

THE FORM AND FUNCTION OF SONG IN FEMALE SONG SPARROWS¹

PETER ARCESE²

Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 2A9, Canada

PHILIP KRAFT STODDARD

Department of Psychology, University of Washington, Seattle, WA 98195

SARA M. HIEBERT

Department of Zoology, University of Washington, Seattle, WA 98195

Abstract. We report on the occurrence and context of female song in the color-marked Song Sparrow (*Melospiza melodia*) population resident on Mandarte Island, British Columbia. Sonograms of three females showed that the structure of female song varied, but was usually less complex than that of males. At least one female's song was within the male range of complexity and could have been mistaken for a male song had the sex of the bird been unknown. Another female sang at least two distinct song types. Further, the songs of females recorded on Mandarte were similar to those recorded elsewhere from wild females and from captive females implanted with testosterone. Overall, singing by females on Mandarte was rare; only 12 of approximately 140 females were heard singing during 267 female-years of intensive observation. With one exception, female song was heard only from late February to mid-April, the period just prior to nest building when territory turnover and settlement by yearlings is most common. Most females (83%) sang during territorial conflicts between female intruders and female territory owners. Female song was more common when population density was high, average breeding success was depressed, and variation in breeding success was increased. We suggest that song results from elevated levels of testosterone in females that are engaged in intrasexual aggression, and we discuss some implications of female song for hypotheses of song learning.

Key words: *Melospiza melodia*; *Song Sparrow*; *territoriality*; *testosterone*; *female aggression*; *song learning*.

INTRODUCTION

Nice (1943) reviewed the occurrence of female bird song and speculated on its evolution. After a considerable gap, renewed interest in the song of female birds has concerned its role in courtship and maintenance of the pair bond, family unit, and territory (Beletsky 1982, 1983a, 1983b; Richison 1983, 1986). In this study, we focused on singing female Song Sparrows (*Melospiza melodia*) in a color-marked island population. We discuss the context of female song, present sonograms from six females, and compare our observations with those of Nice (1943). Finally, we speculate on the function of female song in Song Sparrows.

Except in a few species, singing by female passerines is rare (reviews in Nice 1943, Nottebohm

1975, Richison 1983). Nice (1943) suggested that female passerines fell into two groups, depending on whether song was a common or exceptional aspect of their behavior. She placed Song Sparrows in the latter group. Nice (1943) speculated further that the female Song Sparrows she observed singing were unusually aggressive individuals and had abnormally high levels of androgens. Her suggestion seems reasonable because, in some species in which females rarely or never sing, singing can be induced by implanting testosterone (references in Nice 1943, Nottebohm 1975). However, Wingfield (1984a, 1984b) has shown that in wild Song Sparrows, circulating levels of testosterone in females at the time of territory establishment and just prior to nest building are normally almost as high as those recorded in males at the same time. This is the period during which Nice (1943) heard females singing.

If singing by female Song Sparrows results from unusually high levels of androgens in a few birds,

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² Present address: Serengeti Wildlife Research Institute, P.O. Box 3134, Arusha, Tanzania.

such behavior may be aberrant and therefore unimportant. Alternatively, singing females may be rarely but regularly observed under particular and interesting circumstances, thus suggesting a function for female song. For example, Richison (1983) concluded that singing by female Black-headed Grosbeaks (*Pheucticus melanocephalus*) functioned in family group maintenance: females sang most frequently during the fledgling period and young birds oriented themselves towards their parents' song after becoming separated from them. Beletsky (1983a, 1983b) showed that female Red-winged Blackbirds (*Agelaius phoeniceus*) sang different song types in the context of intrasexual aggression or pair-bond maintenance, and that these songs also differed from the familiar territorial song of males.

In this paper, we show that singing by female Song Sparrows occurred primarily in the context of territory defense against female intruders. We suggest that singing by female Song Sparrows indicates high levels of androgens, and that such high levels are a normal consequence of aggressive interactions. Androgens may be secreted in response to repeated or prolonged conflicts between females for territory ownership, as demonstrated for male Song Sparrows by Wingfield (1984b).

