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EFFECT OF MATING STATUS AND TIME OF DAY ON KIRTLAND'S WARBLER SONG RATES[1]

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Key words: Kirtland's Warbler; Dendroica kirtlandii; song rates.

Song rates of birds vary with environmental temperature, time of day, stage of reproduction, and pairing status (e.g., von Haartman 1956, Mayfield 1960, Verner 1963, Shields 1977, Best 1981, Robbins 1981, Skirvin 1981, Howes-Jones 1985). Males whose mates are removed may also increase their song output relative to controls or preremoval song output (Krebs et al. 1981, Cuthill and Hindmarsh 1985).

Knowledge of factors affecting song rates is important because biologists use song in estimating or monitoring bird populations. Perhaps for no other species have song censuses played such a major role in population assessment and management as for the Kirtland's Warbler (*Dendroica kirtlandii*). In 1951, this endangered songbird was first censused within the known nesting range, which is restricted exclusively to Michigan (Mayfield 1953). The entire population was censused again in 1961 (Mayfield 1962) and every year after 1970. This information has been used to assess the response of this species to various management techniques (e.g., Brown-headed Cowbird [*Molothrus ater*] control). Recruitment to the population has been estimated by assuming that all singing males were paired (Mayfield 1975, 1983; Walkinshaw 1983; Probst, in press) and using known or inferred values for mortality rates, number of young fledged, and other demographic variables. Recently, Probst and Hayes (unpubl.) showed that a significant percentage of these singing males were probably unmated.

If there are differences in singing rates at different times of day or between paired and unpaired males, they could alter any census or demographic analysis of the Kirtland's Warbler. For example, if mated males sang less, they might be less detectable than unmated males and more likely to be missed. This is further complicated because the distribution of mated and unmated males among habitats is quite different (Probst and Hayes, unpubl.).

We report the variation in song rates of mated and unmated Kirtland's Warblers throughout the day. We analyzed data for 52 males (29 paired and 23 unpaired) whose mating status was known. During June and early July of 1982 and 1983, the number of songs and the time during which we listened for songs were recorded for a total of 5,381 min. We started observations when a bird's identity could accurately be confirmed based on song and plumage characteristics and location on the study plot. The plots had been previously censused to determine the number of singing males, and pairing determinations were made on males in the chronological order of their discovery. Typically we obtained data on a single male at a time, while we were determining his pairing status. On a few occasions, the proximity of a male with known pairing status to a male we were currently following allowed us to obtain data for more than one bird at a time. We do not have continuous records of singing for all males, because the priority of following males closely enough to determine their pairing status sometimes prevented us from recording singing. Song data were classified into the following five time categories: 0630 to 0800, 0800 to 0930, 0930 to 1100, 1100 to 1230, and after 1230 e.s.t. No data were collected after 1430 e.s.t. We did observe males earlier than 0630, but during this time males sang so infrequently that we had difficulty establishing their locations and could not always distinguish them from neighbors. Hence we could not adequately record their song rates. For this reason these data were excluded from our analysis. In the few instances when our field notes did not permit a direct classification into a single time category (e.g., if 20 songs were recorded between 0915 and 0945) the number of songs placed in each category was in proportion to the observation time in each category. Periods of silence (non-singing) were included in our calculation of song rates, which was done on a per-bird basis. The amount of time for which song data were recorded for individual birds ranged from 30 to 210 min. As a result of our method of determining pairing status, individual paired birds were observed for less time on average than unpaired birds. Nevertheless, the greater prevalence of paired birds resulted in similar total observation times for paired and unpaired birds (2,267 minutes and 3,114 minutes, respectively, Table 1). The number of minutes of observation per bird was weakly but significantly correlated with song rate ($r = 0.329$, $P = 0.017$),
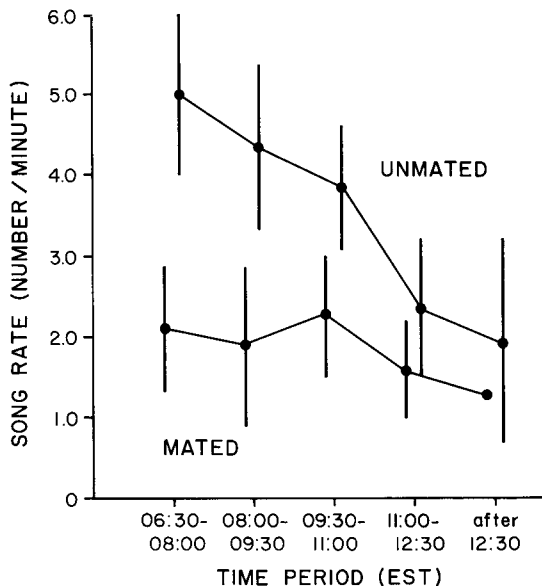
FIGURE 1. Song rates of mated and unmated Kirtland's Warbler males during five diurnal time periods in June and early July 1982 and 1983. Dots indicate the mean, and vertical bars indicate the 95% confidence intervals. No confidence interval is shown for the after-12:30 period for mated males, due to the small sample size for this category.

