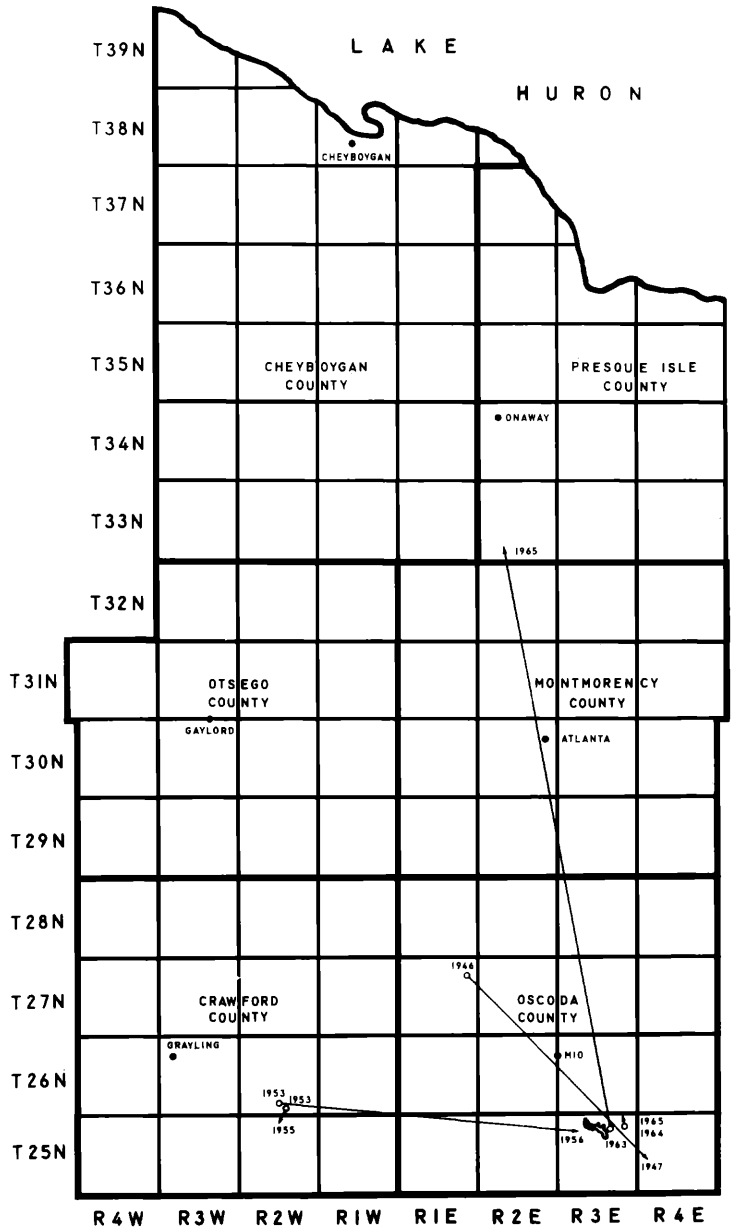
"CHANCES" OF GETTING BANDING RETURNS

It is obvious, of course, that the number (or the percentage) of returns of banded birds that one obtains depends, in part, both on the number of birds banded and on the intensity of effort expended in subsequent years in searching for previously banded birds. The last factor, especially, must be borne in mind in comparisons of returns for the two periods considered: 1931-1957 and 1958-1966.

A prime example of the element of luck, as well as diligence, in discovering banded birds that do not return to their area of banding is the female Kirtland's Warbler found in Presque Isle County by Nicholas and Mabel Cuthbert on 14 July 1965. This bird had been banded as a nestling 45 miles to the south in Oscoda County by Berger on 24 June 1963. (See Fig. 2 and Radabaugh, 1966.)

The detailed historical aspects of the shifting of his study areas by Josselyn Van Tyne as the habitat matured are beyond the scope of this paper. It is pertinent, however, to call attention to Mayfield's statement (1960: 3) that he had "information on 250 nests, but no one person has seen half of them, and very few nests were observed from start to finish." Mayfield added (1960: ix) that Van Tyne returned to the Kirtland's Warbler breeding grounds "for from one to twenty-five days' further work" in 22 of the years between 1930 and 1956.

Figure 2. Returns of five female Kirtland's Warblers banded as nestlings. Map includes data through the 1965 season. Mack Lake is shown in lower right. Town and range lines indicated, each square comprising 36 square miles. For banding details, see Radabaugh (1966).



It is a fact that Van Tyne and his co-workers never were able to devote an entire breeding season to the study of the Kirtland's Warbler. Why Van Tyne did not spend longer periods in the field work is largely conjectural. His inordinate sense of responsibility to the Bird Division of the University of Michigan Museum of Zoology, as well as his heavy load of editorial work throughout the years, however, undoubtedly played an important role in his failure to concentrate more intensively on the breeding biology of the Kirtland's Warbler.

It was not until 1954 that evidence was obtained proving that some Kirtland's Warblers were double-brooded. That finding was, according to Mayfield ("Observations on the Kirtland's Warbler, June 27 to July 10, 1954," unpublished report submitted to Van Tyne and Berger, 1954), "a totally unexpected discovery." Van Tyne had stated that Kirtland's Warbler was single-brooded (1953: 420; Mayfield has pointed out that this account was written in 1946). It seems reasonable to conclude that this belief and assumption—that the Kirtland's Warbler was totally single-brooded—resulted, in part, from the fact that there had been inadequate coverage of the breeding season prior to 1954.

In writing of the discovery of the two cases of double-broodedness in 1954, Mayfield (1960: 79) stated that this "rare event may occur more often than our records show, because not much of our field work has been done late in the nesting season. However, it is not a common occurrence, for diligent field work in several mid-summers has failed to disclose other such renestings" (*sic*). Actually, the 1954 discovery resulted from only 23 days of field work, which, however, were intentionally spaced in June and July: Berger color-banded adult female and nestling warblers for a nine-day period in mid-June, and Mayfield worked the area for 14 days in late June and early July. (Van Tyne was on an expedition to Bylot Island during the summer of 1954, and did not take part in the work).

It became evident during the 1955 breeding season that the study area in Crawford County (a forestry plantation) had matured to the point where profitable field work of a certain type could not be conducted there in 1956. It was decided later to shift the study in 1956 to the Mack Lake region in Oscoda County, where a series of fires had burned off large areas on 2 April 1946. Shifting of study areas obviously reduces the chances of getting banding returns.

