The Auk 111(3):556-562, 1994

SEASONAL AND DIURNAL PATTERNS OF SINGING AND SONG-FLIGHT ACTIVITY IN BLUETHROATS (*LUSCINIA SVECICA*)

JUHA MERILÄ[1] AND JORMA SORJONEN

Department of Biology, University of Joensuu, Box 111, 80101 Joensuu, Finland

ABSTRACT.—To assess the functions of male song in Bluethroat (*Luscinia svecica svecica*), seasonal and diurnal patterns of song and song-flight activity were analyzed by using data on individually marked birds. The seasonal patterns of singing and song-flight activity were found to peak shortly after male arrival and before the onset of egg laying. The diurnal pattern of song production peaked in the early morning (0300-0900), with a less clear increase in song rate around 2200. Male singing activity decreased significantly after clutch initiation. Only unpaired males, or males that failed in their breeding attempt, were heard singing after the egg-laying period. Seasonal and diurnal patterns of song-flight activity were strongly correlated with patterns of singing activity. In addition, male pairing speed was positively correlated with song-flight activity. These results suggest that both song and song flights in Bluethroats serve to attract females. *Received 27 April 1993, accepted 1 July 1993.*

BLUETHROAT (*Luscinia svecica*) males are both visually and acoustically conspicuous birds compared to most northern European passerines. The song of the Bluethroat is complex (Cramp 1989, Sorjonen 1986) and, in contrast to most other passerines, males often perform conspicuous song flights (Armstrong and Westfall 1953). Bright coloration and complex acoustical displays of males may have evolved by two different means: through either intra- or intersexual selection, or both (Searcy and Andersson 1986).

In this paper we describe seasonal and diurnal patterns of song production in the Bluethroat. Our aim was to investigate whether the function of Bluethroat song and song flights was to attract females (result of intersexual selection) rather than to defend territory (result of intrasexual selection; Catchpole 1973, 1982, Searcy and Andersson 1986). By using data on temporal variation in singing behavior, we tested six predictions where the results of each test would be consistent with either female-attraction or territorial function of song. We also used data on the song performance of individual males and related this to their pairing speed.

We predicted (see Catchpole 1973, 1982, Lampe and Espmark 1987, Björklund et al. 1990) that, if Bluethroat song is used mainly in territorial defense, then: (1) singing should continue throughout the breeding season, albeit at the reduced rate; (2) males should sing at a higher rate when other males are singing; and (3) if the song is used to protect paternity, song output should peak during the females' fertile period (i.e. during egg laying; Birkhead and Møller 1992). However, if the primary function of song is to attract and retain mates, then: (1) it should occur at a higher rate before pairing and egg laying, and cease after the start of egg laying; (2) unpaired males should continue singing throughout the breeding season; and (3) males should resume singing after loss of their nests. Similarly, if females use male song and/or song flights as a cue to male or male territory quality, a correlation between singing behavior and mating success would favor the sexual-attraction function of song/song flights (Payne and Payne 1977, Radesäter et al. 1987).

METHODS

Fieldwork was carried out from 16 May to 27 June 1988 in a subalpine mountain birch forest east of lake Kilpisjärvi (69°50′N, 20°50′E) in Finnish Lapland. The study area was approximately 1 km^2, consisting mainly of a mixture of subalpine birch forest, meadows, and small bogs. Detailed descriptions of the habitat and the breeding biology of the Bluethroat population are provided by Järvinen and Pryl (1980) and Järvinen and Pietiäinen (1983; see also Arheimer 1982).

The first Bluethroat was observed on 19 May, and the first song was heard on 20 May. Males were captured using mist nets and song playback after they

---

[1] Present address: Department of Zoology, Section of Animal Ecology, Villavägen 9, 752 36 Uppsala, Sweden.

settled in territories. Each male was color marked with a unique combination of plastic leg bands.

Singing and song-flight rates of males were observed throughout the breeding season in 10-min observation periods (song phrases and/or flight songs per 10 min). We recorded 1,629 periods covering 271.5 h of observation. For each male, observations were made every day (with few exceptions) in a random manner. Most observations were made between 0000 and 1200 (66%), and the distribution of observation periods over breeding season was fairly even (n = 783 and 846 before and after median date of clutch initiation, respectively). Altogether 22 males were followed, but some of these males disappeared, or were not followed later on due to time constraints. Data on these males were included on some analyses to increase sample size (proportion of males singing, diurnal song patterns), but excluded from the analyses of seasonal patterns. Eight males were followed throughout the breeding season and the mean number observation periods per day for these males was 6.4 ± SD of 2.63.

