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**DAILY ORGANIZATION OF VOCALIZATIONS
OF FOREST-EDGE BIRDS IN WISCONSIN**
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ABSTRACT

The daily patterning of vocalizations was determined for 15 species of forest-edge birds at the UWM Field Station. Species that were predominately callers (gave few songs) had very erratic patterns of vocalizations. Species that were primarily singers had distinct morning peaks in singing ("dawn chorus") and, for most species, smaller evening peaks. Some of the singers also had small mid-afternoon peaks when the overall singing rates were low. With the exception of the Field Sparrow, which had a peak before most other species, and the towhee, which had a peak after most other species, there was little interspecific variation in the timing of morning peaks.

INTRODUCTION

An understanding of the daily singing patterns of birds is necessary to test hypotheses concerning whether selection shapes the temporal organization of singing. For example, a number of interrelated hypotheses have been suggested as causes of the "dawn chorus" (reviewed by Kacelnik and Krebs, 1983). These are: 1) microclimatic conditions are particularly favorable for song transmission at dawn (Waser and Waser, 1977, Henwood and Fabrick, 1979); 2) territorial advertisement is especially favored at dawn because of higher rates of territorial intrusions (Kacelnik and Krebs, 1983); and 3) foraging success is low at dawn so birds should sing more at this time (Kacelnik, 1979).

Although there are many references to a "dawn chorus" in birds (Armstrong, 1963) and primates (Tenaza, 1976), we could find few analyses of dawn singing except those concerned with the onset of song in different species (i.e. Zammuto and James, 1982). According to Campbell and Lack (1985) a burst of singing occurs before and just after dawn, singing then abruptly decreases, with a lesser peak at dusk. What proportion of a species' songs occur near dawn? Does an abrupt decrease follow in mid-day with a resurgence of singing later? Is there a "chorus" at dawn produced by different species overlapping their songs? If most species have high song output at dawn, do other patterns occur later in the day?

Heterospecific song may be a significant source of noise for singing birds. Individuals have been shown to avoid this noise by short-term temporal adjustments of singing patterns (Popp et al., 1985), or by alternating song bouts (Cody and Brown, 1969). Another possible mechanism for avoiding interference from heterospecific song would be for species to show different peaks in their daily patterning of vocalizations.

Our principal objective was to provide a preliminary description of the temporal distribution of vocalizing in an avian community. An emphasis was placed on the "dawn chorus" and the daily singing patterns of each species. We have also included calls in our analysis, as they are a considerable component of total vocal output for many passerines.

Song is usually confined to male birds and functions as a territorial advertisement as well as for attracting and stimulating a female. Calls, in contrast, are given by both sexes in a variety of circumstances such as alarm, maintaining contact, etc. Two species we studied, the Great Crested Flycatcher and the Mourning Dove do not produce songs. We predicted that songs and calls would show different daily patterns related to their functions, and we anticipated a more random patterning of calls than songs.

METHODS

Recordings were made at two sites at the University of Wisconsin-Milwaukee Field Station, Ozaukee County, Wisconsin. Both recording sites were near wet areas on the border of a field and an upland hardwood forest, dominated by sugar maple (Acer saccharum), American beech (Fagus grandifolia), white ash (Fraxinus americana) and basswood (Tilia americana).

We used a Nagra 4.2L or Nagra III tape recorder at 9.53 cm/sec with a Sennheiser MKH 104 omni-directional microphone. Vocalizations were recorded continuously from 0400 to 2100 on two days at both sites. Recordings were made on 20 and 24 June 1985 at site A and on 24 June and 1 July at site B. Sunrise occurred at approximately 0515 and sunset at 2035. The dates were selected for favorable weather (average wind speed of 6.5 km/h, 10 to 26° C, sunny) and to prevent inclusion of migrants.

A vocalization rate (vocalizations/min) was determined for each species for each hour of the day (each half hour between 0400 and 0600). This was done by listening to the recordings and noting each time a species vocalized during a 20 min sampling period. The sampling periods were begun at the start of each hour (each half hour between 0400 and 0600). An average vocalization rate for each site was then calculated by taking the mean value for the two recording days. In order to compare species with greatly different vocalization rates, a relative rate of vocalization was calculated for each species by dividing each hourly rate by the maximum hourly rate for that species. During the hour when a species sang the most its relative rate of vocalization would, therefore, be 1.0.

RESULTS AND DISCUSSION

Of the 15 species included in the analysis, nine were principally singers and only occasionally gave calls: Field Sparrow (Spizella pusilla), Song Sparrow (Melospiza melodia), Common Yellowthroat (Geothlypis trichas), Northern Cardinal (Cardinalis cardinalis), Rufous-sided Towhee (Pipilo erythrophthalmus), Blue-winged Warbler (Vermivora pinus), Rose-breasted Grosbeak (Pheucticus

ludovicianus), House Wren (Troglodytes aedon), American Robin (Turdus migratorius). Four species were predominately callers: Black-capped Chickadee (Parus atricapillus), Great Crested Flycatcher (Myiarchus crinitus), American Goldfinch (Carduelis tristis), and Mourning Dove (Zenaida macroura). The Red-winged Blackbird (Agelaius phoeniceus) and Gray Catbird (Dumetella carolinensis) were the only species for which substantial amounts of both calling and singing were recorded. Callers tended to be erratic in the timing of their calls (Fig. 1). For most callers there was little similarity in the patterning of calls between the two sites.

