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The Condor 100:145–148
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SONG SPARROW MALES USE FEMALE-TYPICAL VOCALIZATIONS IN FALL¹

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Abstract. In many species of north temperate-zone passerines, females do not sing, but rather use female-specific calls for acoustic communication. In a resident population in Washington state, banded adult male Song Sparrows (*Melospiza melodia*) outside the breeding season used a vocalization (chitter call) previously believed to be used only by females. This phenomenon has not been observed previously because most field studies of temperate passerines are confined to the breeding season. In this population, juvenile males attempt to establish territories in fall when they do not yet sing fully crystallized songs. Use of female-typical vocalizations by adult males outside the breeding season may allow adults of both sexes to communicate about territories to juvenile males who cannot yet sing the full adult songs males typically use to communicate territorial boundaries.

Key words: *calls, communication, female-typical calls, Melospiza melodia, nonbreeding season, Song Sparrow, territoriality.*

In oscine songbirds, both males and females communicate with vocalizations. Whereas male songs are

used to compete with other males and to attract and increase the receptivity and fecundity of female mates (Searcy and Andersson 1986, Kroodsma and Byers 1991), females of most north temperate species do not sing. Female vocalizations are used socially in competition with other females (Beletsky 1983), to indicate species, sex or individual identity (Beecher et al. 1985), to alert others to the presence of a predator (Marler 1955), in pair bond formation or maintenance (Beletsky 1983), to coordinate reproductive effort within the pair (Lehrman 1964, Cheng 1992), during copulation solicitation (Baker and Baker 1988), and to communicate with young (Beecher et al. 1985, Medvin and Beecher 1986). Song Sparrow (*Melospiza melodia*) females sing only rarely (Nice 1943, Arcese et al. 1988) and have a variety of calls, some of which typically are used only by females (chitter, chet, sweep buzz; Fig. 1c, d, e, respectively; also Nice 1943) and some of which are used by both sexes (low chip contact call, high chip alarm call, threat vocalization growl; Fig. 1a, b, f, respectively; also Nice 1943). The most distinctive of these calls is the chitter. Females direct the chitter call both to their mates as a form of inciting, and to conspecific intruders during the early stages of aggressive encounters. They also use the chitter call during copulation solicitations and upon leaving the nest during incubation (Nice 1943). To date, only females have been reported to use this call. The purpose of this paper is to report observations of males in a resident population using the female-typical chitter call during the nonbreeding season. The chitter call is

¹ Received 27 January 1997. Accepted 2 October 1997.

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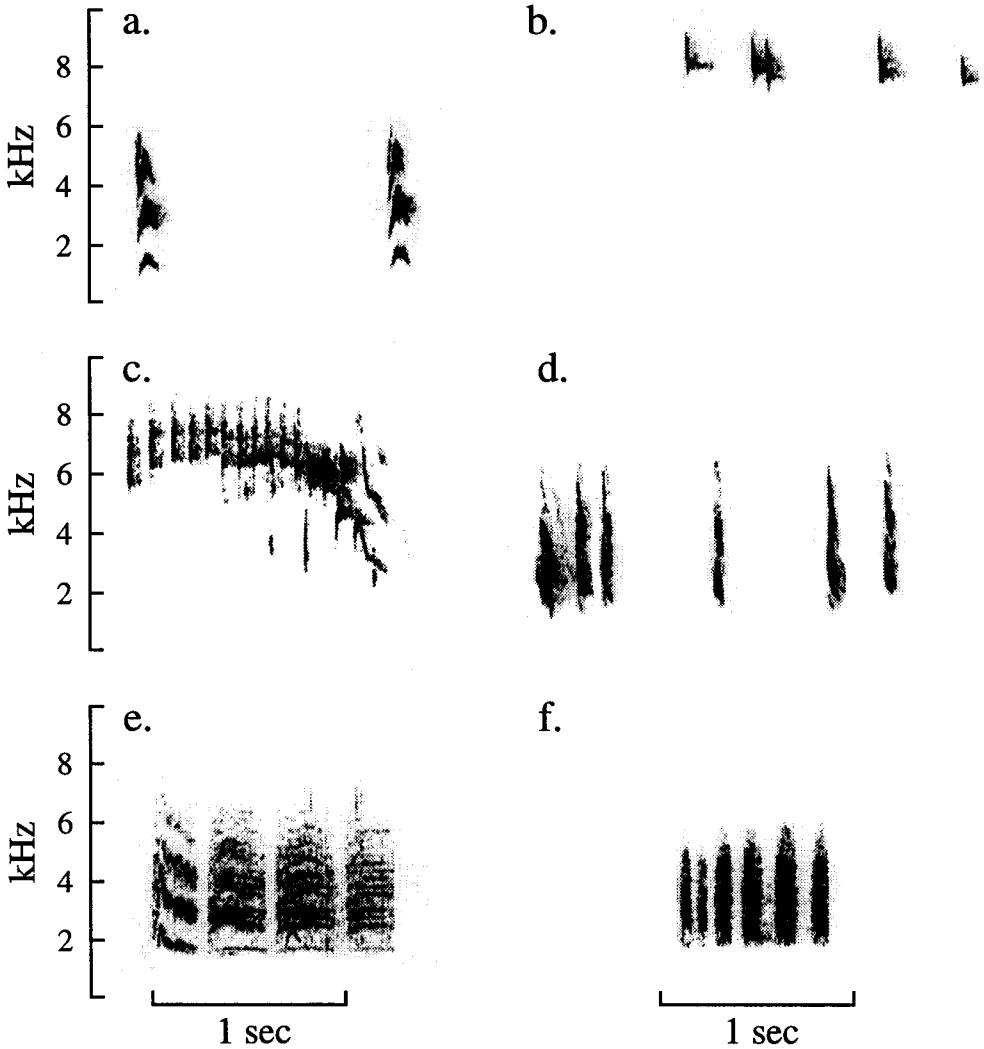