METHODS

Our observations were made during a long-term study of the resident Song Sparrow population on Mandarte Island. Mandarte is a small (6-ha), shrub- and grass-covered rock in the Haro Strait, approximately 64 km south of Vancouver, British Columbia, Canada. Details of the population and the general methods employed there can be found in Tompa (1964) and Smith (1981, in press). From 1982 through 1986, one of us (PA) visited the island for 2 to 5 days at least monthly from September to February, and lived semi-permanently on the island from March through August. During this time, the locations of all birds sighted were recorded on maps drawn from an aerial photograph, and special attention was paid to conflicts over territories.

During the spring of 1985, PKS and SMH recorded three singing females on Mandarte Island. One of these females was recorded while singing spontaneously. The other two sang in response to a playback of songs recorded from a male on a nonadjoining territory. An additional female was recorded by PKS during a song playback

conducted in Discovery Park, Seattle, Washington. In each case, the playback speaker was placed near the center of each female's territory. Songs were recorded on a Uher 4000 tape recorder with a microphone mounted in a 41-cm parabolic reflector. Sonograms of recordings were made on a Kay Elemetrics 6061B Sona-Graph, using a 150 Hz plug-in band-pass filter to reduce ambient noise.

RESULTS

THE FORM OF FEMALE SONG

Female 60194 was first observed to sing on 20 February 1984. The song lasted about 2 sec and was composed of a series of clear, melodic whistles. This female sang in bouts of from one to six songs from a perch above the shrub canopy. The song was loud (audible from three territories distant, about 80 m) and resembled that of a subadult Purple Finch (*Carpodacus purpureus*). The songs of 11 other females heard subsequently varied in volume, length, and complexity, but most resembled the songs of 60194.

The female songs that we recorded were similar to male songs in frequency range, timing, and overall structure (Fig. 1, compare F1-4 with M1-2). P. Marler and S. Peters (pers. comm.) have also recorded songs from live-tutored, captive females that had been implanted with testosterone (Fig. 1, T1-2). Sonograms of recordings from two of these females show a simple (T1) and more complex song (T2) that nearly span the range of song variability that we recorded in the wild (Fig. 1). Overall, males and females sang similar syllable types including pure tones, buzzes, frequency modulated notes and rapid sweeps (Fig. 1). On average, however, females tended to sing songs that included fewer different note types in each song than did males. Nevertheless, the longer, more complex songs could easily pass for male songs to a human listener and might go unrecognized in unbanded populations.

Male Song Sparrows on Mandarte sing four to 12 song types and 30 or more variations on each type (Hiebert, Stoddard, and Arcese, unpubl.). These males sing five to 40 songs of one type, alternating among variations, before switching to another type. The females we recorded sang variations the way males do, and we recorded one female long enough (60 songs) to discover that she had at least two discrete song types.

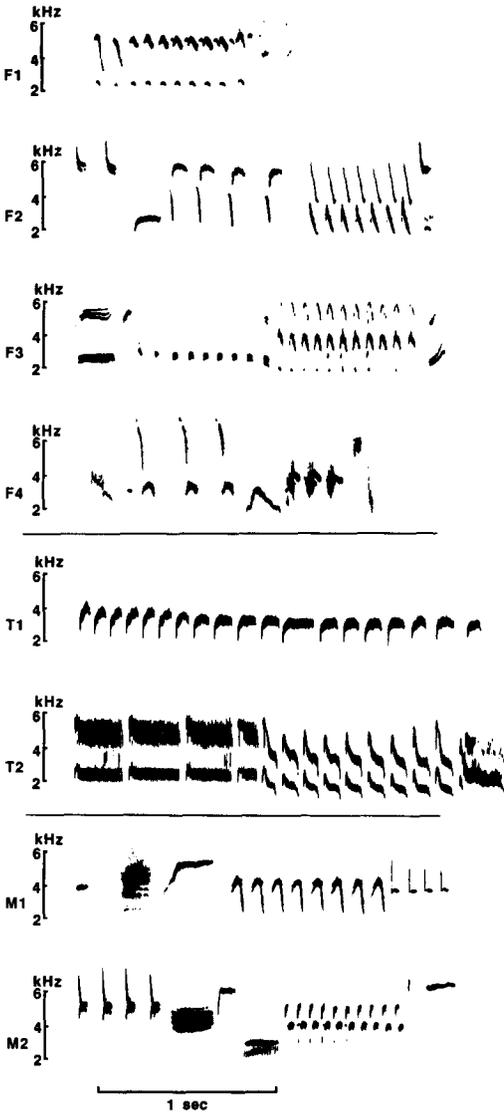


FIGURE 1. Sonograms from three females recorded on Mandarte Island (F1-3), one from a female at Discovery Park, Seattle (F4), and two recorded in New York by P. Marler and S. Peters from captive, live-tutored, females implanted with testosterone (T1-2). Two male songs (M1-2) recorded on Mandarte Island are provided to illustrate the similarity of note types between male and female songs.

