

SONG PATTERNS OF WARBLERS AT DAWN AND DUSK

DOUGLASS H. MORSE¹

ABSTRACT.—Unaccented Ending Songs or their equivalent occurred nearly exclusively in the dawn and dusk singing of male Northern Parula (*Parula americana*), Magnolia (*Dendroica magnolia*), Yellow-rumped (*D. coronata*), Black-throated Green (*D. virens*), and Blackburnian (*D. fusca*) warblers. The proportion of Unaccented Ending Songs at dawn and dusk differed from those given at 06:00, 10:00, and 15:00 when the warblers often sang other songs as well. Total songs/time were low at dawn and dusk, birds were well spaced when singing, and females were not in evidence. I suggest that dawn and dusk songs play an important role in advertising the singer's presence to potential territorial intruders. Received 17 June 1988; accepted 12 Sept. 1988.

The dawn and dusk choruses of birds have traditionally generated considerable interest among ornithologists. However, most of the resulting literature has dealt with the roles of light or meteorological phenomena in eliciting vocalizations and with the sequence of species in joining or quitting the choruses (see Leopold and Eynon 1961). The detailed characteristics of singing behavior at these times have received much less attention, although Craig's (1943) pioneering studies on Wood Pewee (*Contopus virens*) vocalizations clearly indicated that certain song types of that species' repertoire predominated at twilight.

Largely independently of interest in dawn and dusk choruses, the function of bird song has attracted considerable interest over the past 30 years. A topic central to this discussion has been the roles of different songs within a bird's repertoire. It is now known that a rather wide range of species with relatively simple song repertoires may sing their different songs in different contexts (e.g., Craig 1943; Smith 1959; Morse 1967a, 1970).

Several species of wood warblers (Parulinae) have two or more types of songs, which are often given in distinctly different contexts (e.g., Ficken and Ficken 1962, Morse 1967a, Lemon et al. 1987). This pattern is well illustrated by the songs of the Black-throated Green Warbler (*Dendroica virens*) (Morse 1967a, 1970). This species has two distinct songs (Morse 1967a, Lemon et al. 1987). Accented Ending Song (Ficken and Ficken 1962), the song A of some authors, usually occurs when males are unpaired, are in close contact with females, or are foraging below their song

¹ Graduate Program in Ecology and Evolutionary Biology, Div. Biology and Medicine, Brown Univ., Providence, Rhode Island 02912.

perches, where their females are nesting and foraging. Unaccented Ending Song, song B, is associated with territorial proclamation or contact with other males. In large populations it is the song given at high frequency during most of the breeding season, and it reaches its highest frequency immediately after overt encounters between adjacent territory holders have declined. It is also the song usually given by stationary males on elevated singing perches (Morse 1970, 1976a). The contexts in which these two songs are given are consistent with them serving as pair-formation/maintenance songs and territorial-aggressive songs, respectively.

Arguing from Smith's (1965, 1969) message-meaning hypothesis of communication, Lein (1972) proposed a simpler explanation for the function of these songs: that Accented Ending Songs simply occur in the absence of external stimuli that trigger Unaccented Ending Songs. In this scenario, Unaccented Ending Songs could be a response to certain stimuli, and males might sing Accented Ending Songs in the absence of such stimuli, regardless of whether females were present. Although Lein's hypothesis is attractive in its simplicity, it does not invalidate the hypothesis of the two songs playing separate and distinct roles, so data that help to distinguish between them are needed.

Information on the song types sung at dawn and at dusk may provide useful clues to interpreting these songs, since these are times at which contact with other individuals is likely to be minimal. Only limited attention has been paid to the song types of warblers at such times (Lein 1972, Lemon et al. 1987), or for other species, either, with the exception of Craig's (1943) work on Wood Pewees. Here I report the dawn and dusk song types of several warblers, including the Black-throated Green Warbler, that nest in the boreal spruce forest. These songs are highly consistent, and are therefore of potential interest.

METHODS

Dawn and dusk songs were identified to type (Fig. 1) and tallied on 11 mornings and 16 evenings between 8 June and 15 July 1975 in a spruce forest on Hockomock Point, Bremen, Lincoln Co., Maine. This area is described in detail elsewhere (Morse 1976b). Five common warblers were selected for this analysis: Northern Parula (*Parula americana*) and Magnolia (*Dendroica magnolia*), Yellow-rumped (*D. coronata*), Black-throated Green (*D. virens*), and Blackburnian (*D. fusca*) warblers. Five or more males of each *Dendroica* species and three or more *Parula* could be heard clearly from the listening site under calm conditions, to which these observations were confined. A majority of these birds held territories on the study area described in Morse (1976b), and additional birds were located in similar habitats immediately adjacent to that site.

