

Soft song in song sparrows: response of males and females to an enigmatic signal

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Abstract Low-amplitude “soft song” is used by a variety of songbirds; in some species during aggressive encounters, in others during courtship, and yet others in both these contexts. In song sparrows (*Melospiza melodia*), soft song has thus far been observed only in aggressive encounters, where its production is a more reliable predictor of attack than any other signaling behavior. We used song playback to test the response of both male and female song sparrows to soft song. The design of the playback experiments took into account the existence of two classes of soft song: crystallized soft song, which consists of song types also found in the broadcast repertoire, and warbled soft song, which consists of less-structured song types not found in the broadcast repertoire. Female song sparrows responded with significantly less courtship display to the playback of crystallized soft song than to that of normal broadcast song, and response to warbled soft song was if anything lower than to that of crystallized soft song. Male song sparrows responded equally aggressively to normal broadcast song as to crystallized soft song, and equally aggressively to warbled soft song as to crystallized soft song. The female results support the conclusion that neither form of soft song functions in courtship. The male results suggest that the reliability of soft song as a signal of aggressive intent is not maintained by a receiver retaliation rule.

Keywords Soft song · Song sparrow · *Melospiza melodia* · Bird song · Aggressive signaling

Introduction

Low-amplitude song, variously termed as “soft song” (Nice 1943) or “quiet song” (Dabelsteen et al. 1998), is produced by male songbirds in two rather disparate contexts. In some species, for example pied flycatchers (*Ficedula hypoleuca*) and great tits (*Parus major*), males have been observed to produce soft songs only during courtship (Lundberg and Alatalo 1992; Dabelsteen et al. 1998), whereas in others, such as white-throated sparrows (*Zonotrichia albicollis*) and redwings (*Turdus iliacus*), males have been observed to produce soft song only during aggressive encounters (Falls and Kopachena 1994; Dabelsteen et al. 1998). Still in other species, including European blackbirds (*Turdus merula*) and dunnocks (*Prunella modularis*), males are known to produce soft song in both courtship and aggression (Snow 1958; Dabelsteen and Pedersen 1990; Dabelsteen et al. 1998). Observations of the context of soft song thus suggest that this behavior may sometimes function as a courtship signal directed at the opposite sex, sometimes as an aggressive signal directed at rival males, and sometimes as both.

In the song sparrow (*Melospiza melodia*), males thus far have been observed to produce soft song only in aggressive contexts (Nice 1943), never in courtship. Male song sparrows commonly produce soft song in response to conspecific song playback (Beecher et al. 2000), and have also been observed to sing soft song during agonistic chases and between bouts of physical fighting (R. Anderson, personal observation). Nice (1943) described a “challenge” or “puff-sing-wave” behavior, which included soft song,

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by territorial males that were confronting intruders. Nice did not observe neighboring males to exchange soft songs at territorial boundaries. Instead, neighbors at boundaries performed “threat posture,” which did not include soft song. We have found that soft song is a song sparrow’s most reliable signal of aggressive intent, in the sense that a male’s soft song delivery rate is a better predictor of future attack than any other signal that we have measured, including song type matching, song type switching, overall song rate, and wing-waving (Searcy et al. 2006). That soft song functions as a signal of aggressive intent is thus evident.

Whether a soft song also has a courtship function is less clear as the absence of published evidence that soft song is used by males in interacting with females is not conclusive evidence that the song is never used in this way. In this study, we bring experimental evidence to bear on the question by comparing the effectiveness of soft song to that of normal broadcast song in eliciting courtship display from females. If soft song is less effective in eliciting courtship than broadcast song, then this would be evidence that soft song has not evolved as a courtship signal. Dabelsteen and Pedersen (1988) have previously shown in European blackbirds that low-amplitude “twitter” songs evoke less courtship behavior in females than do normal broadcast songs.

