Wilson Bull., 115(3), 2003, pp. 241–245

SONG STRUCTURE MAY DIFFER BETWEEN MALE AND FEMALE LEAST FLYCATCHERS

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ABSTRACT.—Female song rarely has been examined in suboscines. This paper describes the context and structure of female Least Flycatcher (*Empidonax minimus*) songs. During two years, we observed 4 of 19 females singing, and although singing occurred infrequently, it occurred predominantly at the nest during incubation and brooding. Analysis of five songs from one female showed that the mean of this female's songs fell below the distribution of male songs for the internote interval, the minimum and maximum frequency, the frequency range, and the frequency at maximum amplitude of the first note of the two-note song. These results differ from other studies showing no sex differences in song structure of tyrannid flycatchers, suggesting further analyses of female song are warranted. *Received 23 September 2002, accepted 01 May 2003.*

Female song is known to occur in only a small number of suboscine species, most of which are duetting species found in the tropics (Farabaugh 1982). Cases of female song in migratory suboscines are rare, although there are a few laboratory (Kroodsma 1984, 1985), and field (Mumford 1962, Smith 1969, Seutin 1987) studies. In oscines, female song usually differs from male song (Hoelzel 1985, Arcese et al. 1988, Baptista et al. 1993), suggesting that female song may have a different purpose (Langmore 2000). Sex differences in suboscine song structure rarely have been examined, although testosterone implant studies on captive birds showed no structural differences between male and female song (Kroodsma 1984, 1985). Field observers have drawn similar conclusions, although there are no structural analyses owing to the challenges of recording singing females (Seutin 1987).

Here we examine the occurrence and structure of female song in the Least Flycatcher (*Empidonax minimus*) under natural conditions. The Least Flycatcher is a sexually monomorphic, migratory suboscine with a simple two-note song (''che-bec'') used by males in territory advertisement, and which can easily be distinguished from calls due to the intensity and frequency of its use (Briskie 1994). Instances of female song have been documented previously in this species (MacQueen 1950, Mumford 1962, Rappole and Warner 1980), although two of these studies used unmarked birds (MacQueen 1950, Mumford 1962) and none quantified song structure. We observed females singing in eastern Ontario and obtained high quality recordings from one subject. Below we describe the contexts in which females sing and compare the structure of the recorded female's song with a sample of recorded males from the same population.

METHODS

We conducted this study near the Queen's Univ. Biology Station south of Chaffey's Locks, Ontario (44° 34′ N, 76° 19′ W) between May and July during the 2000 and 2001 breeding seasons. A total of 19 paired females was observed (9 during 2000, 10 during 2001). Observations of all females and males began as soon as they arrived on the study site and lasted until the end of the breeding season. Each female was visited and observed daily between sunrise and 14:00 EST for instances of female song.

We recorded all songs during calm and clear conditions using a Marantz portable cassette recorder (Model PMD 222) attached to an Audio-Technica directional microphone (Model AT 815a) through a Saul Mineroff pre-amplifier (Model BA3). We digitized songs using Avisoft SASLab Pro (Specht 1995) at a 22,046-Hz sampling rate and analyzed song structure using a Hamming window and the automatic measurement function

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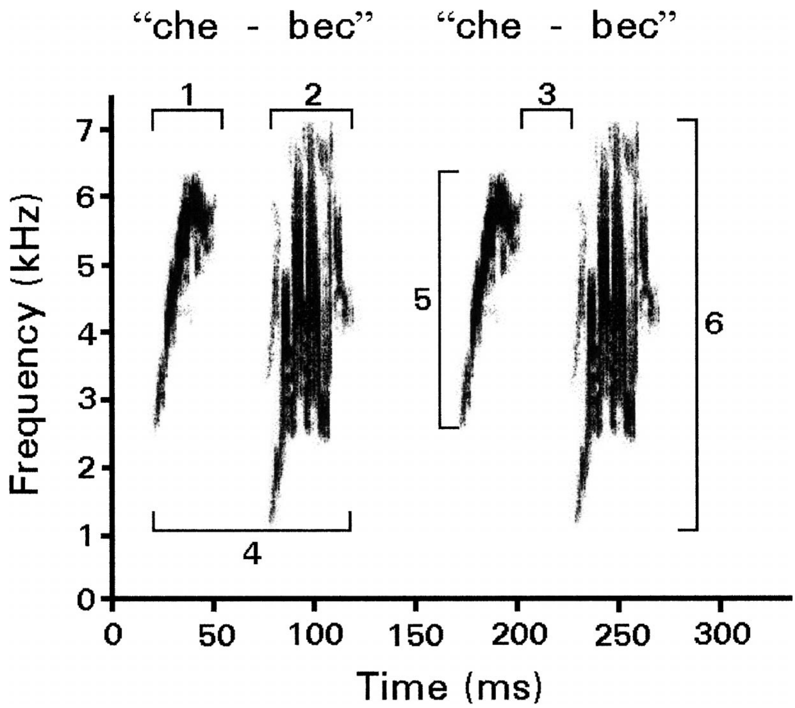