I arrived in the study area to record dawn songs before any warblers had commenced singing. I noted the type of the first song that each species sang, as well as the time at which it first commenced to sing. In addition to tallying the first song of each species, I also recorded

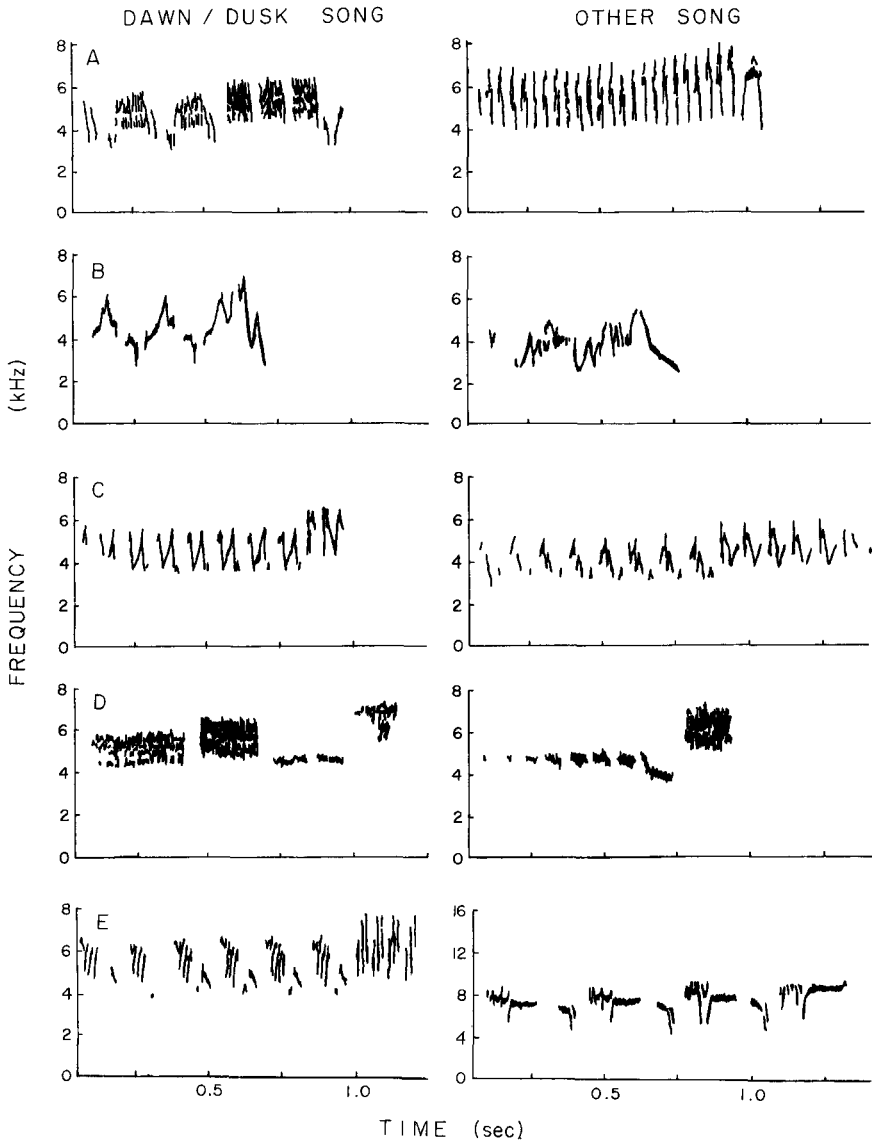


FIG. 1. Sound spectrgrams (tracings) of predominant dawn and dusk songs (called Unaccented Ending Songs) and other principal songs (Accented Ending Songs and others). Note that the other song of the Blackburnian Warbler, the highest of any depicted, has an axis of 0-16 kHz. A = Northern Parula, B = Magnolia Warbler, C = Yellow-rumped Warbler, D = Black-throated Green Warbler, E = Blackburnian Warbler.

the song types of other individuals of each species that commenced to sing within two minutes of the first bird of that species.

For dusk songs I continuously counted the types and times of songs given by each species after 20:15, a time slightly before the different species ceased to sing. This procedure simultaneously allowed me to determine the last songs given by each individual still singing at this time. I remained until singing had completely ceased.