THE OCCURRENCE OF FEMALE SONG

Singing females were rarely observed over the study period (Table 1). Only 12 of approximately 140 females were heard singing during 267 female-years of observation. Of these 12, 10 sang on only one day or two consecutive days. Two

females were heard singing in more than one year. In contrast, territorial males on Mandarte Island sang more or less throughout the year, with peaks during late winter, spring, and fall.

Table 1 shows that female Song Sparrows sang mainly between 20 February and the beginning of egg laying, which occurred between late March and mid-April (Arcese and Smith, in press). Only one female (60300) was heard singing after she had begun to lay eggs. This female sang regularly from 7 April to 18 June 1985, usually when she came up from her nest and before she returned to incubate eggs or brood nestlings.

Singing by females, though always uncommon, has been heard more often in this population when population density was high. F. S. Tompa (pers. comm.) heard a female sing in this population only during the year of highest population density during his 4-year study. This was also the only year in which he observed territorial conflicts between females (Tompa 1964, pers. comm.). J.N.M. Smith (pers. comm.) also heard a female sing in this population in the year of highest density during the period from 1974 to 1979. No female was heard singing in this study prior to 1984, despite intensive observation. Three females were observed singing in 1984, nine in 1985, and two in 1986 (Table 1). Figure 2 shows that fewer than the overall average number of females were observed singing when population density was low, while more than expected were observed in high density years.

THE CONTEXT OF FEMALE SONG

Female song was nearly always associated with territory defense and it resulted most frequently when females disputed territory ownership. This can be seen by considering each observation of a single day or series of 2 days of singing by a female as an event. Of 17 such events, 12 (70.5%) occurred during vigorous conflicts between females for territory ownership (Table 1). In these 12 cases, songs were heard from eight territorial females and four intruders (three neighbor territory holders, one nonterritorial floater).

Figure 3 shows a typical territorial conflict between three females that took place over at least 3 days. Two of these females (60194 and 60279) sang repeatedly as the third (60182) was chased and ultimately evicted. The evicted female later settled two territories distant with an unmated yearling. Two additional females sang when no conflict was apparent. In both cases, however,

TABLE 1. The occurrence and context of female song in the Song Sparrow. No females were observed singing in 1982 or 1983.

Female number	Year		
	1984	1985	1986
60194	20 February: Evicting a female floater. 22 February: Evicting same and settling new boundary.	3 April: In response to male playback. 15 April: Evicting a female floater.	Not heard singing.
60279	20 February: Taking over new territory by evicting former female owner.	Not heard singing.	Not heard singing.
60300	10 March: Taking over new territory by evicting former female owner.	3 April: In response to male playback. 7 April: Evicting a female floater, then regularly to at least 18 June.	Not heard singing.
60204	Not heard singing.	8 April: Evicting a female floater.	(Deceased)
60108	Not heard singing.	25 April: On border as adjacent female is evicted by a female floater.	(Deceased)
60254	Not heard singing.	17 April: No apparent conflict.	Not heard singing.
60126	Not heard singing.	3 April: Response to male playback.	Not heard singing.
59239	(Year of hatch)	19 April: Attempting to settle between established territories.	Not heard singing.
59114	(Year of hatch)	18 April: Taking over adjacent territory by evicting owner.	Not heard singing.
58909	(Year of hatch)	29–30 April: Near female floater that settles on adjacent territory.	(Deceased)
59133	(Year of hatch)	Not heard singing.	16 March: No apparent conflict, but settled within the previous month.
59150	(Year of hatch)	Not heard singing.	3–4 April: During intense fights with female floater.

home ranges of nonterritorial females encompassed part of the singer's territory.

Three additional observations of female song were made when we played a tape recording of male song. One of these observations was made unintentionally while we were trying to stimulate a territorial male to sing. This is the only female (60126) that was not also observed singing under natural circumstances. The two other females that responded to playbacks with song were 60300 and 60194, the most active spontaneous singers observed during the study (Table 1).