FIG. 1. Structural variables of Least Flycatcher songs: (1) duration of first note, (2) duration of the second note, (3) internote interval, (4) total song duration, (5) frequency range of the first note, and (6) frequency range of the second note; see methods for descriptions of six additional variables. Data are from birds breeding in eastern Ontario, Canada, during 2000 and 2001. Recordings were made by M. M. Kasumovic.

in Avisoft. The parameters during the analysis remained constant and were set up to recognize a threshold of −6 dB for element separation and −10 dB for the calculation of spectrum based parameters. We measured a total of 12 variables. Four of the variable were temporal: the duration of the (1) first and (2) second note, the (3) internote interval, and the (4) length of the total song. Seven of the variables were based on frequency: the frequency range of the (5) first and (6) second note, the minimum (7–8) and maximum (9–10) frequency of each note, and the frequency at maximum amplitude of each note (11–12; Fig. 1). Frequency at maximum amplitude was calculated using Cool Edit 2000 (Johnston 2000).

We captured all recorded individuals using a mist net and banded them with an aluminum Canadian Wildlife Service band and a color band for easier identification. We also collected approximately 30 μL of blood. Females were sexed morphologically in the field (Pyle et al. 1987) and sexing was confirmed later in the lab using a molecular sexing protocol (Griffiths et al. 1998).

RESULTS

Four of 19 females that we monitored during the breeding season were observed singing (two during 2000 and two during 2001). We heard all instances of female song before 10:00 EST during incubation and brooding periods. One female captured during the incubation period sang while held in a bird bag. We observed only one of the four females singing more than one song; all recordings were made from this female. This female was the primary female in a polygynous mating. We heard a total of 13 songs from this female during 4 h of observation on three different days. The female sang eight of these songs while incubating eggs; including two given just before she left the nest. We heard the remaining five songs as the female returned from foraging, after which the nestlings began making begging calls.

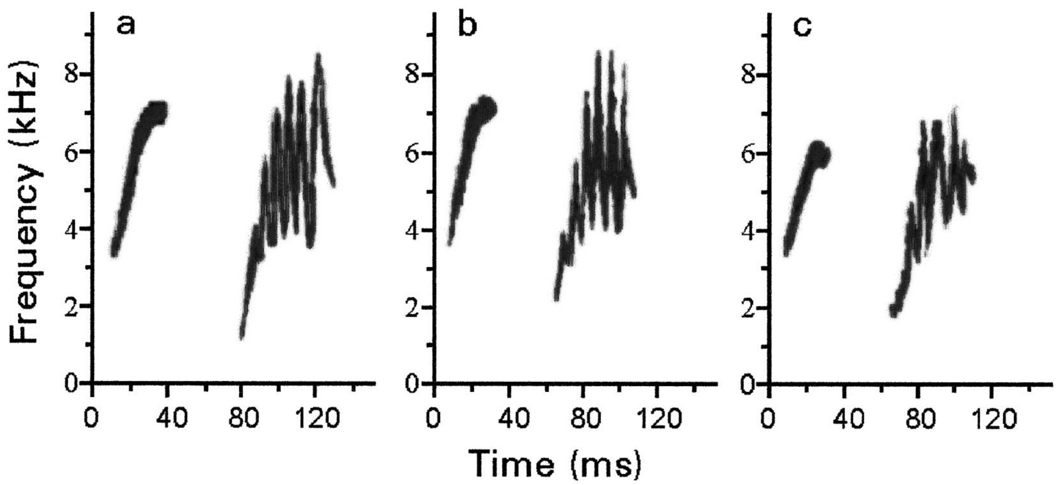

FIG. 2. Sound spectrograms of the songs of Least Flycatchers breeding in eastern Ontario, Canada, during 2000 and 2001; (a–b) two males, (c) one female. Compared to that of males, the first note of the female's song had a lower minimum frequency, lower maximum frequency, lower frequency at maximum amplitude, and a narrower frequency range, and the internote interval was shorter. No differences were seen in the second note. Recordings were made by M. M. Kasumovic.