TABLE 1. Number of birds and min of observation time of paired and unpaired Kirtland's Warblers.

Time of day (e.s.t.)	Number of birds		Minutes observed	
	Paired	Unpaired	Paired	Unpaired
0630–0800	16	13	845	647
0800–0930	12	16	550	902
0930–1100	9	16	328	720
1100–1230	10	10	499	690
After 1230	2	5	45	155
All times	29	23	2,267	3,144

because it took less than 90 min of tracking time to classify all males that we called paired during 1982, so our 1983 data should result in an even higher percent of males whose pairing status was correctly ascertained. Details of the rationale and methodology for determining pairing status are given in Probst and Hayes (unpubl.).

For all time categories combined, the mean song rate of unmated birds (3.91 songs/min) differed significantly ($P < 0.0001$) from that of mated birds (1.95 songs/min). The song rates also differed significantly ($P < 0.01$) between paired and unpaired birds during the 0630 to 0800, 0800 to 0930, and 0930 to 1100 intervals. Song rates were not significantly ($P > 0.05$) different during the 1100 to 1230 interval. No statistical comparison was made for the interval after 1230, due to the small sample size. Singing by unpaired males showed a continuous decline throughout the day (Fig. 1). Paired males sang most between 0930 and 1100, and next most between 0630 and 0830 (Fig. 1). The range in mean song rate for any period was almost three times as large for unpaired males (3.04 songs/min) as for paired males (1.02 songs/min).

If song rates are at or near the threshold of detectability, censusing early in the morning may be biased towards the detection of unpaired birds. These differences may be important for Kirtland's Warblers and other species where censuses are used to estimate production of young, because the birds most likely to be detected are least likely to produce offspring. More singing by unpaired males has been documented for several other species (Davis 1958, Verner 1963, Sayre et al. 1980, Grieg-Smith 1982, Johnson 1983, Logan 1983). These differences should be considered when censuses of singing males are used to estimate the density of breeding pairs.

Our experience with other bird species in northern regions indicates that peak singing activity often occurs in midmorning, especially for warblers. Robbins (1981) found that several taxa (woodpeckers, parids, vireos, orioles, tanagers, and finches) continue to sing throughout the morning with only a gradual decline in rates, and some species have their lowest detectability in the sunrise hour. Verner and Ritter (1986) also found that some species may have their highest detectability in midmorning.

We suggest that future studies compare the detectability of known territorial males over short time periods (5 to 15 min; Best and Peterson 1982, Wilson and Bart 1985) with song rate data. This would help clarify the extent of the potential bias caused by higher song rates of unpaired males.

but paired birds alone ($r = -0.018$, $P \gg 0.05$) and unpaired birds alone ($r = -0.06$, $P \gg 0.05$) showed no correlation of observation time with song rate. This indicates that the overall correlation results from differences in the pairing status of the birds, not from differences in the length of time observed. Song rates of paired and unpaired birds were compared using Student's t-tests.