To reduce the interdependence of song recordings, diurnal patterns of singing and song-flight activity were calculated as follows. If an individual male was recorded more than once within the same hour in the same day, these recordings were averaged, and the resulting figures were used to calculate the mean hourly singing activity of that male over a desired sequence of days (see below), and averaged over different males to yield the mean singing activity of the population for that hour of the day. Since the singing activity of males declined during the egg-laying phase (see Results), only data before this period were included in the analysis of diurnal song patterns.

Seasonal patterns of singing activity were calculated in a similar way. If an individual male was recorded more than once within the same hour in the same day, the average of these values was taken. These individual hourly means were then averaged over a specified span of hours (see below) to yield male daily singing activity. These measures of daily singing activity of individuals were then averaged over different males to yield daily mean singing activity of the population. However, before averaging over different males, male-specific daily singing activities were assigned to a standardized time scale where day 0 represented the date of clutch initiation. For this reason, two males entered in the analysis for example on day −2 (two days before clutch initiation) were not necessarily recorded in the same date, but rather on the same day in relation to their breeding cycle. Furthermore, since the diurnal singing activity of Bluethroats peaked during the morning hours (see Results), we included only song observations made between 0300 and 1200 in this analysis. Diurnal and seasonal song-flight activities were calculated in similar fashion.

In order to investigate whether song or song-flight rates might influence male mating success, we correlated individual pairing speed with individual song-flight and song rates. Since pairing date was not possible to assess accurately due to extreme secretiveness of females, the number of days between a male's arrival date and date of the first egg in his clutch was used as an estimate of pairing speed.

The test for dependence of song/song-flight rate on number of males singing was done using chronological dates since the use of time scale relative to breeding cycle would confound this comparison. Thus, in this test the mean daily singing rate of population was correlated with number males singing in a given day. The song records of males that were not heard singing on one particular day were excluded from this analysis because inclusion of days when most of the males had stopped singing (see Results) had resulted in spurious correlation between song rate and numbers of singing males (if none of the males are singing, song rate must be zero). For this reason, the days when none of the males was singing were excluded from the analysis and, consequently, the sample size dropped (this explains also the difference in n for song rate and song-flight analyses).

Because of the nonnormality of song variables (e.g. 49% of song-rate records made before median date of clutch initiation were zeros), statistical analyses were carried out using nonparametric tests. In the graphical representations of the seasonal and diurnal patterns of singing behavior, we used polynomial regressions to describe trends. In each case, the search for the best fit was initiated starting with linear regression, and then refined using different-order polynomial models. The best-fitting model (highest r^2) was chosen for graphical representation.

Because of the large sampling variance in mean song and song-flight rates (because a number of the observations produced a zero; i.e. no song or song flight recorded during a given period), we also calculated mean song and song-flight rates based on 10 most active observations of each individual. These measures are not independent of mean song and song-flight rates, but provide a way to check robustness of results based on mean values of more heterogenous observations.

All times refer to Finnish summer time (GMT + 3 h). All tests are two-tailed unless otherwise stated.

RESULTS

Seasonal pattern of song production.—Song production was highest directly after male arrival and declined sharply towards the start of egg-laying (Fig. 1A). There was a significant difference in song rates between the period before clutch initiation ($\bar{x}$ = 10.98) and egg-laying period ($\bar{x}$ = 1.18; Wilcoxon sign-rank, $z = -2.36$, $n = 7$, $P = 0.018$), as well as between the period