In analyzing these data I treated each bird-day as an independent observation, since it represented a new experience for each of the birds involved. However, it should be kept in mind that I have gathered these data from a number of individuals that is much smaller than the number of observations reported in Table 1 (see above).

To compare these patterns with songs given at other hours, I used data from song censuses made at various hours in an adjacent spruce forest (Hog Is., Bremen: 8 June–15 July 1966), mostly 06:00–06:30 and 10:00–10:30 h, but with a few censuses at 15:00–15:30 and 19:00–19:30 h. Briefly, I walked a transect of approximately 2 km, recording each song that I heard clearly. This area contained a minimum of eight pairs of Northern Parulas and considerably larger numbers of the other species (also see Morse 1968, 1976b).

For convenience I refer to the predominant song type sung at dawn and dusk as Unaccented Ending Song, which follows its use elsewhere for the Black-throated Green Warbler (Morse 1967a, 1970). Use of similar terminology for the Northern Parula, Magnolia, Yellow-rumped, and Blackburnian warblers is for convenience only and does not make any implications about the function of these songs. The other songs are referred to as Accented Ending Songs, again following its previous usage for the Black-throated Green Warbler. The Unaccented Ending Song is comparable to the serial mode of Lemon and his associates (McNally and Lemon 1985, Lemon et al. 1987), the Accented Ending Song to their repeat mode.

RESULTS

Unaccented Ending Songs were given significantly more often as first dawn songs and last dusk songs by Black-throated Green Warblers. One of the two songs (here called the Unaccented Ending Song) was also given significantly more frequently than the other by each of the remaining species. The only partial exception was the Yellow-rumped Warbler, which in the sample for the first singing of any individual of the species in a day did not differ significantly from random (Table 1). The complete sample of first songs (first songs of all of the individuals of a species) was significant for the Yellow-rumped Warbler, however. In no instance did the first morning singers and last evening singers of a species give Unaccented Ending Songs significantly more or less often than did their conspecifics (Table 1: $P > 0.05$ in χ^2 tests).

Proportions of dawn and dusk songs did not differ significantly from each other in any of the species (Table 1: $P > 0.05$ in Fisher tests). This pattern held, whether the first and last songs from all members of each species were compared, or the first and last songs of each species as a whole on a given day.

The relative frequencies of the different song types given by each species at dusk differed significantly from those given at 06:00 and 10:00 h (Table

TABLE 1
FIRST AND LAST SONGS SUNG BY WARBLERS AT DAWN AND DUSK BETWEEN 8 JUNE AND 15 JULY 1975. SEE TEXT FOR EXPLANATION

Species	Dawn						Dusk					
	First birds		All birds		Last birds		All birds		Last birds		All birds	
	UES ^a	AES ^b	UES ^a	AES ^b	UES ^a	AES ^b	UES ^a	AES ^b	UES ^a	AES ^b	UES ^a	AES ^b
Northern Parula	11	0	<0.001	27	0	<0.001	10	1	<0.05	26	2	<0.01
Magnolia Warbler	11	0	<0.001	32	1	<0.001	16	0	<0.001	62	1	<0.001
Yellow-rumped Warbler	7	3	>0.05	19	3	<0.05	14	0	<0.001	30	0	<0.001
Black-throated Green Warbler	11	0	<0.001	28	0	<0.001	12	1	<0.001	50	3	<0.001
Blackburnian Warbler	10	0	<0.001	23	0	<0.001	11	2	<0.001	29	2	<0.001

^a Unaccented Ending Songs or equivalent.

^b Accented Ending Songs or equivalent.

^c Two-tailed binomial tests.

2) ($P < 0.001$ in χ^2 tests on the original data). Although comparable quantitative data were not taken on dawn songs, the results in Table 1 strongly suggest that the relationship between dawn songs and those sung later in the morning closely follows the pattern for the dusk songs reported in Table 2.

The dawn and dusk results are profitably compared further with the proportions of different song types given at other times of the day (Table 2). The minimum proportion of Unaccented Ending Songs occurred at 06:00 h. The proportion of Unaccented Ending Songs increased by 10:00, but did not approach the dusk (or dawn) results. This pattern occurred in each species over the three times of day for which I have large samples of data (06:00, 10:00, dusk), and is highly significant (X_r^2 [Siegel 1956] = 10.00, $df = 2$, $P < 0.01$ in a Friedman two-way analysis of variance). Conclusions do not change if one incorporates the sparser data from 15:00 and 19:00 into the analysis ($X_r^2 = 18.09$, $df = 4$, $P < 0.01$). Proportions of Unaccented Ending Songs are still lowest at 06:00, mid-day proportions (10:00 and 15:00 h) are higher than the early morning proportions and similar to each other, and evening (19:00) results are intermediate between mid-day and the nearly absolute dominance of Unaccented Ending Songs at dusk. Thus, proportions of song types change through the day, with the greatest diversion from the dawn and dusk pattern occurring soon after dusk (06:00). However, at no period during the day does the dominance of Unaccented Ending Songs to reach that observed at dawn and dusk.