Van Tyne, Mayfield, and Berger worked on the Mack Lake study area in various combinations during June, July and August of 1956. Sixteen nests were found, and Van Tyne and Berger color-banded 10 adult females, 8 adult males, and 16 nestling Kirtland's Warblers during June and July, 1956. This was the largest number of adults that had ever been color-banded in a single season (1932-1956).

Van Tyne died in January, 1957, and the follow-through on the study area the following summer was not as intensive as the work the previous year. Nevertheless, four of the males and four of the females (plus two banded females whose nests were not found)

banded in 1956 were found on the study area in 1957. This, again, was the largest number of returns that had ever been obtained in a single year since the first two Kirtland's Warblers were banded in 1932. (Unfortunately, circumstances were such that Berger was able to do very little field work during 1958 and 1959 and none in 1960.)

Consequently, it seems certain that at no time during the period of 1931-1957 was a study area worked as intensively *throughout the breeding season* as the Mack Lake area in the period 1963-1966. One might expect, therefore, to obtain a higher percentage of returns of banded birds and instances of double-broodedness in the later period.

ANALYSIS OF RETURNS

The data involved in this analysis span the years 1933-1966, inclusive. During this period, 69 individual Kirtland's Warblers (28 males, 41 females) were found in at least one subsequent year. Table 2 gives a breakdown of these returns by year and by sex. These 69 returns represent a 15 percent return of the total birds banded (457).

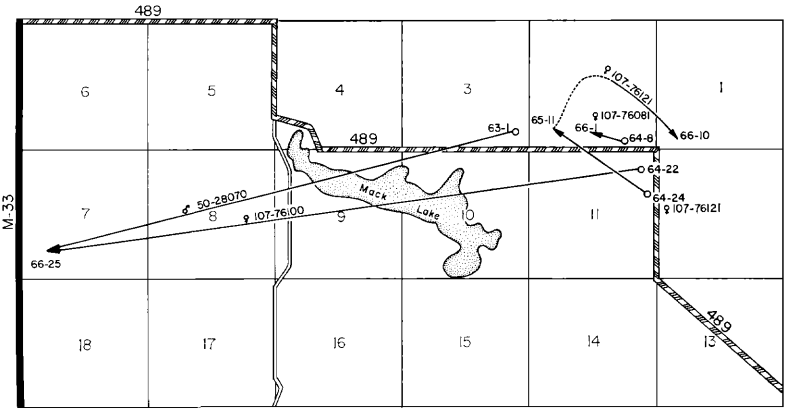
A factor *greatly* modifying the percentage of returns, however, is the large number of Kirtland's Warblers that were banded as nestlings or fledglings. Of the 457 total birds banded, 296 (64.7 percent) were young of the year (primarily nestlings but also a few recently-fledged young). Only eight (2.7 percent) of the 296

TABLE 2. RETURNS OF KIRTLAND'S WARBLERS (NO DUPLICATIONS)*

Year	Males	Females	Totals
1933	1	0	1
1940	0	1	1
41	1	0	1
42	2	1	3
43	1	1	2
44	1	2	3
45	0	1	1
46	0	2	2
47	2	2	4
48	2	1	3
1952	0	2	2
53	1	0	1
54	0	1	1
55	1	6	7
56	0	1	1
57	4	4	8
1964	1	2	3
65	5	7	12
66	6	7	13
	28	41	69

*Birds returning more than once arbitrarily recorded once, the year of their first return.

Figure. 3. Map of Mack Lake Area showing returns of birds banded as nestlings and returning locally. Each numbered square is a surveyor's section (One square mile). Data include the 1966 season.



young birds have been seen again as adults. Five of these eight were seen as adults in the same "colony"[1] in which they were hatched. The other three were found in other colonies some distance away (Figs. 2, 3).

The discovery of these latter three birds was virtually accidental. Because most of the occupied habitats in the Kirtland's Warbler breeding range are not worked in any given season (except for the census years), and because the discovery of those birds banded as young of the year is, therefore, very unlikely, we have chosen to disregard the 296 banded young in our present consideration of the percentage of banded birds returning to the breeding grounds.

If we consider, then, only the 161 Kirtland's Warblers banded as adults (see Table 3), we find 61 of 161 (37.8 percent) of banded birds returning. This figure obviously represents the minimum percentage of returning birds. Another real factor modifying this figure is the number of returning banded adults that are not looked for (or are inadequately looked for) in subsequent years. This can happen, as pointed out earlier, because of lack of time, change of study areas, or cessation of studies altogether. The number of

[1]The Kirtland's Warbler shows a strong tendency to nest in loose groups with the areas between, though seemingly suitable in every way, unoccupied. These "Colonies"—not by any means to be confused with *true* colonies such as those of many species of seabirds, etc.—consist of pairs on territories distributed in such a way that the birds communicate by sight or the sound of their songs. In the field it is normally no problem to delimit a "colony"—indeed many are scattered tens of miles apart on the comparatively tiny range of this species. The term "colony" is used for want of a better term and is traditionally written with quotation marks to distinguish the social arrangement of the Kirtland's Warbler from true colony nesters. For the remainder of this paper we will dispense with the quotation marks.

undiscovered returns is, of course, unknown. It is difficult, or perhaps impossible, to estimate such a number. Although the number may not be great, relative to the returns discovered, it does make the 37.8 percent return figure lower than reality.

There were 27 of 51 (52.9 percent) males banded as adults that were found in a subsequent year. In addition, one of the eight returns of birds banded as young of the year was a male.

There were 34 of 110 (30.9 percent) females returning after being banded as adults. Additionally, seven birds banded as young of the year were discovered to be females upon their return.

Inasmuch as there is no adequate evidence to the contrary, we assume that the sexes are roughly equal in numbers on the nesting grounds. If this is true, then it is likely that the discrepancy between male and female returns in the above figures can be accounted for by further assuming that some or many of the female returns are not found. The singing males, for example, "announce themselves," whereas the females are quite unobtrusive.

Mayfield (1960: 205) commented that, on the Old Mack Lake Area (Sec. 19, T25N, R4E, Oscoda County): "of 22 instances of returns a year later there were four instances of females which were not seen one year but were found the next. On the same area, which was studied extensively, no males were missed one year and found later." We have had similar experiences. The Old Mack Lake Area, as Mayfield pointed out, was such that a thorough search could be made of the entire area each season. In larger, or in less well-worked areas, a few males, too, would be missed.