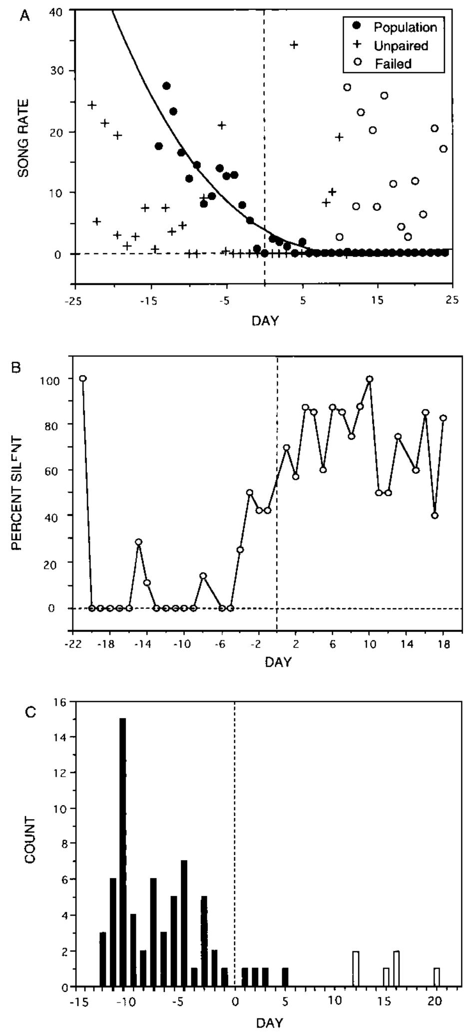

Fig. 1. Seasonal variation in singing behavior in the Kilpisjärvi Bluethroat population. (A) Mean daily song rate (phrases/10 min) of seven paired males (closed circles) and one male that failed to pair (+). Open circles indicate mean daily song rates of two males after breeding failure. (B) Proportion of silent males at different times of breeding season. (C) Distribution of 10 most active song observations of seven paired males. Open bars indicate observations of two males after breeding failure. Vertical line indicates date of clutch initiation (observations for unpaired male are standardized to median laying date of the population). Equation for regression line in panel A is: $Y = 3.732 - 0.744X + 0.04X^2 - 0.01X^3$ ($F = 97.0$, $r^2 = 0.88$, $P < 0.001$).

before and after clutch initiation (excluding egg-laying period; Wilcoxon sign-rank, $z = -2.20$, $n = 6$, $P = 0.028$;). However, the difference in song rate between the egg-laying period and the period after egg laying was not significant (Wilcoxon sign-rank, $z = -1.6$, $n = 6$, $P = 0.109$; one male that failed in breeding was excluded from this and previous test). Three of the seven paired males stopped singing before clutch initiation, and only one of them was heard singing after clutch completion. However, one male that failed to pair continued singing throughout the season (Fig. 1; crosses), and two males that failed in breeding resumed singing after loosing their clutches (Fig. 1, open circles).

The decline in singing as the egg-laying stage approached also is indicated by the dramatic increase of silent males (i.e. males known to be present but not singing) just before the median date of egg laying (9 June; Fig. 1B). Similarly, the distribution of 10 most active singing observations for seven males that were followed throughout the season truncates around the date of clutch initiation (Fig. 1C). However, the mean daily song rate of the population was not correlated with the number of singing males (Spearman rank; $r_s = 0.01$, $n = 28$, $z = 0.08$, $P > 0.90$).

Diurnal pattern of song production.—The mean song rate of population was highest between 0300 and 1100 (Fig. 2A), and another, less clear increase in the song rate occurred around 2200. Little singing was noted between 0000 and 0300, and song rates in afternoon and early evening hours were also low in comparison to the morning hours. The number of silent males increased after 1000 (Fig. 2B), and the distribution of 10 most active song observations for eight males peaked between 0300 and 0900 (Fig. 2C).

Seasonal pattern of song-flight activity.—The seasonal pattern of song-flight activity is similar to that of song (Spearman rank; $r_s = 0.92$, $n = 39$, $z = 5.89$, $P < 0.001$), with the highest rates at the beginning of the breeding season and ceasing before clutch initiation (Fig. 3A). The difference in song flight rates between the prelaying ($\bar{x} = 0.65$) and egg-laying periods ($\bar{x} = 0.03$) was significant (Wilcoxon sign-rank, $z = -2.197$, $n = 7$, $P = 0.028$). There was, however, no significant difference in rates between the egg-laying and postlaying periods ($\bar{x} = 0.03$ and 0.00, respectively; Wilcoxon sign-rank, $z = -1.00$, $n = 6$, $P = 0.32$). Only one male was seen

