

PAIRING SUCCESS OF KIRTLAND'S WARBLERS IN MARGINAL VS. SUITABLE HABITAT

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ABSTRACT.—We compared pairing success of male Kirtland's Warblers (*Dendroica kirtlandii*) in different habitats to test the hypothesis that a lower proportion of males in marginal habitat are mated. Fewer than 60% of the males in marginal habitat were paired, but 95% of the males in suitable habitat were paired. We estimated the overall pairing success of the known breeding population at 85%. We could not estimate the number of females because the adult sex ratio is unknown, and an unknown proportion of Kirtland's Warblers are polygynous. The Kirtland's Warbler population was fairly constant from 1971 to 1983, despite markedly improved nest success resulting from cowbird control measures. If there are more males than females, or if many females fail to breed or must accept mated males or marginal habitat, population growth could be impeded. We combined reduced pairing success with an estimate of fledgling mortality, and revised the estimated number of fall immatures to between 369 and 471 birds—about 36% lower than the uncorrected estimate. Lower annual productivity of a static population implies higher annual survivorship of adults, yearlings, or both. Received 31 October 1985, accepted 17 October 1986.

THE known nesting range of Kirtland's Warbler (*Dendroica kirtlandii*) is restricted to 13 counties in the northern lower peninsula of Michigan. The first census of these birds in 1951 produced a total of 432 singing males (Mayfield 1953). A second census in 1961 found 502 males (Mayfield 1962), but by 1971 the population had declined to 201 singing males (Mayfield 1972). An average of 206 males for the next 10 years (Ryel 1981a) caused concern that the species might become extinct. The concentration of Kirtland's Warblers into a small number of breeding colonies (Probst 1986) provides a unique opportunity for comprehensive studies of population dynamics, habitat distribution, and mating system.

Research on the pairing success of male Kirtland's Warblers and other bird species is important for four reasons. First, the existence of unmated birds has implications for estimates of reproduction and other aspects of avian population dynamics. Second, researchers need an objective methodology for determining mating status of birds in densely vegetated habitats. In the case of Kirtland's Warbler, our methodology can be modified to estimate frequency of polygyny or even to ascertain the adult breeding sex ratio of an entire species. Third, the

proportion of unmated males is information vital to understanding the relative quality of breeding habitats for Kirtland's Warbler and other birds. Last, pairing determinations will be necessary to test a dispersal model that estimates colonization probability and pairing success in habitat that is central, peripheral, or disjunct from the known breeding range.

If some males remain unpaired, population growth will be lower than expected from calculations that assume complete pairing. In a species such as Kirtland's Warbler, with a very small population and a highly transitory breeding habitat, unsuccessful pairing could derive from an unequal breeding sex ratio. Mayfield (1960), Ryel (1979), and Walkinshaw (1983) found unpaired males, but unmated birds were assumed to be insignificant to the population dynamics of the species.

We hypothesize that the pairing-success rate varies in areas of different habitat quality, and is lower in habitat that is of marginal quality. We investigated the pairing success of male Kirtland's Warblers in three classes of habitat: suitable, young marginal, and open marginal. We studied Kirtland's Warbler pairing success in three habitat types, and extrapolated our results to the known breeding population for a reanalysis of demography. More specifically, we extended our results to the habitat distribution of the males within the known nesting range,

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and revised published and unpublished estimates of annual fledgling production (e.g. Mayfield 1978, Walkinshaw 1983).