Although we tabulated song rates as number per min, song activity was usually grouped into distinct periods of singing (about 4 to 7 per min) or not singing. Periods of silence lasted as long as ½ hr or more. When infrequent singing occurred early in the day, we were unable to identify bird locations and could not record periods of silence (zero song rates). For this reason (i.e., because we could not record zero song rates early in the day) and because our observations started when a bird could be located aurally rather than at a randomly selected time, our data may be biased towards higher song rates than actually occurred. The lack of correlation between song rate and amount of observation time, however, suggests that there was no detectable bias.

Pairing status was determined by watching males for a set period of time and classifying those seen with a female or fledgling as paired and other males as unpaired. Observation was terminated upon sighting a female or fledgling with a male, so paired males were observed for shorter periods of time. This enabled us to determine the pairing status of the largest possible number of singing males. The length of an appropriate observation period for pairing determinations was established by plotting the percent of males classified as paired from N. Cuthbert's (unpubl.) data against observation time. An asymptote was reached by 150 min. This analysis indicated that about 90% of all paired males would be correctly classified as paired within 150 min of observation time. Thus, we assumed that this was an adequate observation period to ascertain whether or not a male was paired. In 1983, based on analysis of our 1982 data, we observed birds for 90 min of "tracking time" (defined as the time during which we could see the bird or knew its location based on song). We did this

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POSSIBLE MANIPULATION OF EGGSHELL CONDUCTANCE OF HOST EGGS BY BROWN-HEADED COWBIRDS[1]

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Key words: Eggs; avian parasitism; cowbirds; water-vapor conductance; Red-winged Blackbirds.

Avian parasites, such as Brown-Headed Cowbirds (*Molothrus ater*) use several methods that minimize the competitive advantage of host nestlings and that maximize survival of their own young to fledging (Friedmann 1929, Payne 1977). Ejection of one or more host eggs can reduce the number of host nestlings competing with the parasite nestlings for food, but sometimes this behavior can cause the host to abandon the nest (Payne 1977). Alternatively, the competitive advantage of parasite nestlings can be enhanced without removal of host eggs from the nest by any mechanism that disrupts the structural integrity of the eggshell of host eggs to a sufficient degree that host embryos do not hatch.

The shell thickness and pore area are two features of avian eggs which must meet a set of mutually antagonistic requirements within narrow limits; otherwise, the development of the embryo is disrupted and hatching will not occur. The eggshell must be sufficiently thick to support

the mass of the egg contents and weight of the incubating adult, yet thin enough to permit the embryo to pip and hatch successfully. Additionally, the shell thickness and pore area together comprise the conductance (G) of the eggshell to gaseous diffusion (see Ar et al. 1974). The conductance must be sufficiently great that enough O_2 can diffuse into the egg to meet the needs of the embryo, yet it must be small enough that excessive losses of CO_2 and water vapor are prevented and invasion of bacteria and other infectious agents is minimized (see Carey 1983).

Blankespoor et al. (1982) recently observed that Red-winged Blackbird (*Agelaius phoeniceus*) eggs are more frequently cracked during egg laying and incubation than are cowbird eggs in the same nest. Since Red-winged Blackbird eggs have a thinner shell than cowbird eggs, those authors speculated that Red-winged Blackbird eggs were more likely to become cracked when eggs were jostled against one another in the nest. Further, they hypothesized that the thicker eggshell of cowbird eggs conferred a competitive advantage over Red-winged Blackbird eggs, since cracked eggs were more likely to break and to be removed from the nest by the incubating host. It is also possible that embryos in cracked eggs might not develop and hatch successfully because of excessive loss of water and CO_2 and/or invasion of bacteria, fungi, etc.

The phenomenon documented by Blankespoor et al. (1982) may result from differences in thickness and strength