TABLE 3. BANDING AND PERCENT OF RETURN DATA COMPARING THE PERIODS 1931-1957 AND 1958-1966

Period	Total number banded	Total banded as adults		Number returning				Percent returning
		male	female	Total	male	female	total	
1931-1966*	457				28	41	69	15
		51			27			52.9
			110			34		30.9
				161			61	37.8
1931-1957	336				16	25	41	12.2
		32			16			50
			76			22		28.9
				108			38	35.1
1958-1966*	121				12	16	28	23.1
		19			11			57.8
			34			12		38.2
				53			23	43.3

*Banding through 1965, returns through 1966.

Thus, we have approximately 50 percent of males banded as adults returning. This figure for returning males is even higher (57.8 percent) for the period 1958-1966 (see Table 3). Although we are dealing with only 19 males in this latter period, this evidence suggests an approximate 60 percent return for banded males.

It is essentially impossible to assess accurately how many females are missed and it is also difficult to explain why females might not return as well as the males. Nevertheless, on the available evidence, we are willing to suggest that approximately 60 percent of the females should return as well. Thus, about 20 percent of those females banded as adults and returning are missed by observers. This figure does not seem unduly high to us when one considers the many possibilities of missing a female in the field. Moreover, the opportunities for such sightings usually span only one nesting season inasmuch as most of the Kirtland's Warblers (banded as adults) that return, do so only once.

WARBLERS RETURNING ONLY ONCE

One appreciates, of course, that under the heading of "Warblers Returning Only Once" one actually means those birds which were *found* only once. There is a convenient division between the time period covered by Mayfield's monograph (1931-1957) and the period subsequent to 1957. Aside from convenience, however, there is a natural division between the two periods (when considering returns) because there are still many banded birds surviving from the latter period, whereas it is highly unlikely that there are remaining survivors from the earlier period. Any additional returns from the current group will, of course, remove such returns from the category of returning only once. Here, again, we have

TABLE 4. KIRTLAND'S WARBLERS BANDED AS ADULTS RECORDED AS RETURNING ONLY ONCE (NOT NECESSARILY THE YEAR AFTER BANDING)

Years and Groups	Numbers and Percentages of Return
Both sexes:	
1931-1966	46 of 61 birds (75.4%)
1931-1957	27 of 37 birds (73%)
1958-1966	19 of 24 birds (79%)
Males only:	
1931-1966	20 of 27 birds (74%)
1931-1957	11 of 16 birds (68. 7%)
1958-1966	9 of 11 birds (81.8%)
Females only:	
1931-1966	26 of 34 birds (76.4%)
1931-1957	16 of 21 birds (76.6%)
1958-1966	10 of 13 birds (76.9%)

TABLE 5. KIRTLAND'S WARBLERS BANDED AS ADULTS RECORDED AS RETURNING ONLY ONCE — IN THE YEAR AFTER BANDING

Years and Groups	Numbers and Percentages of Return
Both sexes:	
1931-1966	37 of 61 birds (60.6%)
1931-1957	22 of 37 birds (59.4%)
1958-1966	15 of 24 birds (62.4%)
Males only:	
1931-1966	17 of 27 birds (62.9%)
1931-1957	9 of 16 birds (56.2%)
1958-1966	8 of 11 birds (72.7%)
Females only:	
1931-1966	20 of 34 birds (58.8%)
1931-1957	13 of 21 birds (61.9%)
1958-1966	7 of 13 birds (53.8%)

excluded consideration of the eight birds that returned after being banded as young of the year because the chances of finding them are so small. Table 4 presents data on warblers returning only once—regardless of the number of years after banding. If, however, we take into consideration those birds which were found only once but in some year *other* than the first year after banding, and subtract these birds from the total returning only once, we obtain the data presented in Table 5. One must assume that these birds excluded from the new calculations did, in fact, return more than once but simply were not observed until some later year. Thus, Table 5 modifies Table 4 by skimming off those birds that really returned more than once (but were seen only once) and, therefore, brings us closer to the number of warblers actually returning only once.

Thus, on the basis of the data in Table 5 we can say that approximately 60 percent of those birds banded as adults that are found in subsequent years return to their former breeding area only once—and this return occurs the year following the year of banding. Much of this relates to the longevity of the birds involved.

WARBLERS RETURNING MORE THAN ONCE

The number of warblers returning more than once complements the number returning only once, relative to the total number of returns. It is the purpose of this section to show the distribution of these returns in time.

Fifteen of 61 (24.5 percent) of the birds banded as adults returned more than once. In this group, the difference between returns of males and females is slight: males, 7 of 27 (25.9 percent) birds; females, 8 of 34 (23.2 percent) birds. Data on 12 of these 15 birds are given in the following table:

Sex	Returned in 2 consecutive years		Returned in 3 consecutive years	
	1st & 2nd years after banding	2nd & 3rd years after banding	1st, 2nd & 3rd years after banding	2nd, 3rd & 4th years after banding
Male	4	0	2	0
Female	3	1	1	1

The sightings of the other three birds were as follows: One female returned the first year after banding, "skipped" a year, and then returned again the third year after banding. One female returned in seven consecutive years following the year of banding (returns in 1943-1949, inclusive); one male returned in eight consecutive years following the year of banding (returns in 1942-1949, inclusive).

In addition, we have the nine birds "skimmed off" in the previous section because, though sighted only once as returns, they undoubtedly returned more than once. The following table shows these returns relative to the time of banding:

Sex	Year After Banding		
	1st	2nd	3rd
Male		2	1
Female		5	1

We have used the term "return" to indicate the situation where a bird is seen (with a color-band) or recaptured in some year(s) subsequent to the year of banding. For the above nine birds, however, we have a situation analogous to the tree falling to the ground on an uninhabited island—is sound produced or do we need a listener? Events continue in our absence or ignorance and we are confident that these birds returned the *first* year after banding as well.

LOCATION OF RETURNS RELATIVE TO FORMER NESTS OR COLONIES

We deal with the males and females separately, discussing each in three categories: returning to the same territory, returning to a different territory in the same colony, and returning to a different colony.

Mayfield (1960: 49) states that the average territory for the Kirtland's Warbler (with 12 territories measured—by marking the farthest points reached by the singing males) is 8.4 acres. He also states that the territories are roughly circular. A circle with an area of eight acres would have a diameter of 225 yards. Thus if a bird (male or female) returns to within 225 yards of a former territory (most usually this involves measurements between the last known nest of the former year and the first known nest of the year of return), it is judged to have returned to the same territory.