METHODS

We studied the pairing status of Kirtland's Warblers in three sites during June 1982 and 1983. Each study site was classified as either suitable or marginal habitat. Marginal habitat was divided further into open-marginal or young-marginal categories. Open-marginal habitats were unburned, poorly stocked areas (see below), and young-marginal habitats were adequately stocked areas that had been used by Kirtland's Warblers for less than 3 yr. This distinction between suitable and marginal habitat was derived from the affinity of these birds for areas with a high jack-pine (*Pinus banksiana*) density (Mayfield 1960, Walkinshaw 1983). The period of suitability of any jack-pine area for nesting by Kirtland's Warblers is limited. There is a pattern of a gradual increase in the use of an area, followed by more stable populations that then decline (Probst 1986). To account for this rapid temporal shift in habitat suitability, we classified study sites as suitable only if they had been used by birds for 3 yr or longer. We classified as open marginal all areas that were unburned, naturally regenerated (i.e. poorly stocked), with stem densities estimated to be less than 2,500/ha. Jack-pine stands that were unburned and naturally regenerated had only about one-third the tree density of fire-regenerated stands or areas planted for Kirtland's Warbler use (Probst MS). Wildfire or plantation areas with more than 2,500 stems/ha that had been used for less than 3 yr were classed as young marginal.

During 1982, we studied two Kirtland's Warbler management areas (KWMA) in Oscoda Co., Michigan. Mack Lake KWMA represented suitable habitat. McKinley KWMA represented open-marginal habitat. In 1982, we also observed one other open-marginal habitat and two young-marginal habitats. We revisited these three areas and examined three other young-marginal areas and four other open-marginal areas in 1983 (Table 1). By 1983, Rayburn had been occupied for 3 yr and was reclassified as suitable habitat for the second year of study. One area of young habitat we studied was Bald Hill Burn, a large (800 ha) site that regenerated from wildfire. Large wildfires commonly burn an area that varies with respect to topography and site quality. The mesic microsites are occupied first, and birds colonize the xeric sites with shorter trees in later years. Thus, large wildfire areas are conveniently divided by tree height and density into two or more subareas. The 1975 Bald Hill Burn was divided into the Bald Hill North subarea, with denser jack-pine regeneration, and the more open Bald Hill South subarea. This allowed us to compare the influence of tree density on pairing suc-

cess in an area where distance from other Kirtland's Warbler colonies and other variables were similar.

We collected data mainly from open and young habitats because our data on pairing success in suitable habitats during 1982 agreed with previous experience that most, if not all, Kirtland's Warbler males there find mates (Walkinshaw 1983, Cuthbert unpubl. rept.). These previous assessments of pairing status were conducted primarily in habitat we would classify as suitable. During 1982 and 1983 we classified 27 males in young-marginal habitat, 24 in open-marginal habitat, and 19 in suitable habitat.

Pairing determinations.—Males were classified as mated if they were found with a female or fledglings. A female or fledgling was not always seen with a male during short observation periods, so we established criteria for duration of observation for pairing determinations. To determine the amount of time needed for observation before we could conclude that a male was not mated, we plotted the percentage of males classified as paired against observation time. These data initially were obtained from N. Cuthbert (unpubl. rept.). Data from the first year of our study were used to verify and improve the determination in the second year of the study (see below). As expected, the proportion of males classified as paired increased as observation time increased, but this percentage approached an asymptote below 100% at longer observation times (see Results). The sharp inflection of the curves strongly suggests that males were observed long enough for pairing determinations that compare habitats reliably.

Analysis of the 1981 data (Cuthbert unpubl. rept.) showed that mates of 89% of the Kirtland's Warbler males studied could be found in 150 min of observation per bird. Additional observation time resulted in almost no increase in the percentage of birds classified as paired. Consequently, in 1982 we assessed pairing status by observing individual males for periods of up to 150 min or until the presence of a mate was confirmed. If a bird was seen with a female or fledgling, it was classified as paired, and observation was terminated. If a bird was silent or unseen for 20 min, we stopped accruing observation time and observations were renewed later in the day or later in the season. Furthermore, the habitats we studied were more open than most of the areas Cuthbert studied, which should have made the detection of mates and fledglings easier.