FIGURE 1. Female Song Sparrow vocalizations. a. contact call, shared with male; b. alarm call, shared with male; c. chitter, female typical; d. chets, female typical; e. sweep buzz, female typical; f. growl, shared with male.

easily recognized by human observers and is characterized by a series of single notes, each consisting of a rapid downsweep–upsweep combination. Notes within the chitter often become more frequent as they rise and fall in pitch. It often is followed by chets, notes like those in the chitter call which are given singly, or by a sweep buzz.

METHODS

The study site, Discovery Park, in Seattle, Washington is a 3 km² undeveloped city park along Puget Sound. The Song Sparrow habitat consists of mixed deciduous and coniferous woodland with a dense understory including salmonberry and blackberry (*Rubis sp.*), ferns (*Polypodium sp.*), and nettle (*Urtica dioica*) inter-

persed with open grass fields. The population is resident and typically includes about 150 banded males in any year. In 1990–1995, most adult males in the study area were banded with a unique combination of one aluminum U.S. Fish and Wildlife Service band and three plastic color bands (Beecher et al. 1994). Each part of the study site was censused weekly with the goal of seeing each banded individual at least once each month throughout the year. Most individuals were observed much more frequently. Sightings of an individual typically include both its location and behavior.

RESULTS

All observations occurred in the fall, between 1 September and 30 November in 1990, 1992, and 1995. A

total of 10 banded adult males and 1 banded hatch-year male were observed giving the chitter call typical of female Song Sparrows. Chitters often are heard as originating from within a bush and are presumed to have been given by females. However, in 12 observations of 11 males, each individual was clearly visible and was definitely the source of the vocalization. In the fall of 1990, one adult male was observed to chitter on two occasions. In both cases he was perched and calling on his territory. One hatch year bird was observed giving chitters in response to playback of male songs in the fall of 1992. Four adult males also were observed chittering in fall of 1992; two of these gave the chitter call in response to playback of male song. Finally, six banded adult males were observed chittering in fall of 1995. Of these six, one was a 3-year-old male observed using chitters during fall territorial interactions (as indicated by the wing-wave threat display, called a puff-sing-wave by Nice 1943) with two banded adult males and two unbanded birds. Because all adult males in the vicinity were banded, it is likely that the two unbanded birds were juveniles. At this time of year, very little song is heard, hatch year birds are dispersing, and in this resident population, they are beginning to attempt to gain territories (Beecher et al. 1994).