TABLE 6. DATA SHOWING THE DISTANCE (IN YARDS) AND DIRECTIONS FROM LAST KNOWN NEST OR TERRITORY OF ONE YEAR TO FIRST KNOWN NEST OR TERRITORY OF A SUBSEQUENT YEAR — FOR 28 MALES

Males:	Year After Banding 1st	2nd	3rd	4th	5th	6th	7th	8th
F-30387	65 N							
34-51868	105 N	135 NW	200 E	+	120 SW	150 & 250 (200)†	130 SE	+
34-149331	30 NNE							
39-54175	+							
41-97261	45 NW	385 SE						
41-97265	250 W	350 S	200 SE					
41-97291	+							
41-97293	.....	30 SSE						
42-68862	600 SW	75 NE						
43-46979	45 W							
49-30938	210 S	20 S						
49-30939	.....	.....	+					
50-28021	100 N							
50-28027	150 SW							
50-28070*	.....	.....	6125 W ⁂					
50-28079	295 WNE	195 E	610 & 285 (445)†					
54-12549	100							
54-12550	100							
106-71778	+							
107-76082	100 SE							
107-76087	130 W							
107-76088	+							
107-76090	.....	875 ENE						
107-76095	+	740 SSW						
108-48117	415 WNW							
108-48130	30 & 370 (200)†							
108-48136	395 & 460 (425)†							
108-48200	150 W							
Averages:	185	312	1,742	....	120	200	130	...

Over-all average 392 yards.

*—banded as a fledgling.
+—no nest found, bird returned to the same general area.
⁂returned to another colony.
†two mates—distances averaged, no directions used.

If a bird's returning point is more than the somewhat arbitrary 225 yards, it is judged as returning to a different territory in the same colony—unless, of course, it returns to another colony.

1. Males (N = 28):

a. Eighteen (64 percent) of the males returned to the same breeding territory in subsequent years. Of these males, 14 (50 percent of the total) returned exclusively to the same nesting territory; four of these males also returned, in other seasons, to a different territory in the same colony. The average distance between nests (24 returns to the same territories among the 18 males) was 113 yards (range: 20 to 210 yards).

b. Nine (32 percent) of these males returned to different territories within the same colony. Five males did so exclusively,

TABLE 7. DATA SHOWING THE DISTANCE (IN YARDS) AND DIRECTIONS FROM LAST KNOWN NEST OR TERRITORY OF ONE YEAR TO THE FIRST KNOWN NEST OR TERRITORY OF A SUBSEQUENT YEAR — FOR 41 FEMALES

Females:	1st	2nd	3rd	4th	5th	6th	7th
34-51869	105 N	135 N					
38-70530	.....	200					
41-97249	.....	300 N	500 S				
41-97250	.....	435					
41-97262	45 NW	450 S	600 N	250 S	385 S	50 S	75 NE
41-97270	350 S	.....	700 N				
41-97271	.....	600 E	4 E	400 W			
41-97279	.....	900 NE					
41-97280	33,250 NE ⅋						
41-97295*	33,250 NE ⅋						
43-46990	1,300 SW						
49-30904	155 S						
49-30955*	.....	+					
49-30957	200 NE						
49-30961*	.....	.....	40,450 E ⅋				
50-9452	600 SW						
50-9453	1,500 SW						
50-9454	250 NW						
50-9455	150 NW						
50-9464	750 S						
50-28014	350 SE						
50-28016	300 S						
50-28018	600 SW						
50-28029	+						
50-28072	.....	200 N					
50-28078	.....	130 N					
50-28080*	.....	78,750 ⅋ (N)					
50-28085	.....	.....	750 N				
50-28086	725 E	600 W					
50-28088	715 W	305 SE	1,210 W				
106-71778	.....	+					
107-76080	210 SW	170 W					
107-76081*	.....	700 W					
107-76094	140 E						
107-76096	1,085 E						
107-76100*	.....	8,310 W ⅋					
107-76121*	1,750 W	1,680 E					
108-48106	400 W						
108-48116	415 W						
108-48135	1,870 E						
108-48160	45 W						
Averages:	3,097	5,867	6,316	325	385	50	75

Over-all average 4,065 yards, or, excluding those five returning to another colony, 520 yards.

*—banded as young of the year.

+—no nest found, bird returned to the same general area.

⅋—returned to another colony.

TABLE 8. DIRECTIONS AND DISTANCES OF RETURNS RELATIVE TO FORMER NESTS OR TERRITORIES: 18 MALES*

Sum of net movements for:	Directions								Number of Records
	N	NE	E	SE	S	SW	W	NW	**
1st year after banding	300	0	0	100	210	750	1,135	45	14
2nd year after banding	0	75	1,070	385	1,140	0	0	135	9
3rd-8th year after banding	0	0	200	430	0	120	0	0	4
Totals	300	75	1,270	815	1,350	870	1,135	180	27

*—does not include the male that returned to another colony.
**—see also Table 6.

whereas four others also returned, in other seasons, to the same territories. The average distance between nests or territories for this group (with nine such cases among the nine males) was 478 yards (range: 250-875 yards).

c. One (4.5 percent) male was found as a return in a different colony. The distance between the two nests involved was about 3.8 miles. These two colonies were on opposite sides of Mack Lake and were essentially isolated from each other within a nesting season.

The over-all average distance between nests for the 28 male returns was 392 yards (see Table 6).

2. Females (N = 41):

a. Twelve (29.2 percent) returned to the same territory. Ten of these 12 returned to the same territory exclusively; two others also, in other seasons, returned to different territories in the same colony. The average distance between nests (16 nests among the 12 females) was 126 yards (range: 4-210 yards).

b. Among the females, 23 (56 percent) were found as returns on different territories in the same colony. Of these, 21 did so exclusively; two others also, in other seasons, returned to the same territory occupied in some previous year. The average distance between nests (32 nests of 23 females) was 730 yards (range: 250-1,870 yards).

c. Five (12.1 percent) of the female returns were discovered in other colonies some distance from the colony where they were banded. Four of these five females were banded as young of the year (i.e., nestlings or fledglings).

The over-all average distance of the net movements for the 41 female returns was 4,065 yards (2.31 miles), or, disregarding the returns to other colonies, the average would be 520 yards (see Table 7).

TABLE 9. DIRECTIONS AND DISTANCES OF RETURNS RELATIVE TO FORMER NESTS OR TERRITORIES: 30 FEMALES*

Sum of net movements for:	Directions N	NE	E	SE	S	SW	W	NW	Number of Records **
1st year after banding	105	200	3,820	350	1,555	4,210	3,325	445	26
2nd year after banding	815	900	2,280	305	450	0	1,480	0	12
3rd year after banding	2,050	0	4	0	500	0	1,210	0	6
4th-7th year after banding	475	0	0	0	685	0	0	0	5
Totals	3,445	1,100	6,104	655	3,190	4,210	6,015	445	49

*—does not include five females returning to another colony.
**—See also Table 7.