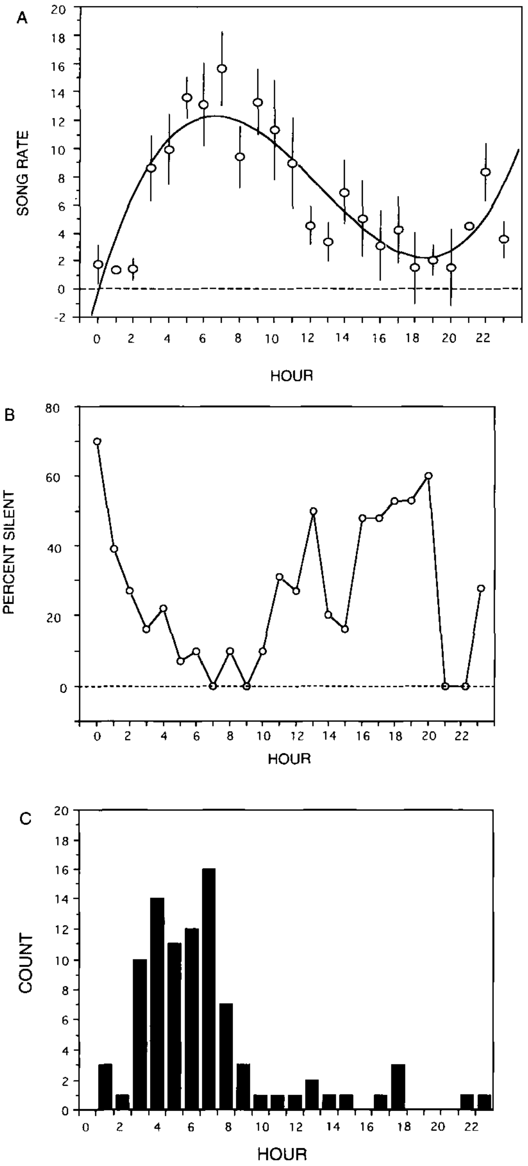

Fig. 2. Diurnal variation in singing behavior of Bluethroats. (A) Mean hourly song rate (± SE). (B) Proportion of silent males at different times of day. (C) Distribution of 10 most active song observations of nine males followed from their arrival to start of egg laying. Equation for regression line in panel A is: $Y = 1.213 + 4.49X - 0.453\ X^2 + 0.12X^3$ ($F = 19.9$, $r^2 = 0.75$, $P < 0.001$).

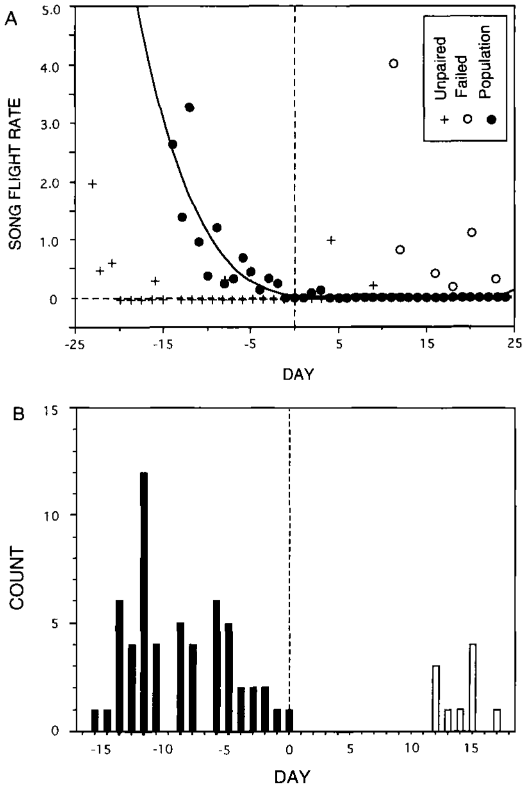

Fig. 3. Seasonal variation in song flight activity of Bluethroats. (A) Mean daily song flight rate of seven males (song flights/10 min). (B) Seasonal distribution of 10 most active song flights for seven males. White bars indicate observations of one male after it failed in breeding. Observe that n in panel does not add up to 70 because of the great individual variation in song-flight activity (i.e. some males performed song flights often enough to add up to 10). Best-fit to data in panel A was provided by regression: $Y = 0.36 - 0.15X + 0.004X^2 - 0.0004X^3 + 0.000009X^4$ ($F = 30.0$, $r^2 = 0.78$, $P < 0.001$).

making song flights during egg laying, while no song flights were observed after clutch completion. The exceptions to this were the unpaired male and one of the two males that failed in breeding attempt (Fig. 3A). This concentration of song flight activity during the period before clutch initiation can be seen also in the distribution of 10 most active song flights of seven males followed throughout the breeding season (Fig. 3B). The mean daily song-flight rate was moderately correlated with number of singing males (Spearman rank; $z = 2.06$, $n = 25$, $r_s = 0.47$, $P = 0.039$).