We also test the response of male song sparrows to the playback of soft song on their territories. Response to territorial playback is sometimes regarded as a test of whether a signal is aggressive, under the assumption that territory owners themselves will respond more aggressively to a highly aggressive signal than to a less aggressive one. In some species of songbirds, however, it has been found that males respond less rather than more aggressively to signals that other evidence suggests are aggressive (Järvi et al. 1980; Catchpole 1983; Searcy and Nowicki 2000). Thus, we do not regard our results on male response as a test of the aggressive-signaling function of soft song. Rather, these results bear on the question of what evolutionary mechanism maintains the reliability of soft song as a signal of aggressive intent. Having demonstrated that soft song reliably signals aggressive intentions in the song sparrow (Searcy et al. 2006), we now ask how this reliability is enforced.

It is widely accepted that communication signals do, on average, provide reliable information about the qualities or intentions of the signaler (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Reliable signaling of aggressive intentions or fighting ability may provide a cheap and efficient mechanism for settling aggressive contests, but reliability in aggressive-signaling systems is particularly vulnerable to cheating in the form of exaggeration or bluff (Dawkins and Krebs 1978; Maynard Smith 1979). Two principal suggestions have been made as to how reliability can be maintained in aggressive signaling despite the

advantages of deception. One suggestion is that signals of aggressive intent are constrained to be reliable because some property of the signal is causally related to the quality being signaled (Maynard Smith and Harper 1995, 2003). For example, dominant frequency of calls in toads may be constrained to be a reliable signal of fighting ability because the minimum dominant frequency that a toad can produce is correlated with the size of its vocal cords; the size of the animal’s vocal cords is determined by its body size, and body size is the most important attribute determining fighting ability (Davies and Halliday 1978; Howard 1978; Arak 1983; Robertson 1986). Whether or not one accepts such constraints as likely in general (Searcy and Nowicki 2005), constraints do not seem likely to apply to soft song. Low-intensity signals should, if anything, be physically less difficult to produce than high-intensity signals. Hence, it does not seem reasonable that birds of low fighting ability or aggressive motivation would be simply unable to produce soft song. Physical constraints thus do not seem a viable explanation for the reliability of soft song as a signal of aggressive intent.

The other major hypothesis to account for the reliability of signals of aggressive intent is that reliability is ensured by costs. If aggressive signals are costly, and their costs fall differentially on individuals of low aggressiveness or fighting ability, then reliable signaling can be evolutionarily stable (Enquist 1985; Grafen 1990). A variety of types of signal costs have been suggested (Vehrencamp 2000; Searcy and Nowicki 2005), but some, such as production costs and developmental costs, seem unlikely to apply to soft song. Production costs are energy costs incurred when a signal is produced. Bird song in general is thought to have a surprisingly low-energy cost (Oberweger and Goller 2001; Ward et al. 2003), and energy costs must if anything be lower for soft songs than for normal songs. Soft songs are no longer than broadcast songs (Anderson 2006) and are not consistently associated with any special posture. Developmental costs are incurred during development of a signal, and thus well before the signal is produced. Song learning may have considerable costs because learning requires investment in the brain nuclei that control the song (Nowicki et al. 1998, 2002). Complexity and stereotypy are the song attributes that require particular investment (Nowicki et al. 2002; Spencer et al. 2004). Analysis of soft song in song sparrows shows that these songs consist of a mix of “crystallized soft songs,” which are normal broadcast songs sung at low amplitudes, and “warbled soft songs,” which are rambling songs of comparatively low stereotypy, again sung at low amplitudes (Fig. 1). Because these songs either repeat those already in the broadcast repertoire or have low stereotypy, they are unlikely to impose substantial developmental costs over and above the normal broadcast repertoire.