Table 8 summarizes data on the directions and distances that banded males moved from a known nesting territory one year to a known nesting territory in a subsequent year. Table 9 presents similar information for banded females. It will be noted that net movements to the North, Northeast and Northwest are small in distance and in number relative to "movements" in other directions. At the present time, all that we can say is that these data simply show that many of the returns are not ending up quite as far north as they were in previous years. Additional information on distances and directions, for specific birds, is given in Table 6 (for males) and Table 7 (for females).

MALES AND FEMALES MATED AGAIN IN SUBSEQUENT YEARS

These birds fall into two categories: 1. mated again in males' former nesting territory, and 2. mated again but in a new nesting territory. Tables 10 and 11 and Figures 4 and 5 present information for both categories.

As pointed out in the previous section, only one out of 28 banded males returned to a different colony. Of the remaining 27 males, 18 returned to the same nesting territory a total of 24 times; nine males returned to the same colony but to different nesting territories nine times. Five of the 41 females banded and returning were found as returns in other colonies, four of these being banded as young of the year. Of the remaining 36 females, 12 returned to the same territory 16 times, and 23 returned to the same colonies, but to different territories, 32 times.

Hence, the data suggest that both males and females return to the same colony with about the same frequency, but that the males end up much closer to their former territories than do the females. This is reflected in the greater average net movements among the

TABLE 10. MALES AND FEMALES MATED IN MORE THAN ONE SEASON: RETURNING TO MALES' FORMER TERRITORY

Male	Female	Seasons in which mated
34-51868*	34-51869*	1941, 1942, 1943
34-51868*	41-97271*	1944, 1948
41-97261*	41-97262*	1942, 1943
42-68862*	41-97262*	1948, 1949
50-28079**	50-28078**	1963, 1965
108-48200**	108-48160**	1965, 1966

*—see Figure 4.
**—see Figure 5.

female returns—520 yards as opposed to 392 yards for the males (when excluding the females returning to different colonies).

Inadequate field work has been done in May (Mayfield, 1960: 44) to justify further comment on the behavior of the females on their return to the breeding grounds in the spring. Nor is there any real evidence to suggest that Kirtland's Warblers develop a pair-bond for more than a single nesting season. Available evidence does suggest, however, that the males arrive first on the breeding grounds. Inasmuch as the homing instinct is so strong in both sexes, we suggest the possibility that the same two birds will be mated in successive years if the female arrives on the male's territory early enough, that is, before another female has reached it so that a new pair-bond has already been formed before the previous mate reaches the male. Perhaps, sometimes, the already-mated male also establishes a pair-bond with a mate from an earlier year. This could be one explanation for the single males that have two mates at the same time (see, however, Fig. 5). There have been four cases of a male with two mates reported to date. Mayfield (1960: 57-58) reports one such case in 1947. The other three instances occurred on the East Mack Lake Area in 1966. It almost certainly occurs more frequently than our examples indicate but, so far at least, cannot be judged a common event.

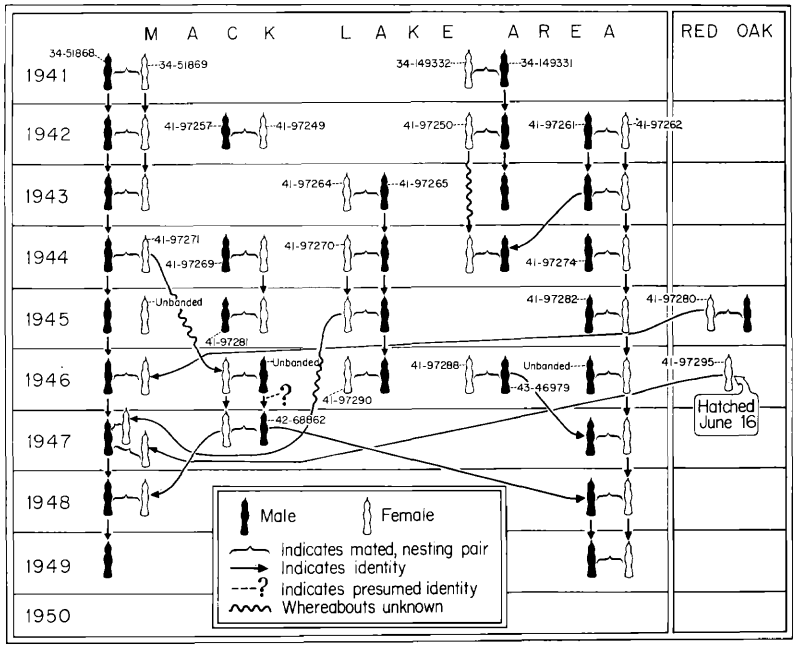
There have been two instances of females returning to the same territory but having a new mate.

TABLE 11. MALES AND FEMALES MATED IN MORE THAN ONE SEASON: ON A NEW TERRITORY

Male	Female	Years mated	Distance between nests
41-97265*	41-97270*	1944 & 1945	350 yards
108-48117**	108-48116**	1965 & 1966	415 yards

*—see Figure 4.
**—see Figure 5.

Figure 4. Chart showing the interrelationships of pairs of Kirtland's Warblers in the Old Mack Lake Colony (Sec. 19, T24N, R3E, Oscoda County) in the period 1941-1949, inclusive. Chart includes data on all pairs known to have mated in more than one season prior to 1965. Modified (by adding band numbers) from Josselyn Van Tyne's original chart (see Mayfield, 1960, Fig. 7).



LONGEVITY

The oldest Kirtland's Warblers known lived to be at least nine years old (male ♂34-51868; 1941-1949) and at least eight years old (female ♂41-97262; 1942-1949).