No other playbacks were conducted during spring or summer, but playbacks were frequently used as an aid during late winter censuses. Fe-

males never responded to these with song, though *threat notes*, *chatters*, *tchunks*, and *caterwauls* (Nice 1943:274) were common. Females were never observed responding to intruding or neighboring males with song, though they did sometimes respond to these birds aggressively (i.e., supplant, chase, and puff-wave posture, similar to "puff-sing-wave" described for males by Nice (1943:274).

DISCUSSION

Recent experimental studies indicate that female song in passerines plays a role in courtship, maintenance of the pair-bond and family group, and territory defense (Beletsky 1982, 1983a, 1983b;

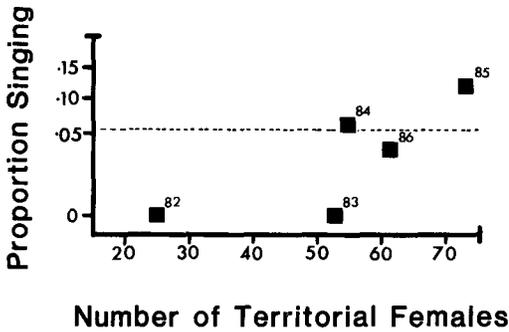


FIGURE 2. The proportion of females (transformed by arcsine square-root) heard singing in relation to the total number of breeding females. The dashed line indicates the average proportion of females in the population heard singing over the entire study. The data are heterogeneous across years ($\chi^2 = 12.78$, $df = 4$, $P < 0.025$).

Richison 1983, 1986). However, these studies have dealt only with species in which females commonly sing. No function has been suggested for female song in species where such behavior is rare (e.g., Rufous-sided Towhee, *Pipilo erythrophthalmus*, and Indigo Bunting, *Passerina cyanea* [Nolan 1958], and Song Sparrow [Nice 1943, this study]). Nice (1943) believed female song served no function in the Song Sparrow, and that it resulted from unusually high levels of androgens in a few abnormal individuals. In the following discussion, we compare our results with those of Nice (1943) and speculate about the implications of female song in our population.

Nice (1943:127) described the song of females that she observed as "short, simple and entirely unmusical," with the exception of one bird (K135). On 2 April 1934, Nice (1943:127) noted that female K135 "has a special place on the locust where she sings; her song is shrill and loud; it reminds me a little of a White-throat [(*Zonotrichia albicollis*)]. There are at least two versions; they are not as unmusical as most female Song Sparrows." The singing behavior of most females that we have heard most closely resembled that described for K135 by Nice. However, not all females that sang on Mandarte produced musical, male-like songs. Sonogram F1 in Figure 1 represents one such song that more closely resembled the songs that Nice reported.

There is also considerable variation in the similarity of song types of males and females across species. For example, in some species in which females commonly sing, such as the Red-winged

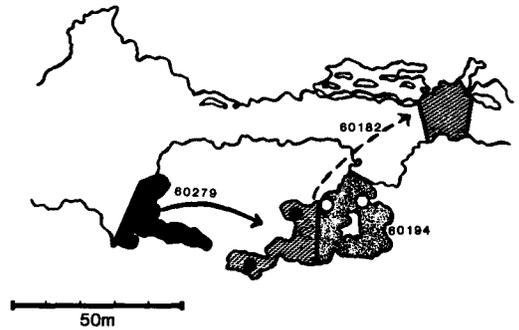


FIGURE 3. Depiction of a conflict between three females for the ownership of a breeding territory (band numbers refer to those in Table 1). Birds defend areas of shrub (outlined area) surrounded by grassland or rocky intertidal. Female 60279 intruded from her previous territory (solid arrow), sang (black dots), and chased female 60182 from her former territory. Female 60194 chased female 60182 whenever she entered her territory and she (60194) sang repeatedly (open circles). Female 60182 settled several days later with an unmated yearling male (broken arrow).