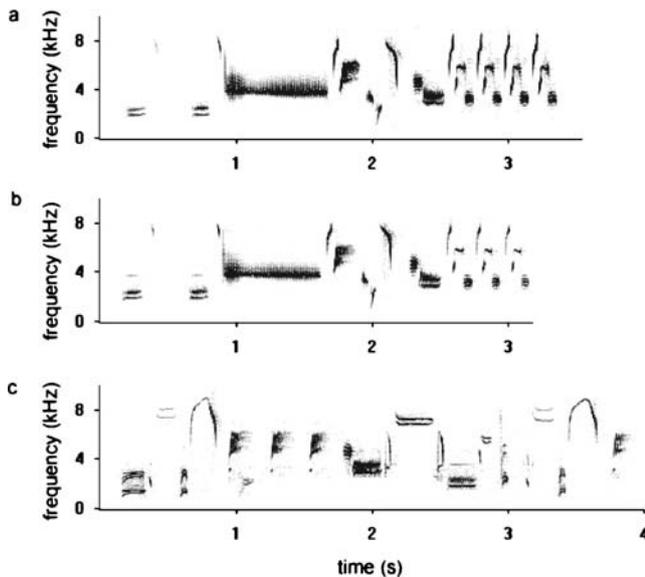


Fig. 1 Spectrograms of the three categories of song sparrow song used in playback: **a** normal broadcast song, **b** crystallized soft song, and **c** warbled soft song. The three songs shown were recorded from the same male. The broadcast song and the crystallized soft song are variants of the same song type; it is typical for crystallized soft songs to be found in the broadcast repertoire (Anderson 2006). Structural differences such as found between **a** and **b** (note the terminal trill) would also be found between different exemplars of a broadcast song type. The darkness of these spectrograms does not convey their relative amplitudes at recording or playback

A remaining category of signal costs, receiver-dependent costs, seems more likely to apply to soft song. In this case, the cost of a signal results from the response that the signal elicits from receivers. One kind of a receiver-dependent cost is a “vulnerability cost,” which arises because “execution of the signal necessarily places the sender in a position of vulnerability to attack and injury by the receiver” (Vehrencamp 2000). Soft song can be argued to impose a vulnerability cost, because transmittal of the signal requires the sender to be near the receiver, and thus vulnerable to attack.

A related type of receiver-dependent cost arises via a “receiver retaliation” rule. In this case, the signal is especially likely to evoke an aggressive response from dangerous adversaries, and reliability is maintained by the “high retaliation cost of signaling a strong state when actually weak” (Vehrencamp 2000). Whereas a vulnerability cost is supposed to stem directly from some aspect of the signal or signaling behavior that makes the signaler physically more vulnerable to attack, a receiver-dependent cost depends only on an arbitrary convention on how receivers respond to the signal. Theory suggests that such retaliation rules can work to ensure the reliability of aggressive signals (Enquist 1985; Hurd 1997), and there are empirical examples that support this hypothesis. For example, in American goldfinches (*Carduelis tristis*), the

most aggressive signals are the ones most effective in deterring opponents, and are also the most likely to provoke attack from opponents (Popp 1987). Furthermore, there is some evidence that singing behaviors with a strong aggressive message in turn elicit a strong aggressive response (Molles and Vehrencamp 2001; Vehrencamp 2001). In this study, we use the approach to territorial playback by male song sparrows to evaluate the receiver retaliation cost of soft song, contrasting response to soft song and broadcast song as we did in the female experiment. Response to song playback has previously been used to measure retaliation costs of song, with the rationale that a strong aggressive response to song playback implies a high receiver retaliation cost (Molles and Vehrencamp 2001; Vehrencamp 2001). As our measure of response, we use approach to the sound source, which has been shown to be an excellent predictor of actual physical attack in song sparrows (Searcy et al. 2006).