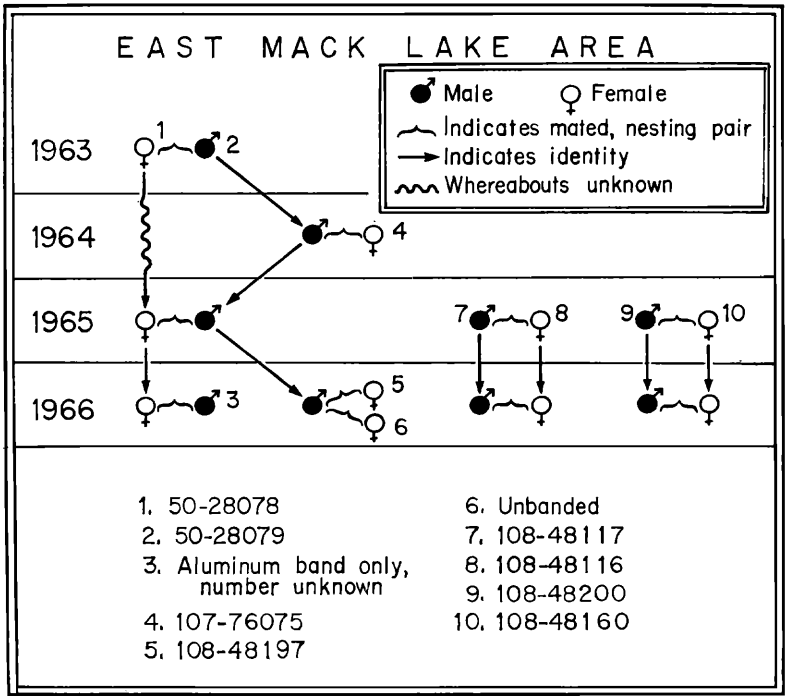
Radabaugh found five birds in 1966 that Berger had banded in 1963. Four of these were banded as adults and thus were at least four years old. Inasmuch as Berger banded only nine adults in 1963, this high return of four-year-old birds suggests a relatively high life expectancy for a songbird. The fifth bird—banded as a fledgling—hatched about 10 June 1963 and was, therefore, 3 years old in 1966.

Mayfield (1960: 206) calculated the life expectancy (or "mean after life") of an adult Kirtland's Warbler in June to be "about 2 years."

RETURNS CORRELATED WITH AGE OF HABITAT

It is possible at this time to make only a few general statements on this subject. As a given habitat declines (as evidenced, for

Figure 5. Chart showing the interrelationships of several pairs of Kirtland's Warblers in the period 1963-1966, inclusive. All pairs known to have been mated in more than one season are shown. Locations include Sections 3, 10, 11 and 12 (T25N, R3E, Oscoda County).



example, by an increase in tree size and concomitant deterioration in other habitat requirements), there is a drop in the population of Kirtland's Warblers. Despite the decrease in total population there may be an increase in the percentage of returns, presumably because those birds are most "accustomed" to homing to a previous nesting area. Such an increase in percentage of returns would seem to be a function of the declining habitat rather than of the total population of warblers.

AGE AT REPRODUCTIVE MATURITY

Two females banded as nestlings have been found during the following nesting season. The data given below show that these birds reached reproductive maturity during the year following their hatching. No males banded as nestlings have been found during the following breeding season.

Female 41-97295 was banded as a nestling in the Red Oak colony (Sec. 12, T27N, R1E, Oscoda County) on 22 June 1946. She was next seen 19 miles (31 km) away in the Old Mack Lake colony (Sec. 19, T25N, R4E) on 14 June 1947 on a nest containing

four warbler eggs. By 16 June this nest was abandoned. A re-nesting for this female was found on 21 June containing two warbler eggs—with the clutch of four being completed on 23 June. The female was still on the nest on 2 and 4 July but on 8 July the nest had been destroyed.

Female 107-76121 was banded as a nestling on the East Mack Lake area (Sec. 11, T25N, R3E) on 19 July 1964. She was next seen about one mile WNW (in the same colony) on 24 June 1965 at a nest containing four newly hatched warblers and one warbler egg—with a possible fledgling for only one of the young at a subsequent date.

RE-NESTING

A single-brooded species is one which attempts to raise only one brood of young to an independent stage during each breeding season. Insofar as we know, all single-brooded passerine species will, however, re-nest one or more times if the first or later nest is destroyed before young are fledged (Walkinshaw, 1941). Similarly, double- or multiple-brooded species may re-nest repeatedly during a single season because of the destruction of nests (Berger, 1951; Nolan, 1955). In order to follow with certainty such sequential nesting, it is essential that one studies color-marked birds.

The interval between the destruction of a nest and the laying of the first egg in the subsequent nest has been determined for several species: e.g., Prothonotary Warbler (*Protonotaria citrea*), 4 to 7 days (Walkinshaw, 1941); Song Sparrow (*Melospiza melodia*), 5 (usually) to 8 days (Nice, 1937: 111), 5 to 7 days (Berger, 1951); American Goldfinch (*Spinus tristis*), 4 to 21 days (Stokes, 1950).

Mayfield (1960: 79) stated: "After a nest has been destroyed or deserted, the female Kirtland's Warbler usually starts building another within one or two days, and lays the first egg of a new set five or six days after the loss of the previous nest. There is some uncertainty about the interval, because the time of the loss of the former nest is never known exactly, but in eight instances where it could be estimated fairly accurately, I judged the probable time in half the nests to be five days, and in half to be six days." In four additional Kirtland's Warbler nests (1964-1966), we found this interval to be 7, 8, 8, and 14 days. The average for the 12 Kirtland's Warbler nests is 6.75 days.

DOUBLE-BROODEDNESS IN THE KIRTLAND'S WARBLER

By definition, a double-brooded species is one which attempts to raise to independence two broods of young per nesting season. The basic criteria for establishing double-broodedness in a species are these: 1. the female, at least, must be uniquely banded; 2. a prior nest of this female must have been found and young must have fledged from it; 3. a subsequent nest of this female must be found containing at least one of her eggs.

Typically, a complete clutch is found in the second nest, but it is not necessary for every second nest to be successful (i.e., to fledge young) for the female to be double-brooded.

To date there have been seven known cases of double-broodedness: two in 1954, two in 1964, and one each in 1963, 1965, and 1966.

In 1954, Berger banded a number of adult and nestling Kirtland's Warblers in June. Mayfield later (late June and early July) followed some of the successful families. Mayfield likely had four "chances" to find second-nests—i.e., four instances where nests fledged early enough and where at least the female was color banded. He found two second-nests—the first ones ever found and the first inkling that at least some female Kirtland's Warblers were double-brooded.

In 1963 we had three "chances" and found one second-nest. In 1964, we found two second-nests out of four "chances." In 1965, one out of two, and in 1966, one out of two. In all, there were 15 "chances"; among these, seven (47 percent) second-nests were found (using a cut-off date of 28 June; see below).