Singers showed a more regular patterning of their songs. Species recorded at both sites had similar daily patterning of vocalizations at the two sites. Morning peaks and late afternoon lulls were typical of almost all singers (Fig. 2). The early morning peak (dawn chorus) occurred at the same time for most of the singers; five of these species had their morning peak at 0430 (grosbeak, cardinal, yellowthroat, Song Sparrow at site B, and Blue-winged Warbler).

The early morning vocalizing patterns were investigated in more detail. The percent of a species' song occurring in each hour of day was calculated (Table 1). For most species a very high proportion of their daily songs occurred during

Table 1. Percent of each species' total songs occurring during early morning.

SPECIES	Time of Day					Average Total Songs Per Day
	0400	0500	0600	0700	0800	
Site A						
Field Sparrow	15.6	6.0	6.9	9.6	9.4	1,432
Song Sparrow	3.9	11.5	17.1	10.6	12.6	1,694
Grosbeak	50.9	23.2	1.2	0	0	259
Yellowthroat	16.2	7.9	0	6.8	0	575
Cardinal	13.5	12.9	21.2	14.1	8.4	179
Robin	10.1	17.9	15.7	4.8	11.7	3,938
Towhee	2.5	11.1	14.6	5.4	10.1	628
Blue-winged Warbler	19.1	10.7	1.1	2.1	2.1	420
Site B						
Field Sparrow	3.7	10.1	8.8	8.9	8.2	2,503
Song Sparrow	12.5	10.8	11.0	13.8	5.8	625
Yellowthroat	9.3	8.3	1.5	7.1	12.3	1,395
Cardinal	23.1	6.7	11.3	23.7	5.1	707
Robin	21.6	15.4	4.6	8.7	11.8	916
House Wren	2.7	8.7	12.3	12.2	7.1	3,296

Figure 1. Daily patterning of vocalization for species that were callers. Relative vocalization rates for each hour of the day were calculated by dividing each hourly rate by the maximum hourly rate for that species. The maximum hourly rate (songs/min.) for each species at each site (A and B) is given in parentheses: (a) Red-winged Blackbird (A, 6.68; B, 8.00), (b) Gray Catbird (A, 2.43), (c) Great Crested Flycatcher (A, 2.57; B, 8.08), (d) Black-capped Chickadee (A, 1.40; B, 4.35), (e) Mourning Dove (A, 1.10; B, 0.78), and (f) American Goldfinch (A, 2.71; B, 3.15). Squares indicate Site A and circles Site B.

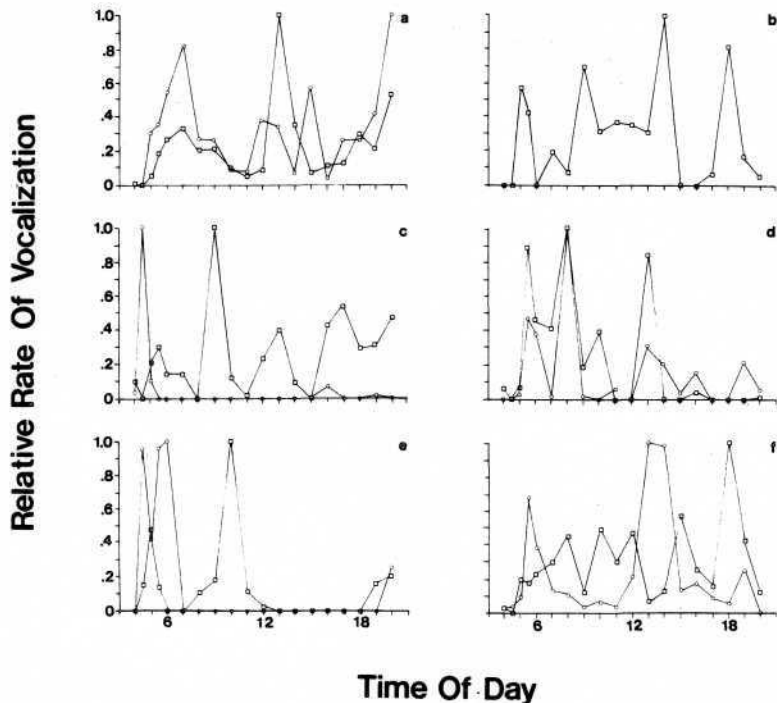
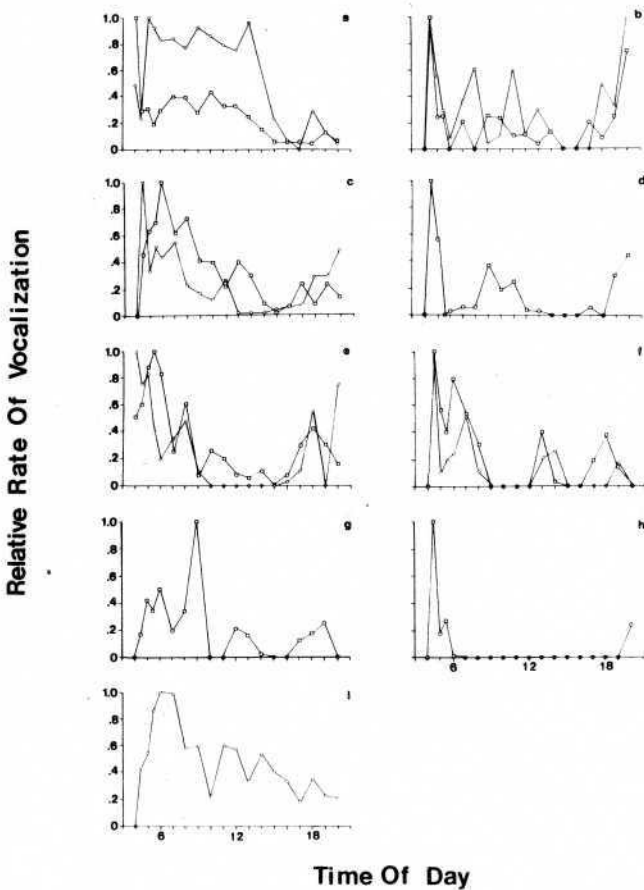