DISCUSSION

The Unaccented Ending Songs given by Black-throated Green and Blackburnian warblers at dawn and dusk were the same songs that these birds used when countersinging with conspecific males, as well as preceding and following hostile encounters with other males (Morse 1967a, 1970; Lein 1972). This pattern was also observed in Northern Parulas (Morse 1967b). While giving twilight songs the males were well-spaced from each other and stationary. I never observed any evidence of female activity at these times: females usually remain much lower in the vegetation than the elevated perches used by males in stationary singing (Morse 1967a) and probably were on their nests at this time. Since the densities of warblers at Hockomock Point and Hog Island are similar (Morse 1976b), total numbers of songs should also be similar; although they were recorded from more birds in the Hog Island sample, because that census was run on a transect and the Hockomock Point census at a single point. However, the numbers of Northern Parula, Black-throated Green, and Blackburnian warbler songs given at dusk at Hockomock Point are lower than those

TABLE 2
 PERCENTAGES OF UNACCENTED ENDING SONGS OR EQUIVALENTS (UES) SUNG BY WARBLERS DURING 30 MIN CENSUS ON HOG ISLAND. SEE
 TEXT FOR EXPLANATION

Species	06:00 (17 censuses)		10:00 (17 censuses)		15:00 (3 censuses)		19:00 (2 censuses)		Dusk (16 censuses)	
	UES	N ^a	UES	N ^a	UES	N ^a	UES	N ^a	UES	N ^a
Northern Parula	38.3	962	54.1	885	80.0	50	96.7	30	98.1	160
Magnolia Warbler	71.4	1016	78.3	769	58.6	29	85.7	91	99.7	896
Yellow-rumped Warbler	46.9	484	75.6	400	75.0	4	87.3	55	100.0	417
Black-throated Green Warbler	63.3	3638	87.6	3831	82.3	260	91.9	272	98.1	324
Blackburnian Warbler	32.4	1470	70.7	1581	73.8	84	77.2	70	98.3	233

^a Total of all songs.

run at 06:00 and 10:00 on Hog Island. This difference is striking for the commonest species, the Black-throated Green and Blackburnian warblers. Thus, the high proportion of Unaccented Ending Songs given by these species at dawn and dusk is not a consequence of abundant conspecific song—if controlled on the basis of the number of songs given, Accented Ending Songs should predominate at these times. The results thus suggest that dawn and dusk songs are associated with territorial maintenance, even if they do not involve close or intense contact with contenders.

Since the warblers sing their twilight songs when vocalizations are not being given in large numbers, other environmental disturbances (wind, turbulence, etc.) are apt to be low, and atmospheric conditions ideal for sound transmission (Wiley and Richards 1978, Henwood and Fabrick 1979), they may be useful in territorial proclamation far out of proportion to their number. I do not have adequate data on the contexts of Magnolia and Yellow-rumped warbler songs at other times of the day to comment substantively on their patterns; however, the great preponderance of a single song type at dawn and dusk invites an explanation similar to that offered for the other three species.

The nearly exclusive use of Unaccented Ending Songs at dawn and dusk, times of minimal vocal and physical interference, does not cleanly fit Lein's hypothesis of song function (1972, 1978), which proposes that Unaccented Ending Songs are given in response to strong external stimuli, such as the presence of a conspecific male, the song of a conspecific, or location on the edge of a territory. According to this hypothesis, in the absence of conflicting external stimuli, including lack of interaction with other males as well as association with females, Accented Ending Songs should occur. Unless one imposes special conditions for the dawn and dusk song patterns, this hypothesis thus does not predict Unaccented Ending Song at dawn or dusk, given the scenario I have described; rather, it would predict Accented Ending Song. Lein (1972) included low light intensity as a strong external stimulus eliciting Unaccented Ending Songs, but did not explain the relation of this special condition to the others that generate Unaccented Ending Songs.