There is, of course, uncertainty concerning possible second nests that were not found. Nevertheless, it appears that *at least* half of the females that successfully fledged a brood by 28 June go on to second-nest. The fledging dates from the first nests in these seven known instances of double-broodedness were: 19, 21, 22, 24, 25, 25, and 28 June (either known dates or ones estimated as closely as possible).

If we consider those pairs fledging a nest by 25 June, six (55 percent) second-nests were found out of 11 "chances." Further, if we consider those pairs fledging a nest by 22 June, three (75 percent) second-nests were found out of four "chances."

This line of evidence suggests that if female Kirtland's Warblers were to fledge first nests early enough they would *all* second-nest. Thus, although more data are clearly desired, we are willing to propose that the Kirtland's Warbler is a fully double-brooded species. We suggest that the relatively small number of second nests found to date results from several factors: the length of the Kirtland's Warbler breeding cycle and a concomitant relatively early cut-off date, after which the birds will not begin another nest; the uncertainty of climatic conditions during May and early June at the latitude (44-45° N.) of the breeding grounds, which may inhibit early nesting or cause either the desertion or the destruction of first nests; the destruction or desertion of many first nests owing to cowbird interference; the difficulty of finding second nests in July.

The interval between fledging of a brood from one nest and the laying of the first egg in the second nest is known (or could be estimated closely) for four nests (one each in 1963, 1964, 1965, and 1966): 5, 8, 10, and 15 days. This interval probably was six days for another nesting in 1964.

Berger color-banded an adult female and her five nestlings (estimated to be 4-5 days old) in nest 54-12 on 19 June 1954. Mayfield estimated that these young probably left the nest about 22 June. He found the banded female on nest 54-17 with four eggs on 30 June, only eight days after the estimated fledging date of the first brood.

Insufficient data are available to suggest a correlation between the size of brood fledged and the interval between fledging and the laying of the first egg in the second nest.

CUT-OFF DATE FOR DOUBLE-BROODEDNESS

There are two main considerations pertaining to the cut-off date for double-broodedness as used herein: 1. it is the date of successful fledging from a nest, and 2. it is the date beyond which the female will not build a second nest.

Such a cut-off date may vary somewhat from year to year. Thus we tend to seek the latest cut-off date and such a date, if discovered, might not apply every year.

Further individual variation may also be found among the females in any given season. For them there would be a cut-off "period" (covering several days), rather than a definite date. Each female presumably has her own cut-off date, and it is the latest which we attempt to find.

The latest cut-off date for double-broodedness found thus far is 28 June (1966). Five young warblers fledged from the first nest on 28 June. The female built a second nest, completing a clutch of four eggs about 9 July. Only one of these eggs hatched—on 22 July.

We know of only one nest later than this (one found in 1963), in which a warbler hatched on 24 July (two days later than the 1966 nest). We know nothing about possible prior nests for the 1963 pair, but it gives a suggestion as to how late the birds may nest. Mayfield (1960: 113) reports a nest found by Mary Jane Williams on 23 July 1946, which contained young birds about two days old (indicating a hatching date about 21 July).

It may be, then, that 30 June would be as late a cut-off date as we can expect. In any event, we can use the 28 June figure with certainty at this time.

Because only about 50 percent of the warblers fledging a brood prior to 28 June have actually been found with second nests, it is conceivable that there is a genetic strain that is double-brooded and another strain that is single-brooded. There is, however, no evidence to support such a hypothesis at this time.

LOSS OF PLASTIC BANDS

If an adult Kirtland's Warbler is seen on the nesting grounds bearing an aluminum band only, the bird may well be a return to that specific area. If the bird is not caught so that the band number can be read, however, it is lost to the records. Such birds, therefore, are a factor when one considers return data, and a word on the loss of plastic bands is pertinent here.

The following birds in point were banded as adults on the Mack Lake area in 1963 and 1964:

Female: yellow left, 50-28069 right—banded 21 June 1963—color band missing when she was re-caught 18 July 1963.

Male: yellow left, 50-28079 right—banded 24 June 1963—color band missing when re-caught 25 June 1964 (at which date another color band was put on the left tarsus)—this latter color band remained through the 1965 season, but was in the process of coming off during July 1966 (slipping downward over the toes).

Female: white over 50-28085 right—banded 19 July 1963—color band missing when re-caught 20 June 1966 (bird not seen in 1964 or 1965).

Female: green left, 107-76079 right—banded 15 June 1964—color band was missing when she was re-caught 24 June 1964.

Female: mauve left, 107-76096 right—banded 3 July 1964—color band missing when she was re-caught 22 June 1965.

Male: white left, 107-76090 right—banded 30 June 1964—color band was missing when he was re-caught 24 June 1966 (he was not seen in 1965).

One must not assume from the above that females lose plastic bands more frequently than males. Firstly, there are only six birds dealt with and, secondly, the 2:1 ratio of females to males matches the ratio of the sexes in total number banded in 1963 and 1964. Female number 50-28085 is the only bird *in this group* to have lost a color band when it was on the same tarsus as, and above, the aluminum band. Our data are too few to suggest that this placement is more secure (in fact it does not seem to be—see examples below).

Of the eight Kirtland's Warblers returning after being banded as nestlings, only three were color banded (at the original banding). None of these three had lost color bands when found again in subsequent years.

In 1964, there were four singing males bearing aluminum bands only that were not recaptured (nestlings from the previous years were color-banded). Three singing males in 1965 and two in 1966 similarly bore aluminum bands only; nestlings in 1964 and 1965 were banded with aluminum bands only. Judging by the territories occupied from one year to the next, there probably were not nine different males, but there was a minimum of four aluminum-banded-only male birds. These, plus the six birds that lost bands and were recaptured, constitute 22.7 percent of the 44 warblers banded as adults during the period 1963-1965, inclusive. We can, therefore, apparently expect to recapture about three-fifths of the birds lacking colored bands. Hence, only about 10 percent of the birds are lost from consideration because of the loss of colored bands.

