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Kirtland's Warbler, Victim of Its Own Rarity?

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The recent history of the population of the Kirtland's Warbler (*Dendroica kirtlandii*) presents some baffling questions. The population declined from about 500 singing males in 1961 (Mayfield 1962) to about 200 in 1971 (Mayfield 1972) under intolerable pressure from nest parasitism by the Brown-headed Cowbird (*Molothrus ater*), which has expanded its breeding range to include that of the warbler only in the last 100 yr (Mayfield 1960). The cowbird has continued to increase. In the late 1960's it parasitized 70% or more of all Kirtland's Warbler nests and depressed the production of young to less than one fledgling per pair of adults per year (Ryel 1981). Measures to control the cowbird started in 1972 and are continuing with remarkable success, reducing parasitism to negligible levels (Shake and Mattson 1975). The production of young warblers immediately rose to rates never seen before and has remained at these high levels (Walkinshaw 1977, Nicholas L. Cuthbert unpubl.), setting to rest any doubts about the fecundity of the species. The decline in the population was arrested, but the number of adults has not increased as expected. The number of singing males has remained nearly level from 1971 to 1982, fluctuating between 167 and 243 (Ryel 1982).

What factors hold the population down in spite of excellent nesting success and survival of adults? Plainly, some combination of factors has been operating selectively against the young with special force in the last two decades. I will consider several possibilities, beginning with problems in the breeding season.

Intuitively, most biologists turn first to the breeding habitat. Indeed, this is restricted and specialized, consisting of extensive homogeneous stands of young jack pines (*Pinus banksiana*) on poor sandy soil in northern lower Michigan. This habitat is a transitory

phase in the forest succession occurring naturally after forest fire and in a modified form after cutting and planting. We suspect the habitat was most extensive in historical times during the 1880's and 1890's in Michigan and perhaps also in Ontario, Wisconsin, and Minnesota at the height of lumbering in the region, when forest fires were frequent and unretarded. At that time Kirtland's Warblers were found on their wintering grounds in the Bahama Islands much more frequently than today (Mayfield 1960). Jerome Weinrich (unpubl.) has calculated that suitable habitat also declined 40% from 1961 to 1971 along with the recent decline in warblers. Thus, a probable maximum and a recent minimum in population have corresponded with gross trends in the extent of suitable habitat. Without doubt, at some level of population, the available habitat would limit the number of birds, and, therefore, efforts to increase the habitat would be a wise conservation measure, but field study has not turned up evidence that the present habitat is inadequate.

Nesting success is good. Unmated individuals are rare. In nesting "colonies" the area used by each pair always seems much smaller than the space available to them. Measured territories have a mean area less than 4 ha (Mayfield 1960), but the area available on occupied tracts usually amounts to more than 12 ha per pair. When mapped, the territories are rarely contiguous on all sides as though crowded. In addition, many tracts of young pines that appear suitable to human eyes are not used by warblers. An example is a large cutover tract in Oscoda County that held the following numbers of singing males in the years beginning in 1975: 0, 6, 0, 1, 1, 10, 14, 22. If it was suitable in 1976 when it held six males, it was surely not less so in the next three years when it had virtually none. In 1980 it became more productive.

For many species losses are heavy among juveniles soon after fledging. In Prairie Warblers (*Dendroica discolor*), 28% disappeared in the 32 days between fledging and independence (Nolan 1978). Mortality in this period has not been measured for Kirtland's Warblers, but observations of postnesting family groups lead us to suspect that these juveniles, living in a barren land with few predators and competitors, may fare better than many other small birds (Mayfield 1960). Losses at this stage of the annual cycle are an important consideration, but we have no reason to believe they have increased in recent years.

Migration may hold the threat of occasional disaster, for this species traverses the hurricane zone between the United States and the Bahamas twice each year (Trautman 1979). Population counts in 14 separate years, however, have not shown declines corresponding to major storms (Ryel 1981). Also, one must note that the migration period, spread over 6 weeks, puts few individuals in flight at one time, and the devastation of each hurricane strikes only a small part of the winter range. Further, this hazard, whatever its seriousness, has been surmounted for thousands of years.

There has been speculation about unknown limiting factors on the winter range, where the bird spends two-thirds of each year. Here, for example, it may be under pressure of competition from fluctuating numbers of other North American visitors, particularly the Palm Warbler (*Dendroica palmarum*), which is abundant in the same islands (Fretwell 1981). This idea remains untested, because there is so little information about the numbers and interactions of the species involved. Modern observers have had mere glimpses of the Kirtland's Warbler in winter, suggesting that the birds are widely dispersed and perhaps solitary. The only evidence thus far of a variable effect of wintering conditions comes from analyses of winter rainfall in the Bahamas. Recent fluctuations in the breeding counts show a strong positive correlation with November-April rainfall and presumably food supply (Ryel 1981). This factor is not new, however,

Unlike many tropical regions, the interiors of these islands have been little altered by man in modern times. These infertile, scrub-covered lands have few human inhabitants, whose attention has been turned mainly toward the sea. Concern has been voiced about the lumbering of pines on portions of the three northernmost islands in the 1950's and 1960's (Radabaugh 1974). Yet, this most recent cutting proceeded down through the chain for 18 yr, and vigorous regrowth was established on the first tract before extensive cutting began on the third, so the removal of trees by loggers may not have been unlike the effect of recurrent local fires down through the centuries. Also, it is noteworthy that most winter sightings of Kirtland's Warblers have taken place on islands without pines. In any case, there is a good likelihood that

pines on these islands are more recent than the warbler (Olson 1982).