Because we were able to record songs from only a single female, we did not compare sex differences in song structure with statistical tests of significance. Instead, we calculated a mean for each individual male's songs (based on 5–10 songs from each male, $n = 40$ songs in all), and then examined the means of the female's songs ($n = 5$ songs) with respect to the distribution and the mean of all the males' means. The means of the female's songs fell within the distribution of male means for all except the following five variables, where the mean of the female's songs was below the distribution of the males' means. The first note of the female's song had a lower minimum frequency (female: 4,362 Hz ± 226 SE; males: 5,145 Hz ± 128 SE, range = 4,722–5,576 Hz), a lower maximum frequency (female: 6,006 Hz ± 62 SE; males: 7,064 Hz ± 51 SE, range = 6,876–7,159 Hz), a lower frequency at maximum amplitude (female: 5,655 Hz ± 156 SE; males: 6,637 ± 67, range = 6,355–6,817 Hz), a narrower frequency range (female: 1,644 Hz ± 190 SE; males: 2,462 Hz ± 468 SE, range = 1,814–2,154 Hz), and a shorter internote interval (female: 0.0568 s ± 0.0012 SE; males: 0.0674 s ± 0.0032 SE, range = 0.0602–0.0822 s). Fig. 2 shows the sound spectrogram of a female song (Fig. 2c) compared to two typical male songs from two different males (Fig. 2a, b).

DISCUSSION

Male Least Flycatchers sing at high rates throughout the breeding season (MacQueen 1950). Although females are highly vocal using "whit" and "weep" calls during the breeding season (Briskie 1994), female song is very rare. Our results confirm previous studies stating that female Least Flycatchers sing male-like songs, as seen in other *Empidonax* species (Seutin 1987). A previous study noted that females sang during the nest selection period (Mumford 1962), whereas we observed females singing only during incubation and brooding periods. While it is possible that we missed hearing some female song during the nest selection period, we think this is unlikely as we followed marked females extensively during nest building in order to locate nests.

The results of our structural analysis should be treated with caution since we were able to analyze songs from only a single female. Larger sample sizes are necessary to determine whether male and female songs truly differ in structure. Although females sing male-like songs, our study suggests there may be sex differences in song structure, with the first note of a female's songs having a lower minimum and maximum frequency, frequency at maximum amplitude, and shorter internote interval than male songs. This finding contrasts with previous studies examining song in a total of five testosterone-implanted female tyrannids where no differences were found (Kroodsma 1984, 1985). It is possible that under natural conditions, female song may serve a different signaling purpose than the aggressive and sexual functions of male song.

A recent study has shown that female Willow Flycatchers (*Empidonax traillii*) aggressively defended territories on the wintering grounds using song (Koronkiewicz 2002). Furthermore, breeding female Willow Flycatchers responded aggressively to intruders (Seutin 1987) and sang from the nest during aggressive interactions (Sogge et al. 1997). We observed similar situations in Least Flycatchers where females also are known to participate in territory defence (MacQueen 1950). The female that we recorded sang most often when her mate was silent and away from the nest. The presence of a secondary female on this male's territory might have increased female aggression as observed in female Yellow Warblers (*Dendroica petechia*; Hobson and Sealy 1990). Finally, one female also sang while being held in a bird bag. Hence, our observations coupled with those on Willow Flycatchers suggest that female *Empidonax* flycatchers may use songs during aggressive interactions, or as a warning in situations of distress. Further studies are necessary to determine whether female song is associated with increased aggression in the absence of the resident male.

Experimental work investigating the song of females in this species may prove interesting, since songs in suboscines are innate rather than learned (Kroodsma 1984). Other species of migratory tyrannids also have been documented to sing (Smith 1969; Kroodsma 1984, 1985; Seutin 1987; Sogge et al. 1997), which suggests that female song in this taxon may be common. More observations of marked birds of known sex are needed to determine the prevalence of female song in other suboscines, and to elucidate its functions.

ACKNOWLEDGMENTS

We are grateful to P. Christie and D. J. Mennill for help with analyzing the songs and for initial comments on the manuscript. We also thank J. A. Smallwood and three anonymous reviewers for helpful suggestions that improved the manuscript. This research was supported by a student research award from the American Ornithologists' Union and a Taverner Award from the Society of Canadian Ornithologists to MMK, and grants from the Natural Sciences and Engineering Research Council of Canada to LMR and PTB.

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