Figure 2. Daily patterning of vocalization for species that were singers. Relative vocalization rates for each hour of the day were calculated by dividing each hourly rate by the maximum hourly rate for that species. The maximum hourly rate (songs/min.) for each species at each site (A and B) is given in parentheses: (a) Field Sparrow (A, 5.75; B, 4.41), (b) Common Yellowthroat (A, 3.10; B, 4.65); (c) Song Sparrow (A, 4.83; B, 2.60); (d) Blue-winged Warbler (A, 2.68), (e) American Robin (A, 12.48; B, 3.75), (f) Northern Cardinal (A, 0.80; B, 5.45), (g) Rufous-sided Towhee (A, 3.05), (h) Rose-breasted Grosbeak (A, 4.40), and (i) House Wren (B, 6.78). Squares indicate Site A and circles Site B.



the period of 0400 to 0500. If birds sang with equal frequency throughout the day, they would have given 5.9% of their songs in each hour period. Most species gave at least twice as many songs as expected during the dawn period, although there were some exceptions (Field Sparrow at site A, towhee, House Wren).

Although advantages may accrue to singing at dawn, one disadvantage might be acoustic interference from other singers. With two exceptions there was no tendency for species to have morning peaks that avoided the noisy "dawn chorus". The exceptions were the Field Sparrow and the towhee; the Field Sparrow had a morning peak before most other species began singing (0400) and the towhee had a morning peak after those of most other species (0900).

Was there a second peak at dusk? We analyzed singing between 1700 and 2000. Only four species had evening peaks during which they gave more than 5.9% of their songs during an hour period: grosbeak, yellowthroat, Blue-winged Warbler, robin (Table 2). For the yellowthroat, the evening peak was as great as the morning peak. Species could, thus, be divided into ones showing a definite evening peak and those with only a small or no increase in singing at dusk.

Table 2. Percent of each species total songs occurring during the evening hours.

Species	Time of Day				Average Total Songs per Day
	1700	1800	1900	2000	
Site A					
Field Sparrow	1.5	1.3	3.2	1.7	1,432
Song Sparrow	4.1	1.4	3.9	2.5	1,694
Grosbeak	0	0	0.5	24.3	259
Yellowthroat	6.5	2.6	7.8	24.0	575
Cardinal	5.0	10.1	3.4	0	179
Robin	5.6	8.2	5.9	3.0	3,938
Towhee	3.6	5.0	7.2	0	628
Blue-winged Warbler	2.1	0	11.9	17.1	420
Site B					
Field Sparrow	0	3.1	1.4	0.5	2,503
Song Sparrow	1.9	7.2	7.2	12.0	625
Yellowthroat	0	9.9	6.5	20.0	1,395
Cardinal	0	0	8.1	0	707
Robin	2.6	13.4	0	18.7	916
House Wren	2.3	4.5	2.8	2.6	3,296

Although most species did not appear to be avoiding noisy periods by adjusting their morning singing peaks, two other trends suggested ways individuals might have insured their song was being heard. First, some species had a smaller midday peak when the overall level of singing was lower (cardinal 1200-1500; Blue-winged Warbler 0800-1200; towhee 1100-1400). Secondly, some species maintained a high level of singing throughout the morning (Field Sparrow; wren).

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