Finally, I turn to a factor not mentioned heretofore and perhaps unique to this species. As the numbers of birds and the extent of their nesting range diminishes, pinpoint accuracy in migration becomes more important. We do not know how Kirtland's Warblers steer to their nesting sites, but we know that experienced adults negotiate the trip very well. I estimate a survival rate of close to 65%, because 60% of banded adults are actually found in the next year, and a few probably escape detection (Ryel 1981). Nearly all adults return to the same nesting "colony," that is, within 1-2 km of the site where banded. This navigational feat, however, is almost certainly more difficult for young birds in their first northward flight. With a population so precariously situated, a few lost each year from this cause could impede recovery. That some birds of this species stray is proved by the discovery of singing males from time to time far outside the normal range. In 1978 alone, four males, two of them banded as nestlings in previous years in Michigan, remained for weeks in Wisconsin, Ontario, and Quebec. Individuals occupied some of these same locations in 4 of the last 6 yr. Surely, most such birds escape detection in the vast pine zone of the Great Lakes region.

The proportion of birds banded as nestlings and recovered in later years is very small in this species, as in other small migratory birds (Ryel 1979). Therefore, the rate of survival in the first year can be inferred only from the number needed to balance the prevailing mortality of adults. At present, this is about 23%. Through control of cowbirds, the production of fledglings per pair of adults tripled in the 1970's as compared to the 1960's, while the survival rate of adults has remained constant. Yet, the population has not increased, and therefore recent losses have fallen disproportionately on the young in their first year of life.

A possible factor operating with increasing force in recent years and selectively against inexperienced birds is the shrinkage of the nesting area the birds must find to breed successfully. In 1951 and 1961 about 500 pairs nested in about nine counties scattered over an area 100 km north to south and 160 km east to west, defining a rectangle of about 16,000 km². When the population crashed in the 1960's, it did not decline evenly across the range but collapsed back into the heart of the range, where the birds nested as densely as ever. In 1982, if one ignores two isolated males not known to be mated, the entire population of 207 pairs (Ryel 1982) nested in a region 50 km north to south and 68 km east to west, defining a rectangle of about 3,400 km². Thus, the width of the range has been reduced almost two-thirds and the area more than two-thirds.

Yearlings may be especially prone to migration errors, because young of other species, if displaced

in long-distance flight, as by lateral winds, have shown a tendency to persist in their original bearing, while adults experienced in the route have made the necessary corrections (Matthews 1964). A similar question might be raised about the navigational difficulties in southward migration, but the Bahamas present a far larger target than the breeding ground, and they have not shrunk in recent years.

The reduction of the nesting range to a mere dot on the continental map may have progressed over a century or more. I suspect that suitable habitat was widely distributed along the front of the Wisconsin Ice Sheet up until about 10,000 yr ago. There is some evidence suggesting that in the last century the species may have been distributed more widely than at present in the Great Lakes States and southern Canada (Mayfield 1960). Interglacial periods like the present were the exception rather than the rule in the Pleistocene, and it is hard to believe the species has teetered along the brink of extinction for thousands of years.

Kirtland's Warblers that miss their target in migration are likely to be wasted. Dispersed individuals of such a rare species are unlikely to encounter a possible mate, and in this case the importance of finding others of their kind for successful breeding involves more than just male-finds-female. This importance is indicated by the birds' tendency to clump into colonies more than habitat constraints would require, as illustrated by the collapse of the population back into the central groups in the 1960's. It is not known how widely the warblers search for nesting sites after arrival in spring nor how widely the juveniles wander in late summer to become "imprinted" with localities other than the birthplaces. Adults and juveniles have been found up until migration time in mid-September still in the vicinity of their nests, and they have been found nowhere else (Mayfield 1960, Weinrich unpubl.). I have not detected any appreciable influx into established colonies in mid-season nor any other indications that the birds are still moving around. On the contrary, isolated unmated males have held to singing territories for weeks, and one outside the range in Ontario returned to the same unproductive site for at least 2 yr. Females have never been found in breeding season except in the vicinity of nests.

Among songbirds, the yearlings returning to the location where they hatched ordinarily are not sufficient to replace the annual decrement of adults. Replacements come from young hatched elsewhere. Thus, the tendency to scatter is valuable as long as it does not come at too high a cost in lost opportunities to breed. The well-studied Prairie Warbler in Indiana offers a comparison with the Kirtland's Warbler. The migration routes of both species are similar, and the return rates of adults are almost identical. In both warblers the rediscovery rate of yearlings is very small, about 4% of fledglings in the Prairie Warbler. Yet, the calculated survival rate of yearlings is about

40%. Thus, nine-tenths of the young die or locate elsewhere (Nolan 1978). Prairie Warblers may stray hundreds of miles away and still find mates and nesting habitat, however, because the bird nests from the Great Plains to the Eastern Seaboard. A Kirtland's Warbler that strays even slightly may find itself separated from others of its kind by the wide expanse of Lake Huron or Lake Michigan.

For the Kirtland's Warbler one can perceive this unique scenario of new difficulties superimposed on its age-old problems of survival. First, the population was restrained by shrinking habitat, then the cowbird delivered an almost fatal blow, and finally the range and population have become so small that some inexperienced birds are unable to find it.

In biology we learn to beware of single causes and simple solutions. In identifying a few factors bearing on the rarity of the Kirtland's Warbler, I do not mean to imply that other factors are not involved also.

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