The detection of pairing success may vary in different habitats (e.g. densely vegetated vs. open habitats). We developed a measure of observability based on track time for the second study year. Track time was defined as the time for which an individual bird was observed without losing visual or audible contact. By comparing the amount of track time with total observation time, we estimated observability for a particular study area or habitat type. We compared pairing success in different habitat types by estab-

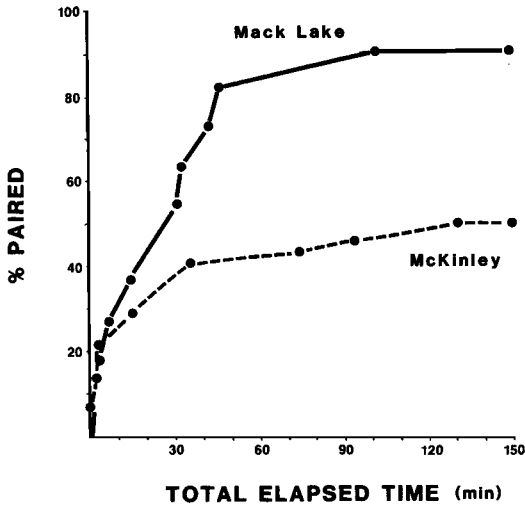


Fig. 1. The percentage of Kirtland's Warblers determined to be mated vs. total elapsed time for 1982. The curves level off after about 90 min total search time.

lishing the criterion for the required amount of observation in terms of track time alone. In 1982 all paired birds were classified as paired in less than 75 min of track time (see Results). Accordingly, in 1983 we refined our pairing determinations by observing birds for up to 90 min of track time.

Pairing determinations were made for males that were present during 5–30 June 1982, and 18–28 June 1983. Males that died, deserted, or relocated (presumably because of failure to attract or hold a mate) were excluded. If most of these males failed to attract a female at a new location, pairing success was overestimated. Because some desertions of territory were offset by immigration of new males, we assumed that few of the missing males died (see Nolan 1978). The annual mortality rate of adult male Kirtland's Warblers is about 25% (Probst 1986); hence, the mortality rate during the month of June should be no more than 2%. We assumed that seasonal survivorship is highest during the breeding season. The principal

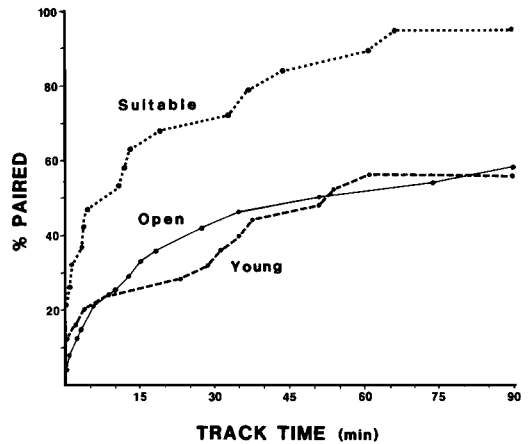


Fig. 2. The cumulative percentage of males classified as mated in 3 habitat classes in 1982 and 1983. Track time is that part of observation time for which the males actually were followed. The curves level off at about 60 min track time.

reason for low pairing-success estimates presumably was that birds we classified as unpaired became paired after our observation period ended. We also may have missed a few females because of insufficient observation time.

Finally, data on male pairing success were extrapolated to the known breeding population in 1982 and 1983 (Ryel 1982, 1983) by classifying occupied habitat as marginal or suitable using the criteria described above. The data on pairing success were combined with other published demographic data to estimate upper and lower bounds of annual fledgling production.

Statistical analysis.—We used Chi-square tests with a correction for continuity to compare numbers of paired and unpaired birds in different habitat types. The 95% confidence interval for pairing success in all marginal habitat combined was calculated using a normal approximation to a binomial distribution with a correction for continuity (Snedecor and Cochran 1967). Sample sizes were too small in suitable, young,

TABLE 1. Relative observability of male Kirtland's Warblers by habitat class.