Materials and methods

Female playback experiments

Subjects for the female experiments were ten adult female song sparrows captured in the vicinity of Hartstown, Crawford County, PA, USA during May, 2003. Subjects were captured using walk-in traps baited with grain and then transported to a laboratory where they were each held singly in cages housed in individual sound attenuation chambers (AC-1, Industrial Acoustics, Bronx, NY, USA). Each female was given an implant of 17- β -estradiol, which was inserted under the skin after application of a topical anesthetic. Implants were made of silastic tubing of 1.96 mm outside diameter, were 14 mm in total length, and contained 8–10 mm of hormone. After testing, we removed the implants (again with application of topical anesthetic) and released all subjects at the site of their capture.

We began testing the females 7 days after the estradiol was implanted. Songs were played to one female at a time, with the door of her chamber open and the other chambers closed. Songs were played from a Nagra DSM loudspeaker placed at a fixed location. Responses were observed using a video camera aimed through the open chamber door and connected to a monitor in another room. We used the number of solicitation displays as the sole measure of response (King and West 1977; Searcy and Marler 1981).

We performed two experiments with females. One, the crystallized vs. warbled experiment, compared response to the two categories of soft song, crystallized soft song and warbled soft song (Fig. 1). The second, the broadcast vs. crystallized experiment, compared response to normal

broadcast song and soft song, using crystallized soft song to represent soft song (Fig. 1). Each female was tested on two consecutive days with a given pair of stimuli, the first time with order counterbalanced across subjects, and the second time with order reversed. On each day of testing, the two contrasting stimuli were presented at least 3 h apart, to minimize habituation from the first test to the second. In each test, a female was presented with 3 min of a single song, repeated at a rate of one song per 10 s; this rate is within the range given by male song sparrows in nature. Male song sparrows sometimes repeat both crystallized and warbled soft songs in bouts of the same type (Anderson 2006). Responses were compared within-subjects (i.e., in a paired design).

In the crystallized vs. warbled experiment, we used ten crystallized soft songs and ten warbled soft songs that we had recorded from territorial males in Crawford County during simulated intrusions on their territories. These songs were played at a mean amplitude of 61 dB Sound Pressure Level (SPL; range 58–64) measured at 1 m. Soft songs are produced in nature at levels ranging from 50 to 77 dB SPL measured at 1 m (Anderson 2006). The cages of the female subjects were 2–4 m from the loudspeaker during playback. In the broadcast vs. crystallized experiment, we used the same set of ten crystallized soft songs (61 dB SPL) plus ten normal broadcast songs also recorded in Crawford County. Each subject was presented with a different crystallized soft song in the first and second experiments. The normal broadcast songs were played at a mean amplitude of 83 dB SPL (range 80–85). Broadcast songs are given in nature at 78–85 dB SPL.

Male playback experiments

Playback experiments with males were carried out in the vicinity of Linesville and Hartstown, Crawford County, PA, USA during June and July of 2004. The subjects were male song sparrows defending territories in edge habitat between deciduous forest and either old fields or mowed areas. The two experiments with males paralleled those with females: One (crystallized vs. warbled) compared response to crystallized soft song and warbled soft and the other (broadcast vs. crystallized) compared response to soft song and normal broadcast song, using crystallized soft song to represent soft song. Trials for the broadcast vs. crystallized experiment were performed between June 3 and June 15, and trials for the crystallized vs. warbled experiment were performed between June 18 and July 2. Both experiments incorporated a paired design in which the contrasting stimuli were presented to the same subjects in a counterbalanced order and at least 2 days apart. Response could then be compared within subjects. Each experiment

had a sample size of 15 males; seven males were used in both experiments, while an additional 16 males were used in just one or the other. Individual male subjects were identified for consecutive playbacks using unique color band combinations or by territory location. To control for effects of familiarity with playback songs, we used in all trials songs that had been recorded at least 2 km distant from the subject, so that all would be equally unfamiliar. We used 15 warbled soft songs, 15 crystallized soft songs, and 15 normal broadcast songs, all recorded in Crawford County. A different exemplar of each category of song was used for playback to each subject.

