

Soft song is a reliable signal of aggressive intent in song sparrows

Christopher N. Templeton · Çağlar Akçay ·
S. Elizabeth Campbell · Michael D. Beecher

Received: 18 May 2012 / Revised: 21 August 2012 / Accepted: 21 August 2012 / Published online: 5 September 2012
© Springer-Verlag 2012

Abstract Animals frequently use signals to modulate aggressive interactions. Establishing that a signal is aggressive or threatening requires demonstrating that it is more commonly used in agonistic contexts, that it predicts subsequent aggressive behaviors by the sender, and that receivers respond differently to this signal. Like many birds, song sparrows (*Melospiza melodia*) produce a low-amplitude “soft song” vocalization that has been hypothesized to be an aggressive signal. Soft song meets the first two criteria, but previous research has failed to demonstrate that soft song provokes aggression or that receivers even perceive soft song differently from normal loud song. We used a playback experiment with taxidermic mount presentation to test whether territorial male song sparrows respond differently to loud and soft song playbacks. Subjects reacted more strongly to the soft song playback by approaching the mount more closely, increasing wing wave displays, and increasing the proportion of their own songs that were soft songs, with further trends toward increasing the number of flights and attacks. These results confirm that soft song is a conventional signal of aggression in song sparrows and that increased receiver retaliation maintains its reliability.

Keywords Aggression · Bird song · Honest signaling · Song sparrow · Territoriality

Introduction

Animal signals produced during aggressive interactions have been the focus of much research, both empirical and theoretical. While classical ethologists were mostly concerned with the motivational basis and the evolutionary origin of aggressive displays, the focus on aggressive signaling shifted to the question of honesty with the advent of the evolutionary game theory in the 1970s. Early game theoretic models (Maynard Smith 1974; Maynard Smith 1979) suggested that when individuals had conflicting interests in the outcome of the interaction, as in an aggressive interaction, the winning strategy would be to signal at the maximum intensity. Thus, signals would not carry any reliable information regarding the subsequent aggressive behavior (e.g., the likelihood of escalation or attack) of the signaler (termed as “aggressive intent”). Nonetheless, subsequent models showed that signals can be honest when they are costly, in particular, when cheating is more costly for lower-quality individuals (Zahavi 1975; Zahavi 1977; Grafen 1990; Maynard Smith and Harper 2003; Searcy and Nowicki 2005).

It is easy to see how some signals used in aggressive contexts should be honest and costly or even impossible to cheat (e.g., when a display emphasizes the body size or weaponry of the signaler (Davies and Halliday 1978; Clutton-Brock and Albon 1979)). Other aggressive signals, however, seem to carry few production costs and do not seem to reflect any trait related to the outcome of a potential fight. Bird song as a signal of aggressive intent falls into this category (Gil and Gahr 2002).

In many songbirds, normal broadcast song has been hypothesized to be low in the threat signal hierarchy and to function primarily as a “keep-out” signal by which the

Communicated by H. Brumm

C. N. Templeton · S. E. Campbell · M. D. Beecher
Department of Biology, University of Washington,
Seattle, WA 98105, USA

Ç. Akçay · S. E. Campbell · M. D. Beecher
Department of Psychology, University of Washington,
Seattle, WA 98105, USA

C. N. Templeton (✉)
School of Biology, University of St Andrews,
St Andrews KY16 9TS, UK
e-mail: ct510@st-andrews.ac.uk

Ç. Akçay
Cornell Lab of Ornithology, Cornell University,
Ithaca, NY 14850, USA

bird “posts” or advertises his territory (Searcy and Beecher 2009). Normal broadcast song is sung at a surprisingly high amplitude given the small size of the bird (Brumm 2009) and is thus aptly referred to as “loud song” (Anderson et al. 2008). Typically, loud song can be heard several territories away from the singer (Catchpole and Slater 2008), though amplitude can vary depending on the social situation (Brumm and Todt 2004; Ritschard et al. 2012). That broadcast song is an effective keep-out signal is revealed by our observations of male birds failing to hold their territory after losing their voice due to viral infections (personal observations) and field experiments in which the bird is surgically devocalized: he is first disregarded and ultimately replaced by a singing conspecific despite attempts to defend his territory (McDonald 1989). Experiments where the male is removed from his territory and replaced with a playback of his songs (or not) have also revealed the keep-out function of the broadcast song (Krebs et al. 1978; Nowicki et al. 1998). Loud song, however, seems to be a relatively unreliable signal as it consistently fails to predict aggressive behavior (reviews in Beecher 2008; Searcy and Beecher 2009). Instead, when aggressive interactions, either real or experimentally manipulated ones, escalate, many birds switch from loud song to other types of signals (Searcy and Beecher 2009).