Habitat class	Average total time elapsed ^a (min)		Average track time ^b (min)		Average ratio track/elapsed	
	All males (n)	Paired males (n)	All males	Paired males	All males	Paired males
Suitable habitat	49 (19)	41 (18)	24	24	0.62	0.61
Young marginal	90 (25)	54 (14)	48	31	0.68	0.67
Open marginal	96 (24)	59 (14)	53	25	0.59	0.59
All habitats	80 (68)	50 (46)	43	26	0.62	0.62

^a Total search time for female.

^b Actual observation time for Kirtland's Warbler male.

and open habitats to use the normal approximation for pairing success, so the 95% binomial confidence intervals were used for those three habitat classes (Blyth and Still 1983).

RESULTS

We were able to classify most mated males within 90 min elapsed time (Fig. 1) or 60 min track time (Fig. 2). The percentage of track time relative to observation time (Table 1) provided a measure of the observability in each habitat.

In suitable habitat (Mack Lake 1982 and Rayburn 1983), 18 of 19 males were paired (Tables 2 and 3), confirming Cuthbert's previous conclusions about pairing success in most habitats for this species. In open-marginal habitat, however, only 14 of 24 males were paired, and in young-marginal habitat only 16 of 27 were paired. The frequency of paired males was significantly different between suitable habitat and all marginal habitats combined ($\chi^2 = 6.70$, $df = 1$, $P < 0.01$). The frequency of paired males did not differ significantly between young-marginal and open-marginal habitat ($\chi^2 = 0.086$, $df = 1$, $P > 0.75$). Moreover, habitat that was less suitable for female Kirtland's Warblers was not

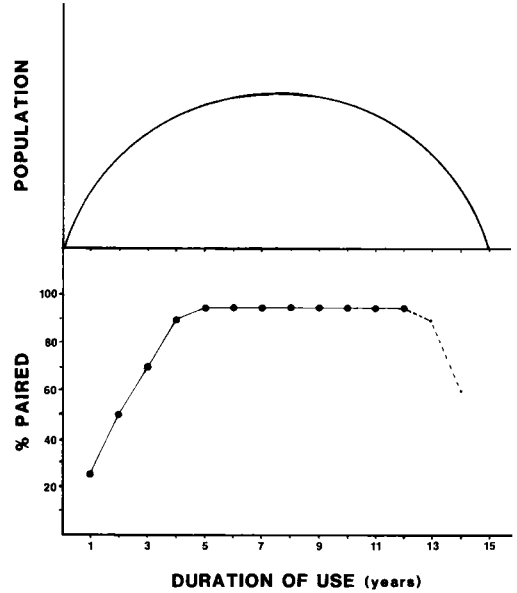


Fig. 3. Hypothetical curves of male Kirtland's Warbler population (top) and percentage of paired males for larger colonies of suitable habitat (bottom). The decrease in pairing success in older habitat is unconfirmed (dashed line) because we did not obtain data in that age of habitat.

TABLE 2. Habitat classification and pairing status of male Kirtland's Warblers.

	Year	Total males	Absent/relocated*	Un-paired	Paired	Proportion paired
Suitable habitat						
Mack Lake (S.3)	1982	14	3+	1	10	10/11
Rayburn	1983	8	0	0	8	8/8
All suitable habitat		22	3+	1	18	18/19 (95%)
Marginal habitat						
Young						
Rayburn	1982	6	1	2	3	3/5
Bald Hill NW	1983	6	0	1	5	5/6
Bald Hill SE	1983	12	0	7	5	5/12
Briggs Road	1983	2	0	1	1	1/2
Lovells (S.6)	1982 and 1983	2	0	0	2	2/2
All young habitat		28	1	11	16	16/27 (59%)
Open						
McKinley	1982	17-21	3-7	7	7	7/14
Parmalee	1982 and 1983	2	0	0	2	2/2
Briggs Road	1983	1	0	0	1	1/1
Meridian	1983	4	1	1	2	2/3
Canoe	1983	2	0	1	1	1/2
Manistee	1983	2	0	1	1	1/2
All open habitat		28-32	4-8	10	14	14/24 (58%)
All marginal habitat						30/51 (59%)

* Number of singing males that were absent after initial censuses; presumed to have relocated.