A Marantz PMD 670 digital recorder and a Fender AmpCan speaker were used for male playbacks. The speaker was positioned well within the territory, and its position was marked for the first trial in each pair so that the same position could be used on the second trial. Broadcast songs were played at a mean amplitude of 85 dB SPL (measured at 1 m with a GenRad 1565D sound level meter on C setting). Both categories of soft song were played at a mean of 64 dB SPL. Amplitude of the soft song playback was low enough that territorial males might have easily failed to hear the playback of soft song, given the size of song sparrow territories and the amount of background noise in the environment. To ensure that subjects did hear the soft song playback, we began each trial by playing an initial song type (a nonexperimental stranger song) at broadcast song amplitude (85 dB SPL) to draw the subject to the vicinity of the speaker. The initial song was played at 10-s intervals until the subject approached within 4 m of the speaker or until the song had been repeated six times. If the subject failed to meet the 4 m criterion by the time the sixth song had been played, we stopped that trial, and tried another test with that subject on a subsequent day. Trials in which the experimental stimulus was a normal broadcast song were also begun with playback of this initial song, with the same 4 m approach criterion, to avoid bias.

Once the 4 m criterion was met, we began a 3 min playback of the experimental stimulus (normal broadcast song, crystallized soft song, or warbled soft song). Playbacks were followed by a 3 min postplayback period during which we continued to monitor the subject's behavior. We measured the aggressive response to the different playback treatments using the variables: (1) distance to the playback speaker averaged over the 3 min playback, (2) distance averaged over the 3 min postplayback, and (3) time spent within 2 m during the 6 min trial. Estimation of distances was aided by placing markers at measured distances of 2, 4, and 8 m from the speaker before the trial. Mean distance to the speaker was calculated using the method of Peters et al. (1980). Proximity to a loudspeaker is a good predictor of attack in song sparrows

(Searcy et al. 2006) and is therefore a valid measure of aggressive response. We used principal components analysis (PCA) to combine the three response measures into a single multivariate measure, which we also compared between treatments.

Results

Female playback experiments

In the crystallized vs. warbled experiment, female subjects performed a mean of 3.1 (± 1.5 SE) solicitation displays in response to crystallized soft song, compared to a mean of 0.8 (± 0.3) displays in response to warbled soft song. The difference in response was not significant according to a Wilcoxon Matched Pairs Signed Ranks test ($N=9$ subjects with non-tied responses, $z=-1.549$, $P=0.12$). In the broadcast vs. crystallized experiment, females performed a mean of 6.4 (± 1.7) displays in response to normal broadcast songs, compared to a mean of 2.0 (± 0.8) displays in response to crystallized soft song. This difference in response was significant by a Wilcoxon test ($N=9$ subjects with non-tied responses, $z=-2.504$, $P=0.012$).

Response to crystallized soft song was lower in the second experiment than in the first, although not significantly lower ($z=-0.689$, $P=0.49$). Again, each subject was presented with a different crystallized soft song in the two experiments. The downward trend in response to the same category of stimuli is probably explained by a general decrease in responsiveness of test females over successive tests, which past experience suggests is a general phenomenon with this testing paradigm. Because response generally tends to decrease over successive tests, a comparison of response to warbled soft song in the first experiment to response to normal broadcast song in the second experiment is conservative with respect to the conclusion that response was higher for broadcast song ($N=9$, $z=-2.821$, $P=0.005$).

Male playback experiments

In the crystallized vs. warbled experiment, order of presentation had no effect on any of the three univariate response measures for either playback treatment (Mann–Whitney U tests; $P>0.25$ in all cases). The subjects responded strongly to both crystallized soft song and warbled soft song, and their responses were similar on all three measures (Table 1). No significant differences in response were found. When we combined the response measures using PCA, the first principal component explained 82% of the variance. The two distance measures loaded negatively, and time in proximity loaded positively, so this component corresponds to response strength. Mean PC1 scores were higher for warbled soft song (0.16) than for crystallized soft song (-0.16), but the difference was not significant ($t=1.171$, $P=0.26$ by a paired t -test).