DISCUSSION

Most previous research on Song Sparrows focused on migrant populations in which birds are not present on their territories in the fall. Therefore, male Song Sparrows had not been previously observed giving the female-typical chitter vocalization in the fall. In resident populations, territory establishment begins in fall when juveniles disperse and behave as floaters on the territories of several adult males. During this period, young males also learn the songs they will sing as adults. Most of these males eventually settle in the areas where they were floaters and share songs with most if not all of the males in this area (Beecher et al. 1994). Although adult males will sing during fall territorial interactions, song rates are lower than those in spring and summer (Beecher, pers. comm.). The additional use of the female-typical chitter call during fall territorial interactions may facilitate two-way vocal interactions between adults and juveniles. In fall, most of the juveniles are not singing or are singing plastic song (Beecher et al. 1994). Previous research on the development of avian vocalizations suggests that in many, but not all, species of birds, calls are innate rather than learned (Kroodsma 1982, Slater 1983), so that juveniles may be able to use the chitter call before they are able to sing. Although males do not use this call during prebreeding territorial establishment or breeding season territorial interactions (Nice 1943, pers. observ.), the use of chitters during fall territorial interactions as described above is consistent with how the calls are used by females (Nice 1943, pers. observ.). Thus, this use of the chitter by males preserves one of the signal functions of this call which may already be known to the juveniles. Furthermore, during fall and winter male Song Sparrows experience basal levels of testosterone and undergo a seasonal regression in the size of the song control regions in the brain (Wingfield

and Hahn 1994, Smith, 1995). During this time, adult males exhibit less stereotypy while singing, but unlike canaries do not learn new songs or modify the songs they sing (G. T. Smith, pers. comm.). Thus, chitters may be more dependable signals than songs during fall territorial interactions because both adults and juveniles would be able to reliably produce the signal.

Comparisons between oscine and suboscine Passeriformes suggest that singing with its associated specialized forebrain song nuclei and dependence on learning is the evolutionarily derived state, with the use of innate vocalizations including calls as the ancestral state (Kroodsma 1988, 1996). In ancestral Song Sparrows, the chitter vocalization may have been used as a territorial signal by both sexes. Females retained the chitter as the primary territorial signal, only switching to song under conditions of high density (Arcese et al. 1988). The switch from the use of chitters to the use of song may be mediated by testosterone, as testosterone implants induce song in female Song Sparrows, and the forebrain song nuclei are known to bind androgens (Ball 1990). Although juvenile males already have masculinized forebrain song nuclei in fall, due to the organizational effects of estradiol metabolized in the brain from gonadal testosterone (Gurney and Konishi 1980, Schlinger and Arnold 1992a, 1992b), they have not yet experienced the photoperiod induced spring increase in testosterone secretion which activates their prebreeding territorial behaviors and crystallizes their songs (Konishi 1989, Doupe 1994). Thus, while juvenile males can produce plastic song in fall, the chitter may be the most stable territorial signal. High levels of testosterone in adult males during the breeding season may prohibit the use of the chitter call in favor of song (Wingfield and Hahn 1994). In fact, to date no adult males have been observed giving the chitter during the early spring prebreeding or late spring and summer breeding seasons (pers. observ.).

Alternatively, the use of the chitter call by males during territorial interactions may have evolved later as an alternative to song at a time of the year when low levels of testosterone yield low song rates in adults and prolonged plastic song in juveniles. In contrast to the previous hypothesis, the secondary use of chitters by males does not require ancestral Song Sparrows to possess a shared territorial signal. Because females are capable of song and males and females share a number of calls, the first hypothesis, that the chitter is basal, is more likely.

The use of the female-typical chitter vocalization for territorial interactions by females in the prebreeding and breeding seasons and by adult males during fall territorial interactions, suggests that outside the breeding season male territorial behavior may be mediated more similarly to female territorial behavior. In resident populations, females, like males, are territorial throughout the year, but their testosterone levels never reach those of males and for most of the year are comparable to basal male levels (Wingfield 1984). It may be that for Song Sparrows, testosterone plays a larger role in male song than it does in aggression by members of either sex. Finally, in resident populations, female song is rare, occurring only during periods of

high density. Male chitters, however, may be relatively common.

I thank S. Elizabeth Campbell and Cynthia Horning for assistance in the field, the staff of Discovery Park for hosting the field work, and Michael D. Beecher, Philip K. Stoddard, and Les Beletsky for helpful comments on the manuscript. This research was supported in part by dissertation improvement grants from Sigma Xi and the American Psychological Association.

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