TABLE 3. 95% confidence intervals (CI) for pairing success in 4 habitats.

	Paired/total	Percent-age paired	95% CI*
Suitable	(18/19)	95	0.75-1.00
Young	(16/27)	59	0.40-0.77
Open	(14/24)	58	0.37-0.77
All marginal	(30/51)	59	0.44-0.72

*Intervals for $n \leq 30$ are from table 2 in Blyth and Still (1983); for $n > 30$ (all marginal habitat) the normal approximation with continuity correlation was obtained from the same source.

restricted to the more open, unburned stands. The results from Rayburn 1982 and Bald Hill suggest that unmated males are more likely to occur in stands of wildfire origin if the area is small (Rayburn) or young (Bald Hill and Rayburn) or relatively isolated (Rollways). The data from recently occupied areas (Rollways, Lovells, Rayburn, Bald Hill) indicate that over 40% of the males in such areas were unpaired. The importance of tree density to pairing success also was seen within the Bald Hill burn, where 5 of 6 singing males were mated at the denser northern region, but only 5 of 12 were mated at the more open southern site. Less than 60% of the singing males in young- and open-marginal habitat were paired. We have no data to support or refute the hypothesis that males in declining habitat have a lower probability of finding mates (Fig. 3), but previous observations (Mayfield 1960) support this idea.

Male distribution among habitats.—We estimated that about 160 and 147 males were found in suitable habitat in 1982 and 1983, respectively, and about 47 and 68 males (Table 4) were found in breeding areas that were either smaller, younger, or more open (i.e. marginal habitat). We extrapolated the pairing success results from suitable habitat (95% paired) to 73% of the males, and applied the data from the marginal habitat (59% paired) to the remaining 27% of the males. This yielded an estimated average for 1982 and 1983 of 292 mated males out of 307 males in suitable habitat, and 68 mated males out of 115 males in marginal habitat. Eighty-five percent of the 422 males were paired in 1982 and 1983 combined.

The results of male pairing success were combined with other demographic factors to predict the annual reproduction of the known Kirtland's Warbler population. This analysis was facilitated by the relatively stable popula-

TABLE 4. Kirtland's Warbler males in marginal* vs. suitable habitat, 1971-1983.

	Total no. males	No. males in		Percent-age of males in suitable habitat
		Marginal habitat	Suitable habitat	
1971	201	13	188	94
1972	200	14	186	93
1973	216	45	171	79
1974	167	49	118	71
1975	179	32	147	82
1976	200	48	152	76
1977	218	48	170	78
1978	196	29	167	85
1979	210	29	181	86
1980	242	25	217	90
1981	232	32	200	86
1982	207	47	160	77
1983	215	68	147	68
Average	206	36.8	169.5	82

* Habitat that is younger, older, or poorly stocked with trees relative to suitable habitat.

tion between 1976 and 1985. To examine the influence of reduced pairing success relative to other demographic factors, we estimated both low and high values of productivity and recruitment (Table 5). The first example assumes an operational sex ratio (OSR; Emlen and Oring 1977) of 0.90 and the second an OSR of 0.80 females per male. Fledgling production averages 2.6 fledglings per nest (Kelly and DeCapita 1982) or 3.1 fledglings per pair, which includes renestings (Walkinshaw 1983). Fledgling survivorship to independence for passerine birds ranges from 60 to 80% (e.g. Hann 1937, Walkinshaw and Faust 1975, Nolan 1978, data from Walkinshaw 1983). We used 75% survival of adults based on a 60% annual return of banded males (Mayfield 1960) plus an estimate of 15% relocations between years (Probst 1986). If we assume that our estimate of pairing success is not strongly offset by polygynous matings or late pairing by unmated males, then decreased pairing success combined with fledgling mortality reduces the estimate of fall immature Kirtland's Warblers to between 369 and 471 birds (Table 5). Uncorrected estimates ranged from 600 to 700 (Ryel 1981b, Walkinshaw 1983, Probst 1986). The number of new recruits each spring was calculated by assuming a stable population. Our data and assumptions indicated a 21-26% spring return rate of fall immature birds.