In the broadcast vs. crystallized experiment, order of presentation again had no effect on any of the univariate response measures ($P>0.25$ in all cases). Response to normal broadcast song was more intense than response to crystallized soft song on all three measures (lower distances, greater time in proximity), but none of the differences was significant (Table 1). The first principal component explained 77% of the variance in response, and the factor loadings were very similar to those in the crystallized vs. warbled experiment. Mean PC1 scores were higher for normal song (0.24) than for soft song (-0.24), but the difference was not significant ($t=1.525$, $P=0.15$ by a paired t -test).

Comparing across the two experiments, response to warbled soft song was extremely similar to response to normal broadcast song for each of the three original response measures (Table 1).

Discussion

Female song sparrows responded much less strongly to crystallized soft songs played at 61 dB than to normal

Table 1 Response of male song sparrows to playback of soft songs and normal songs on their territories (means \pm SE)

	Distance during playback (m)	Distance after playback (m)	Time within 2 m (min)
Crystallized vs. warbled			
Crystallized soft	2.3 \pm 0.5	5.1 \pm 1.6	3.5 \pm 0.5
Warbled soft	1.7 \pm 0.5	3.6 \pm 0.7	3.9 \pm 0.5
P value	0.24	0.50	0.73
Broadcast vs. crystallized			
Normal broadcast	1.6 \pm 0.2	3.4 \pm 0.6	4.1 \pm 0.4
Crystallized soft	2.1 \pm 0.4	4.3 \pm 0.7	3.3 \pm 0.5
P value	0.41	0.30	0.08

P values are from Wilcoxon Matched Pairs Signed Ranks tests

broadcast songs played at 85 dB. As the acoustic structure of crystallized soft song seems to be highly similar to that of normal broadcast songs except in amplitude (Anderson 2006), this difference in female response must be attributed to the amplitude difference. Female preferences for louder male signals have previously been demonstrated in a variety of anurans and acoustic insects (Fellers 1979; Arak 1983; Latimer and Sippel 1987; Gerhardt and Huber 2002), in European blackbirds (Dabelsteen and Pedersen (1988), and in red-winged blackbirds (*Agelaius phoeniceus*; Searcy 1996). Such preferences may, in general, be adaptive because louder males are on average closer to the receiver, or because louder males are on average larger or more vigorous. Preferences for louder males might also be simply a byproduct of neural and sensory mechanisms that give greater attention to more intense signals. In the case of soft song in song sparrows, however, another possibility is that females discriminate against soft song because soft song is a signal of aggressive intent. Females have been shown to discriminate against male aggressive signals in a variety of species of anurans (Schwartz 1987; Wells and Bard 1987; Brenowitz and Rose 1999; Gerhardt and Huber 2002). Our finding that female song sparrows respond even less to warbled soft song than to crystallized soft song is in accord with this last possibility: Crystallized soft song might represent a distant male singing broadcast song, whereas warbled soft song is unambiguously a signal of aggressive intent. At any rate, the low response to both forms of soft song is strong evidence against the possibility that soft song functions as a courtship signal in this species.

We found no evidence of a receiver-retaliation rule for soft song in song sparrows. Approach to a loudspeaker playing conspecific song has been shown to be a strong predictor of attack in song sparrows (Searcy et al. 2006), so the measures we made for proximity to the playback speaker are valid measures of aggressive response. Furthermore, the response measures we used were similar to those that have been used to support a receiver retaliation rule for other song features in other species of songbirds (Molles and Vehrencamp 2001; Vehrencamp 2001), and that have been used successfully to demonstrate differential response to other categories of song in song sparrows (Peters et al. 1980; Searcy et al. 1997). The summary response measure provided by PCA showed that the overall response was substantially in the opposite direction from that predicted by the receiver-retaliation hypothesis, with a stronger response to normal broadcast song than to soft song. We conclude that a receiver-dependent cost through a receiver retaliation rule is not supported for soft song in song sparrows.