Blackbird, female songs do not resemble those of males (Beletsky 1983a, 1983b). In others, however, females sing songs that are either nearly as well-developed as males (e.g., Black-headed Grosbeak, Richison 1983) or equally well-developed (reviewed in Farabaugh 1982). In species in which females rarely sing, female songs are usually less well-developed than those of males, and are often described as resembling those of immature males (e.g., Nice 1943, Nolan 1958, this study). This suggests that there may be a reduced capacity for female song learning and/or performance in species in which males commonly sing but females rarely do so.

Nice (1943) defined five stages and Mulligan (1966) four in the song development of male Song Sparrows. These began with a soft warbling stage and culminated in full crystallized song. The females we recorded appeared to be nearing the final stage. More of their vocalizations were song fragments than we would expect of a mature male, but they did sing some full, complex songs. Further, in all of the female songs that we recorded, internote intervals were similar to those of crystallized male song. This suggests either that: (1) practice-singing by females is not as important in song development as in males, (2) that some females practice singing as yearlings, or (3) that the song learning process is somewhat different for male and female Song Sparrows.

Nice (1943:127) observed young, unbanded

birds which she suspected were females singing in fall; a female that she hand-raised also produced juvenile male-like warbles. However, we have never made such observations on color-banded, juvenile females. We therefore suggest that practice-singing is less important for female Song Sparrows than it is for males, perhaps because females sing fewer and simpler song types. Further, the song learning process for males and females might differ if female song learning functioned in species recognition, mate choice, or inbreeding avoidance (review in Payne 1983) as well as in territory establishment and defense. In this case, song learning in females might be more highly developed for recognition than for performance.

We observed singing females almost exclusively during the period just prior to nest building (late February to early April). This period matches closely the dates given by Nice (1943:127) of 12 February for the earliest song and 19 April for the latest. Nice (1943) also notes that Wetherbee (cited in Nice 1943) reported a color-banded female Song Sparrow that sang frequently from April through at least 17 June, matching our record for female 60300 (Table 1).

Nice (1943) observed at least two females singing when they participated with their mates in evicting intruding birds. For example, "On Feb. 26, 1932, K56 was singing almost constantly, whenever she was resting from chasing 120M [a male], a new arrival that morning. At times she chased while her mate sang. She perched on top of elders and sang very loudly, often answering her mate's songs" (Nice 1943:127). Nice (1943) mentioned no territorial conflicts when she observed other females singing.

Our observations are consistent with Nice's, with the notable exception that 83% (10 of 12) of the females that we heard singing were involved in conflicts with other females over territory ownership. In contrast, we never observed females to sing when nonterritorial male floaters attempted to evict territorial males or to settle between territorial neighbors, even though such attempts were common during the study (Arcese, in press). This clearly shows that on Mandarte Island, singing by female Song Sparrows is related to competition with other females for breeding space. In this regard, our observation of an increase in the incidence of female song with breeding density is consistent with two effects of density on breeding performance: average reproductive success is strongly depressed

(Arcese and Smith, in press), but variation in reproductive success is increased among females (Smith and Arcese 1986).

We suggest that, as population density and variation in reproductive success increase, competition among females for high quality territories or males becomes more intense. Such competition commonly leads to territorial conflicts between females at high population densities (Arcese, unpubl. data). Androgen levels may increase in females involved in prolonged conflicts, as has been demonstrated in wild male Song Sparrows (Wingfield 1984b), P. Marler and S. Peters (pers. comm.) have repeatedly found that singing can be easily induced in female Song Sparrows with testosterone implants. It is therefore reasonable to conclude that conflict-induced elevations in androgen would have a similar effect in highly stimulated females. Androgen levels in wild female Song Sparrows are known to normally approach the levels observed in males during the periods in which we and Nice (1943) observed females singing (Wingfield 1984a, 1984b).

We therefore suggest that singing by female Song Sparrows is a rare, but normal aspect of female behavior that can be explained in two ways: (1) mechanistically, in terms of the relationship between circulating levels of androgens and the frequency and intensity of aggressive interactions; and (2) evolutionarily, in terms of the role of female vocalizations in aggressive contests over resources that affect reproductive success. Our conclusions remain tentative, however, because the specific relation of androgen levels to territorial conflict in females has not been studied. Therefore, experimental studies are now needed to test if female songs or other vocalizations (e.g., *caterwauls*, *chatters*, *threat notes* [Nice 1943:274]) in the Song Sparrow serve a territorial function as in species such as the Blue Grouse (*Dendragapus obscurus*, Hannon 1980).

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