DISCUSSION

The principal cause for the decline of Kirtland's Warbler between 1961 and 1971 was hypothesized to be nest parasitism by the Brown-headed Cowbird (*Molothrus ater*). In response, the U.S. Fish and Wildlife Service initiated an intensive cowbird trapping program in 1972. This reduced the rate of nest parasitism by cowbirds from 50-70% of the nests before the initiation of trapping (Mayfield 1960, Walkinshaw and Faust 1975) to an average of 3.4% from 1972 to 1982 (Kelly and DeCapita 1982). The number of fledglings per nest increased from 0.81 to 2.76 during the same period (Kelly and DeCapita 1982).

During 1971-1983 the Kirtland's Warbler population fluctuated between 167 and 242 singing males (\bar{x} = 206; Table 4). Thus, cowbird control did not promote a substantial recovery of the species. A variety of explanations for this has been offered. Ryel (1981b) suggested that the population may be limited on its wintering grounds. Probst (1986) suggested that low pairing success (ability to attract and hold mates), fledgling mortality, and yearling dispersal may account for a static situation or a slow recovery of the population.

The results on pairing success of Kirtland's Warbler may be important for revising past productivity estimates. In the period 1973-1977 an average of 23% of male Kirtland's Warblers were in either declining breeding areas or young, developing colonies (Table 4). Many of these birds may not have paired successfully, which may have contributed to the slow recovery of the population. During the years 1978-1981, 87% of the males were in larger colonies of suitable habitat; almost all of them presumably paired successfully. In 1983 the proportion of males in suitable habitat was only 68%. The trend toward a high proportion of males in marginal habitat should continue from 1984 to 1989, because most males probably will be in young or declining habitat in those years. We have not related our 1982 and 1983 estimates of pairing success to the proportion of males in marginal habitat in other years, because the distribution of females may have changed under different habitat conditions in different years. In addition, our estimate of males in marginal habitat in 1982 and 1983 may be conservative because we excluded those males that were in old marginal habitat.

TABLE 5. Estimates of Kirtland's Warbler annual productivity and recruitment (1982 and 1983 average).

Estimate	No. of females	Fledglings/ pair ^a	Fledgling survivorship	[Subtotal]	x	Calculated survivorship of immatures	+	[Subtotal]	+	Adult survivorship ^b	=	No. of spring Kirtland's Warblers
High productivity	(190 ^c	x 3.1	x 0.80 ^d)	[=471]	x	0.21	+	[=100]	+	(402 x 0.75)	=	402 (212 males)
Low productivity	(170 ^e	x 3.1	x 0.70 ^f)	[=369]	x	0.26	+	[=95]	+	(382 x 0.75)	=	382 (212 males)

^a Walkinshaw 1983.

^b 60% return rate plus estimate of 15% relocations (Probst 1986).

^c 0.90 operational sex ratio (assumes equal OSR in primary habitat).

^d High estimate for fledgling survival (data from Walkinshaw 1983: table 39).

^e 0.80 operational sex ratio (assumes that polygyny is rare and that pairing success is reduced in old, declining habitat).

^f Low estimate for fledgling survival (Walkinshaw and Faust 1975).

Mating system and habitat.—Polygynous mating systems are more likely to evolve in species that have minimal male parental care and in habitats where the vegetation has little vertical complexity, such as marshes or grasslands (Verner and Willson 1966). Verner and Willson argued that two-dimensional habitats are characterized by a more patchy distribution of resource productivity, and male territories of more varied quality, than habitats with greater vertical structure. Nevertheless, polygyny could evolve in more uniform habitats if males divide resources unequally (Vehrencamp and Bradbury 1984). Under such circumstances, it could be more advantageous for a female to pair with a mated male in a highly suitable territory than to choose an unmated male in an unsuitable or marginal one. Thus, polygyny could evolve in a species without a surplus of females (Verner 1964, Orians 1969; but see below). Birds with polygynous mating systems may occupy habitats with unmated, monogamous, and polygynous males present in the same stand. In some cases, the mating status of the males has been correlated with habitat variables (e.g. Verner 1964, Willson 1966, Pleszczyńska 1978, Carey and Nolan 1979, Zimmerman 1982).