Rejection of a receiver-retaliation cost leaves open the question of what mechanism maintains the reliability of soft song as a signal of aggressive intent. One possibility is that soft song imposes a vulnerability cost, in the sense that the

execution of the signal leaves the signaler more open to injury (Vehrencamp 2000). This hypothesis has some appeal, because a signaler must be fairly near a receiver for the receiver to be able to hear soft song, and soft song undoubtedly is on average given nearer to receivers during aggressive encounters between song sparrows than broadcast song. One problem with this hypothesis is that it is not clear that a male who is close to the receiver is any more vulnerable when he sings a soft song than when he sings a broadcast song. The amplitude experienced by the receiver of a broadcast song given at 1 m would be unambiguously greater than that of broadcast song given at 10 m, and therefore would also necessarily convey that the signaler is close. Another problem with the vulnerability hypothesis is that it makes few or no testable predictions.

A second possibility is that production of soft song imposes what we term a “competing functions cost,” a cost that arises when signaling has multiple functions, and signaling to maximize one function minimizes another. In the current case, singing functions in both male–male aggressive signaling and in female attraction and courtship. Soft song may maximize the aggressive signaling function, but at a cost to the male–female function. The fact that females discriminate against soft song is in accord with this kind of cost. Singing to females is known to contribute to male fitness in a number of ways: by attracting females to a territory (Eriksson and Wallin 1986; Johnson and Searcy 1996), by stimulating courtship and copulation (King and West 1977; Searcy and Marler 1981; West et al. 1981), and by stimulating nesting (Hinde and Steel 1976; Kroodsmma 1976). Thus, switching to soft song ought to have some negative fitness consequences for male song sparrows through diminished effectiveness in communicating to females. A problem with this hypothesis is that the total time males spend in escalated interactions with rival males, and therefore the total time spent producing soft song seems likely to be very small. Thus, the overall cost from reduced male–female signaling may well be negligible.

Another approach to explaining the use of soft song in aggressive contexts is to ask how a territory owner might benefit from using soft song during aggressive interactions. One hypothesis is that the signal’s low amplitude minimizes the opportunity that others have to eavesdrop on the interaction (McGregor and Dabelsteen 1996; Dabelsteen et al. 1998). Territory owners could benefit from concealing that an encounter is taking place from several classes of potential eavesdroppers, including conspecific males, who might take advantage of the owner’s preoccupation to trespass on his territory, and predators, who might use the opportunity of the owner’s distraction to attack him. Experimental simulation of singing interactions has shown, however, that a territorial male song sparrow that uses soft song in confronting an intruder actually increases, rather

than decreases, the likelihood that other males will trespass on his territory (Searcy and Nowicki 2006). Thus, responding to a singing intruder with soft song appears to be counterproductive with respect to eavesdropping males. Furthermore, experimental simulation of an increased threat of predation does not cause territory owners to increase their reliance on soft song (Searcy and Nowicki 2006). In fact, playback of alarm calls decreased, rather than increased, the proportionate use of soft song by focal males in response to a simulated rival male. It appears that the eavesdropping hypothesis, although intuitively appealing, does not explain the use of soft song as a signal of aggressive intent in song sparrows.

In conclusion, it is clear from our results that soft song does not function as a courtship signal in song sparrows, as it seems to do in some other species of songbirds (Lundberg and Alatalo 1992; Dabelsteen et al. 1998). Thus, soft song in song sparrows appears to be exclusively a signal of aggressive intent. It is not clear what if any cost acts to maintain the reliability of soft song as a signal of aggressive intent in song sparrows. Theory suggests that some cost must be in place to select against the use of soft song as a bluff. A receiver-retaliation cost is the most likely kind of cost to apply to this type of signal, but such a cost is not supported by our results.

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