Diurnal pattern of song-flight activity.—The diurnal pattern of song-flight activity was similar to that of singing activity ($r_s = 0.85$, $n = 24$, $z = 4.08$, $P = 0.001$). Song-flight activity peaked dur-

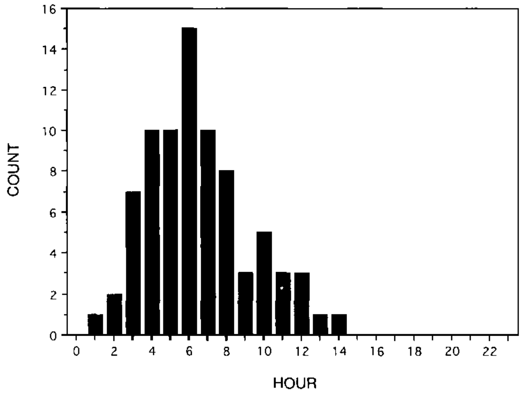

Fig. 4. Diurnal variation in song-flight activity of Bluethroats as indicated by distribution of 10 most active song-flight observations for nine males.

ing the morning (0500–1200), and few flight songs were performed between 1700 and 0300. This can be seen also from the distribution of 10 most active song flight recordings made for different males (Fig. 4).

Individual variation in singing behavior and pairing speed.—Song rates differed significantly among 7 paired males, as measured by mean daily song rates (Kruskall Wallis, $H = 15.86$, $P < 0.05$), and the song rate in 10 most active observations ($H = 39.51$, $P < 0.001$). Similarly, there was significant heterogeneity in song-flight rates as measured by 10 most active observations ($H = 34.61$, $P < 0.001$), but heterogeneity was not evident when mean daily song rates were used ($H = 3.57$, $P = 0.81$). However, using the first measure of song-flight rate, males with higher song-flight rates were also those that mated first (Table 1). However, mean daily song-flight rate was not significantly associated with pairing speed (Table 1). No significant association was found between pairing speed and different measures of song activity. Further, there was no correlation between pairing speed and arrival date (Table 1).

DISCUSSION

Our results show that the singing period of Bluethroats is short, peaking before or during pair formation and ceasing shortly thereafter. These data suggest that song in Bluethroat functions primarily, if not solely, in mate attraction and not in territorial defense; if it did function in territorial defense, song should continue after mate acquisition (Catchpole 1973, 1982). This interpretation is further supported by the fact that no paired males were heard singing after clutch completion, a phenomenon also observed in Sedge Warblers (*Acrocephalus schoenobaenus*; Catchpole 1973, 1980, 1982; for a sharp decrease in song rate after mate acquisition see also: Nice 1943, Stenger and Falls 1959, Lowther and Falls 1968, Dowsett-Lemaire 1981, Wallin 1986). By contrast, one unmated male was observed to continue singing until the end of the study period. Similarly, males that failed in their breeding (due to predation or desertion) resumed singing after loss of their clutch (for similar examples, see Wasserman 1977, Krebs et al. 1981, Johnson 1983, Cuthill and Hindmarsh 1985). All of these facts are consistent with mate attraction being the chief function of Bluethroat song. Furthermore, if males sing mainly in territorial defense, one should find a correlation between number of simultaneously singing males and their singing activity (Lampe and Espmark 1987). This was not the case in our study—singing rate was independent of the number of males singing, as has been also found in study of Swedish Great Tits (*Parus major*; Björklund et al. 1990). Thus, although the hypothesis that males use song in territorial defense cannot be ruled out, the evidence suggests that Bluethroat song functions primarily in mate attraction. On one occasion, when making a song playback in the territory of a disappeared male, we observed a female approaching the tape recorder on the ground. From the behavior of the female it was obvious that she was attracted to the broadcasted song. This observation parallels the experimental results of Eriksson and Wallin

TABLE 1. Spearman rank correlation coefficients between singing behavior and pairing speed (time elapsed between arrival and first egg) among seven Bluethroat males.