There are 14 published incidents of polygyny reported for Kirtland's Warbler (Mayfield 1960, Radabaugh 1972, Walkinshaw 1983). Radabaugh (1972) estimated a maximum of 12% (9/72) of the males in one subsample had two mates (a larger sample of male Kirtland's Warbler may not have been observed long enough to confirm all possible cases of polygyny).

Kirtland's Warblers differ from other examples of the evolution of polygyny in at least two respects. First, males are actively involved in nesting at all stages of the cycle. They help build the nest, feed the female during incubation, care for nestlings, and help feed fledglings (Mayfield 1960, Walkinshaw 1983). Thus, Kirtland's Warbler should have an unusually high polygyny threshold (Verner and Willson 1966, Orians 1969) for selection to favor sharing of male parental care relative to pairing with unmated males. For example, if male Seaside Sparrows (*Ammodramus maritimus*) are removed experimentally, reproduction suffers (Greenlaw and Post 1985), so male assistance can be significant to nesting success in species where males help regularly. Second, the jack-pine habitat has more vegetative complexity vertically than marshes or grasslands, but less

than forests. Nevertheless, the patchy distribution of trees in the Kirtland's Warbler shrubland habitat has potential for male territories of unequal quality, so it still would be advantageous for a female to pair with a mated male if her reproductive success could be higher than it would be on a poorer territory with an unmated male.

Number of breeding females and annual productivity.—Although male pairing success is a useful criterion for ranking habitat quality, reproductive estimates must be made from the number of breeding females. Polygynous matings compensate for unpaired males to an unknown degree. Similarly, successive monogamy could add to the number of females estimated from the number of males alone. The possible alternatives that would explain the existence of unmated males in marginal habitat have consequences, however, that lower the production of fledglings relative to a habitat situation where almost all pairs are monogamous in suitable habitat: (1) successive monogamy or late pairing, (2) polygynous mating, (3) unequal tertiary sex ratio, or (4) females unmated for an entire breeding season.

The Kirtland's Warbler mating system may vary with changes in habitat quantity and distribution. When suitable habitat is relatively abundant, monogamy should be more prevalent. Polygyny should become more widespread as suitable habitat becomes scarce or dispersed, a situation that probably occurred in the 1960's and early 1970's. At present, habitat is relatively scarce and scattered. This situation should favor a mix of unmated, monogamous, and polygynous males. Similar habitat conditions are occurring now, and by 1989 5 or 6 major breeding areas should have negligible populations. Most Kirtland's Warblers may be concentrated in two major wildfire areas by that time. Polygyny may become more prevalent, and scattered males may occupy a number of smaller stands where their pairing success is low. If the population is to remain constant, these declines must be offset by large numbers of breeding females in two major wildfire areas that should comprise a large part of suitable Kirtland's Warbler habitat in the future. Thus, the Kirtland's Warbler mating system may result from the species' fragmented and transitory habitat within a limited breeding range. The proportion of unmated and polygynous males may fluctuate with habitat conditions through time.

We recommended that Kirtland's Warbler habitat managers raise the tree-stocking level to 2,500-3,800 stems/ha in situations where this is not already being done. This suggestion, accepted by the USDA Forest Service, should maximize pairing success in areas managed for Kirtland's Warbler. Previously, Probst (1985) also suggested that stand rotations within Kirtland's Warbler Management Areas should be planned for more temporal overlap to increase Kirtland's Warbler colonization success and male pairing success during the early period of Kirtland's Warbler occupancy of a stand.

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