Since a territory holder's song may function in advertising his presence and thereby discourage entry by would-be intruders (Göransson et al. 1974, Krebs 1977, Krebs et al. 1978), clear communication at such times might assume considerable importance. Consistent with this interpretation, Mace (1986) found that male Great Tits (*Parus major*) continued their dawn singing bout longer when their females were held in their nest boxes than if they were free to leave. This result is consistent with a basically male-male function for dawn song in that species at least, a pattern eventually broken by the appearance of the females. It is also

consistent with the relatively high number of Accented Ending Songs by the warblers in the early morning (06:00) song censuses (Table 2).

The dawn and dusk warbler songs may thus be of particular importance in maintaining territorial integrity, although observations on isolated birds (Morse 1970) and experiments are needed to test their role further. These results do not support the notion that song types (or silence) can be predicted in any simple way solely on the basis of the external stimuli acting on them at the moment.

ACKNOWLEDGMENTS

I thank M. S. Ficken, E. S. Morton, and F. E. Wasserman for comments on the manuscript, and D. E. Kroodsmas for helpful correspondence. M. S. Ficken and E. S. Morton generously provided the sonagrams for Figure 1. The National Audubon Society kindly permitted use of their property.

LITERATURE CITED

- CRAIG, W. 1943. The song of the Wood Pewee *Myiochanes virens* Linnaeus: a study of bird music. New York State Mus. Bull. 334:1-186.
- FICKEN, M. S. AND R. W. FICKEN. 1962. The comparative ethology of the wood warblers: a review. Living Bird 1:103-122.
- GÖRANSSON, G., G. HÖGSTEDT, J. KARLSSON, H. KÄLLANDER, AND S. ULFSTRAND. 1974. Sångensroll för revirhållandet hos naktergal *Luscinia luscinia nagra* experiment med playbackteknik. Vår Fågelvärld 33:201-209.
- HENWOOD, K. AND A. FABRICK. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. Amer. Nat. 114:260-274.
- KREBS, J. R. 1977. Song and territory in the Great Tit *Parus major*. Pp. 47-62 in Evolutionary ecology (B. Stonehouse and C. Perrins, eds.). Univ. Park Press, Baltimore, Maryland.
- , R. ASHCROFT, AND M. WEBBER. 1978. Song repertoires and territory defence in the Great Tit. Nature 271:539-542.
- LEIN, M. R. 1972. Territorial and courtship songs of birds. Nature 237:48-49.
- . 1978. Song variation in a population of Chestnut-sided Warblers (*Dendroica pensylvanica*): its nature and suggested significance. Can. J. Zool. 56:1266-1283.
- LEMON, R. E., S. MONETTE, AND D. ROFF. 1987. Song repertoires of American warblers (Parulinae): honest advertising or assessment? Ethology 74:265-284.
- LEOPOLD, A. AND A. E. EYNON. 1961. Avian daybreak and evening song in relation to time and light intensity. Condor 63:269-293.
- MACE, R. 1986. Importance of female behaviour in the dawn chorus. Anim. Behav. 34:621-622.
- McNALLY, R. C. AND R. E. LEMON. 1985. Repeat and serial modes of singing in American Redstarts (*Setophaga ruticilla*): a test of functional hypotheses. Z. Tierpsychol. 69:191-202.
- MORSE, D. H. 1967a. The contexts of songs in the Black-throated Green and Blackburnian warblers. Wilson Bull. 79:62-72.
- . 1967b. Competitive relationships between Parula Warblers and other species during the breeding season. Auk 84:490-502.

- . 1968. A quantitative study of foraging of male and female spruce woods warblers. *Ecology* 49:779–784.
- . 1970. Differences between courtship and territorial songs. *Nature* 226:659–661.
- . 1976a. Hostile encounters among spruce-woods warblers (*Dendroica*, Parulidae). *Anim. Behav.* 24:764–771.
- . 1976b. Variables determining the density and territory size of breeding spruce-woods warblers. *Ecology* 57:290–301.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.
- SMITH, R. L. 1959. The songs of the Grasshopper Sparrow. *Wilson Bull.* 71:141–152.
- SMITH, W. J. 1965. Message, meaning, and context in ethology. *Amer. Nat.* 99:405–409.
- . 1969. Messages of vertebrate communication. *Science* 165:145–150.
- WILEY, R. H. AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3:69–94.

WILSON SOCIETY ANNUAL MEETINGS

The 1989 annual meeting of the Wilson Ornithological Society will be held 25–28 May, at St. Mary's College, Notre Dame, Indiana. Doris J. Watt will chair the Committee on Arrangements. Richard C. Banks will chair the Scientific Program Committee. A special feature of this meeting will be a round table discussion of "How to get a paper accepted" for publication in the ornithological literature. Several editors and ex-editors will participate in the discussion.