Dependent variable	r_s	z	P^a
Arrival date	−0.54	−1.52	0.12
Singing rate			
Mean daily	−0.16	−0.40	0.34
10 most active[b]	−0.40	−1.07	0.14
Song-flight rate			
Mean daily	−0.47	−1.14	0.13
10 most active[b]	−0.63	−1.60	0.05

[a] One-tailed test, except for arrival date (two-tailed).

[b] Based on 10 most active song/song-flight observations of each male.

(1986), who found that female Pied and Collared flycatchers (*Ficedula hypoleuca* and *F. albicollis*, respectively) were attracted by male song. Bluethroat song could function also, at least incidentally, in territorial maintenance during the females' fertile period (Göranson et al. 1974). However, because song output peaked before onset of the female fertile period, approaching zero during the egg-laying period, Bluethroat song seems not to function to ensure paternity (for further discussion, see Birkhead and Møller 1992). Nevertheless, since some of the paired males were heard singing during the egg-laying period (albeit at a greatly reduced rate), this could indicate that song is also used in female retention. For example, Catchpole (1973) observed that male Sedge Warblers that momentarily lost contact with their mate during egg-laying phase sometimes resumed singing.

The seasonal pattern of song flights was similar to that of song. Song flights were restricted to the period before clutch initiation, and only unpaired males, or males that failed in their breeding attempt, performed song flights after this. These observations taken together suggest that flight songs serve a sexual-attraction function. The time in which males acquired a mate was negatively associated with our measure of song-flight activity; this draws further attention to a possible sexual function of Bluethroat song flights (Table 1; i.e. the higher the song-flight rate, the more quickly the male acquired a mate). The relationships between pairing speed and other measures of song-flight activity and song rate are consistent with previous results, but lack statistical significance. Larger samples and more accurate estimates for pairing date would be needed to guard against acceptance of false null hypotheses (i.e. that song performance does not affect pairing speed).

Further indications that flight songs are used in sexual attraction are provided by observations where males in a flight song were seen to approach females. On four occasions we observed several (two or three) males making intensive flight songs in the presence of a single female in one of the male's territory. These kinds of intrusions (sometimes extending over several territories) were apparently related to the presence of a female on the other males' territory (see also Schmidt-Koenig 1956). During fieldwork we also found that males responded to the song playbacks with song flights directed towards the tape-recorder (unpubl. data). Response occurred at the beginning of the breeding season, but not after clutch completion. This, together with the fact that mean song-flight rate was positively associated with the number of singing males, may indicate that song flights also function in male-male interactions. Thus, song flights may be used both to attract females and to keep intruders away from the males' territory during the pair-formation period.

ACKNOWLEDGMENTS

We thank Antero Järvinen, the head of Kilpisjärvi Biological Station (University of Helsinki), for providing us the opportunity to stay at the station during the fieldwork, and Rauni Partanen and Aulikki Tervonen for giving their helping hand during the fieldwork. Thanks also to Mats Björklund, Gary D. Schnell, Staffan Ulfstrand, and three anonymous reviewers whose comments have improved this manuscript. This study was supported by a grant from Joensuu University to Jorma Sorjonen.

LITERATURE CITED

ARHEIMER, O. 1982. The breeding biology of the Bluethroat *Luscinia svecica* in subalpine birch forest at Ammarnäs, Swedish Lapland. Vår Fågelvärd 41:249–260 [in Swedish, with English summary].

ARMSTRONG, E. A., AND P. R. WESTALL. 1953. The song-flights of some northern birds. Ibis 95:143–145.

BIRKHEAD, T., AND A. P. MØLLER. 1992. Sperm competition in birds. Evolutionary causes and consequences. Academic Press, Cambridge.

BJÖRKLUND, M., B. WESTMAN, AND K. ALLANDER. 1990. Song in Swedish Great Tits: Intra- or intersexual communication? Behaviour 111:257–269.

CATCHPOLE, C. 1973. The functions of the advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). Behaviour 46:300–320.

CATCHPOLE, C. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74:149–166.