It is possible, although not probable, that some types of color bands (e.g., a thin, butt-end type) could be pecked off by a Kirtland's Warbler. Both wild and hand-raised Kirtland's Warblers,

TABLE 12. COWBIRDS BANDED ON KIRTLAND'S WARBLER HABITATS

Year	Band number	Nest (if banded as a nestling)	Location
1952	48-173828	KW 52-4	7 Mi. NNE of Roscommon (?)
1955	53-150016	KW 55-10	Sec. 33, T26N, R2 W
	53-150017	"	" " "
1956	50-153901	KW 56-9	"West Mack Lake"
	50-153902	KW 56-5	"
	50-153903	KW 56-3	"
	50-153904	KW 56-12	"
	50-153905	"	"
	50-153906	KW 56-14	"East Mack Lake"
	53-150025	KW 56-8	"West Mack Lake"
	53-150026	"	"
	53-150027	KW 56-11	"
	53-150038	KW 56-15	"
	53-150039	"	"
	53-150040	KW 56-16	"
	53-150041	"	"
	53-150042	KW-56-17	"
	53-162609	KW 56-2	"
	53-162610	"	"
1957	53-150047	KW 57-13	"
1958	53-150053	KW 58-5	"
	53-150054	"	"
	53-150055	KW 58-7	"
	53-150056	Black-and-White Warbler	"
	53-150057	" " " "	"
1963	53-150066	KW 63-8	"East Mack Lake"
1964	64-194859	KW 64-5	"
	64-194860	KW 64-12	"
	64-194861	KW 64-10	"
	64-194862	KW 64-12	"
	64-194863	KW 64-20	"
	64-194864	KW "	"
	64-194870	KW 64-26	"
	101-139339	Adult female*	"
1965	61-157301	KW 65-22	Presque Isle
	61-157302	"	"
1966	61-157307	Nashville Warbler	"East Mack Lake"

*—caught in mist net (Sec. 11)

however, seem to become adjusted to their bands in a short time and soon ignore them. Some plastic bands are defective; these might break fairly soon. Weathering would continue with the passage of time, so that the loss of color bands might be expected to increase with time periods longer than those in the examples given above. Early losses of bands, however, probably would be greatest either because of faulty application or because circumstances forced one to band nestlings that were too young.

Nevertheless, the great majority of color bands remain on very well. Mayfield sent us data on the returns of 41 Kirtland's Warblers (25 females, 16 males), which returned a total of 67 times. Of these, 51 (76 percent) were recorded on a sight basis; some also were recaptured. Among the 41 birds, two females had lost colored bands that had been placed above the aluminum band on the same tarsus.

The longest-lived male Kirtland's was banded 34-51868 right, yellow left in 1941, and was recorded as a return, on a sight basis, every year thereafter to and including 1949. The longest-lived female was banded 41-97262 right, green left in 1942, and was recorded as a return, on a sight basis, every year thereafter, to and including 1949.

COWBIRDS BANDED ON KIRTLAND'S WARBLER HABITATS

Van Tyne, Berger, and Radabaugh banded 37 Brown-headed Cowbirds (*Molothrus ater*) on Kirtland's Warbler nesting areas (most of them in Kirtland's Warbler nests) during the period 1952-1966. We know of no returns for any of these birds. (We have no information on Cowbirds which Van Tyne may have banded prior to 1952.)

The cowbird removal program carried out by Nicholas Cuthbert on the Kirtland's Warbler Management Area (Mack Lake) in 1965 and 1966 did not turn up any cowbirds banded by Berger or Radabaugh (although Cuthbert's operation afforded an excellent opportunity for doing so).

SUMMARY

Lawrence H. Walkinshaw banded the first Kirtland's Warbler (a female) ever banded, on 25 June 1932. Josselyn Van Tyne banded the second (a male) on 29 June 1932. On 21 May 1933, Van Tyne found a second male as the first return for this species. The second return (a female) was one banded by Walkinshaw in 1938 and found by him again in 1940.

This analysis is based on 457 banded Kirtland's Warblers: 110 adult females, 51 adult males, and 296 banded as young of the year (principally nestlings).

A total of 69 Kirtland's Warblers (28 males, 41 females) have returned at least once (a 15 percent return). Of the 296 birds banded as young of the year, however, only eight (2.7 percent) have been seen in subsequent years. We have, therefore, elected to disregard the warblers banded as young of the year in this discussion.

Of Kirtland's Warblers banded as adults, 61 of 161 birds (37.8 percent) returned. There were 27 of 51 (52.9 percent) males banded as adults that returned; 34 of 110 (30.9 percent) females returned. We assume that females return to the breeding grounds as well as the males and that about 20 percent of these females are missed by observers.

Approximately 60 percent of birds banded as adults return only once. Of 28 male returns, 18 (64 percent) returned to the same

territory (territory averages 8.4 acres) a total of 24 times, nine returned to a different territory in the same colony once each, and one returned to a different colony. The over-all average distance in the "movements" from year to year was 392 yards.

Of 41 female returns, 12 (29.2 percent) returned to the same territory 16 times, 23 returned to a different territory in the same colony 32 times, and five returned to a different colony. The over-all average distance of the "movements" was 520 yards (disregarding the five returns to other colonies).

Males and females return to the same colony with about the same frequency, but the males are more likely to establish themselves on their former territory.

The males presumably arrive first on the breeding grounds in the spring. Because the homing instinct is so strong in both sexes, it seems possible that the same two birds will remate in successive years if the female arrives early enough—before another female has established a pair-bond with the male. Available evidence suggests, however, that a pair-bond usually lasts only during a single nesting season. Data on eight pairs of Kirtland's Warblers, mated in at least two seasons, are presented.

The oldest Kirtland's Warblers known were a male that lived at least nine years and a female that lived at least eight years. Four of nine birds banded as adults in 1963 returned in 1966, suggesting a relatively high life expectancy for a songbird.

Only two females (and *no* males) banded as nestlings have been found the following year. Both were found nesting when approximately one year old.

The interval between the destruction or desertion of one nest and the laying of the first egg in the subsequent nest is known (or could be estimated closely) for 12 cases. This interval varied from 5 to 14 days and averaged 6.75 days.

The analogous intervals for four second-brood nests were 7, 8, 8, and 14 days. No correlation is yet evident between the size of brood fledged and the number of days before the first egg is laid in the second nest.

The latest cut-off date (a date beyond which the females will not start another nesting cycle) found thus far is 28 June (1966), although we have some less conclusive evidence that this date may be as late as 30 June. Seven of 15 (46.6 percent females that successfully fledged a brood by 28 June have been found with second nests. In a smaller sample, about 55 percent of females that fledged young by 25 June second-nested; second nests were built by three out of four females that fledged young by 22 June.

Approximately 85 percent of the returns of Kirtland's Warblers have been judged on a sight basis (colored leg bands). Evidence suggests that about 10 percent of the returns are missed because of a loss of color bands.

No Brown-headed Cowbirds banded as nestlings on Kirtland's Warbler study areas have thus far been seen in subsequent years.

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Received April, 1967.