CATCHPOLE, C. 1982. The evolution of bird sounds in relation to mating and spacing behaviour. Pages 297–319 *in* Acoustic communication in birds, vol. 1. (D. E. Kroodsma, E. H. Miller, and H. Ouellet, Eds.). Academic Press, New York.

CRAMP, S. (Ed.) 1989. The birds of the western Palearctic. Handbook of the birds of Europe, The Middle East and North Africa, vol. 5. Oxford Univ. Press, Oxford.

CUTHILL, I., AND A. HINDMARSH. 1985. Increase in starling song activity with removal of mate. Anim. Behav. 33:326–328.

DOWSETT-LEMAIRE, F. 1981. Eco-ethological aspects of breeding in the Marsh Warbler, *Acrocephalus palustris*. Rev. Ecol. 35:437-491.

ERIKSSON, D., AND L. WALLIN 1986. Male bird song attracts females—A field experiment. Behav. Ecol. Sociobiol. 19:297-299.

GÖRANSON, G., G. HÖGSTEDT, J. KARLSSON, H. KÄLLANDER, AND S. ULFSTRAND. 1974. Sångensroll för revirhållandet hos näktergal *Luscinia luscinia*—Några experiment med playbackteknik. Vår Fågelvärd 33:201-209.

GREIG-SMITH, P. W. 1982. Seasonal patterns of song production by male Stonechats *Saxicola torquata*. Ornis Scand. 13:225-231.

JÄRVINEN, A., AND M. PRYL. 1980. Nesting habits of the Bluethroat *Luscinia svecica* at Kilpisjärvi, Finnish Lapland. Kilpisjärvi Notes 4:1-7.

JÄRVINEN, A., AND H. PIETIÄINEN. 1983. The Bluethroat *Luscinia s. svecica* population at Kilpisjärvi, Finnish Lapland: Density, habitat selection, age structure and nesting success in 1981. Pages 189-194 *in* Proc. III Nordic Congr. Ornithol., Copenhagen 1981 (E. D. Fjeldså and H. Meltofte, Eds.). Dansk Orn. För. & Zool. Mus., Copenhagen.

JOHNSON, L. S. 1983. Effect of mate loss on song performance in the Plain Titmouse. Condor 85: 378-380.

KREBS, J. R., M. AVERY, AND R. J. COWIE. 1981. Effect of removal of mate on the singing behaviour of Great Tits. Anim. Behav. 29:635-637.

LAMPE, H. M., AND Y. O. ESPMARK. 1987. Singing activity and song pattern of the Redwing *Turdus iliacus* during the breeding season. Ornis Scand. 18:179-185.

LOWTHER, J. K., AND J. B. FALLS. 1968. White-throated Sparrows. Pages 1364-1392 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237.

NICE, M. M. 1943. Studies in the life histories of the Song Sparrow II. The behavior of the Song Sparrow and other passerines. Trans. Linn. Soc. 6:1-328.

PAYNE, R. B., AND K. PAYNE. 1977. Social organization and mating success in local song populations of Village Indigobirds (*Passerina cyane*). Z. Tierpsychol. 45:113-173.

RADESÄTER, T., S. JAKOBSSON, N. ANDBJER, A. BYLIN, AND K. NYSTRÖM. 1987. Song rate and pair formation in the Willow Warbler, *Phylloscopus trochilus*. Anim. Behav. 35:1645-1651.

SCHMIDT-KOENIG VON, K. 1956. Über Rückkenr, Revierbesetzung und Durchzug des weißsternigen Blaukehlchens (*Luscinia svecica cyanecula*) im Frühjahr. Vogelwarte 18:185-197.

SEARCY, W., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. Annu. Rev. Ecol. Syst. 17:507-533.

SORJONEN, J. 1986. Song structure and singing strategies in the genus *Luscinia* in different habitats and geographical areas. Behaviour 91:274-285.

STENGER, J., AND J. B. FALLS. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125-140.

WALLIN, L. 1986. Divergent character displacement in the song of two allospecies: The Pied Flycatcher *Ficedula hypoleuca* and the Collared Flycatcher *Ficedula albicollis*. Ibis 128:251-259.

WASSERMAN, F. E. 1977. Mate attraction function of song in the White-throated Sparrow (*Zonotrichia albicollis*). Condor 79:125-127.