One such signal is “soft song” or “quiet song.” Soft songs are low-amplitude songs that are sung 10–30 dB lower than normal broadcast song and generally cannot be heard unless the receiver is within 10–20 m of the singer (Dabelsteen et al. 1998). Soft song occurs in many avian species (e.g., Nice 1943; Lack 1965; Dabelsteen and Pedersen 1990; Titus 1998; Anderson et al. 2008; Reichard et al. 2011; Rek and Osiejuk 2011). Although soft song is characterized by low amplitude, its acoustic structure can also vary, and in some species, such as song sparrows (*Melospiza melodia*), soft song can take two different forms, with a given species often employing both. Soft “crystallized” song is simply a low-amplitude version of normal broadcast (loud) song. In contrast, soft “warbled” song differs from normal broadcast song by the presence of very low- and high-frequency elements not found in crystallized song and by the absence of the trills that are typically found in loud song. Crystallized song can be produced at either a loud or soft amplitude, but warbled song is only produced at low amplitude. Although soft song occurs in either mating or aggressive contexts in different species, much of the recent research has been focused on soft song as a reliable signal of aggression.

To establish that a given signal, such as soft song, is a reliable signal of aggression, Searcy and Beecher (2009) suggested that three criteria must be demonstrated. First, the signal should increase in agonistic contexts, e.g., in territorial disputes (“context” criterion). This criterion establishes that the signal is agonistic, but not specifically that it is aggressive (e.g., it might be a submissive signal). Next,

the “predictive” criterion—does the signal predict increased aggression by the signaler?—can establish that the signal is aggressive but does not establish that it is salient to receivers. Finally, the “response” criterion—does the receiver respond differently to the signal than to an appropriate control?—demonstrates that the signal is salient to receivers and that it elicits increased aggression or retaliation. Thus, satisfying these criteria would make a strong case that a given signal is a functional and reliable threat signal.

In song sparrows, soft song is observed only when a bird is near a rival (real or simulated) and involved in aggressive interactions (Nice 1943), thus meeting the context criterion. Searcy et al. (2006) provided the first evidence that soft song production was the one signal that reliably predicted an immediate attack on a taxidermic mount. Similar evidence has been found in another population of song sparrows (Akçay et al. 2011), for the congeneric swamp sparrow (*Melospiza georgiana*, Ballentine et al. 2008), and in other avian species (Hof and Hazlett 2010; Rek and Osiejuk 2011). Thus, strong evidence exists for the predictive criterion and indicates that soft song is a reliable signal of aggressive intent.

Despite this evidence on the reliability of soft song for predicting aggression, it is not clear what maintains this reliability. One possibility is that singing softly increases the likelihood of retaliation from the receiver. Theory suggests that receiver retaliation can be an effective mechanism for maintaining signal reliability, and there are examples in the literature of otherwise non-costly signals being maintained by receiver retaliation (e.g., Rohwer and Rohwer 1978; Molles and Vehrencamp 2001; Tibbetts and Dale 2004). As indicated by Searcy and Beecher’s (2009) response criterion, if soft song is a signal of aggression, the receiver retaliation hypothesis predicts that subjects should respond more strongly to the playback of soft song compared to the playback of loud song.

Anderson et al. (2007) tested the receiver retaliation prediction, but surprisingly, they did not find evidence that song sparrows retaliated more to intruders producing soft song than loud song. Instead, their experiment indicated that soft song and loud song provoked similar levels of aggression in receivers. Several features of the Anderson et al. (2007) experiment may have worked against soft song evoking a more aggressive response than broadcast song, and the current study was designed to deal with these issues. First, an on-territory intrusion can produce a “ceiling” effect, where the subjects respond at high levels to this maximum threat; response measures that otherwise can distinguish aggressive vs. non-aggressive behavior at the territory boundary may prove too crude to reveal an effect when the test is within the territory. In other words, regardless of whether an intruder sings loud song or soft song, his presence in the center of the territory poses the same immediate threat to the territorial integrity, and therefore, the effect of

the song type or quality will likely be subtle. Second, unlike many recent studies, Anderson et al. did not use a taxidermic mount. The absence of a mount both eliminates attack as a measure of aggressive response and removes a target toward which the subject can direct his signaling effort (indeed, Anderson et al. did not examine signaling effort). For example, Akçay et al. (2011) found many differences, especially in signaling behaviors between the response of song sparrows to simulated intruders when the intrusion consisted of a mount plus playback vs. only playback. Third, in their design, Anderson et al. (2007) directly compared broadcast song only with soft crystallized song (birds responded equally aggressively to both), and soft crystallized song only with warbled soft song (birds responded equally aggressively to both). Transitivity would suggest that birds should respond equally aggressively to both broadcast song and warbled soft song, but this direct comparison was not actually made. Song sparrows typically intermix both types of soft songs together in a given singing bout (personal observation; Anderson et al. 2007), so a more direct test would be to compare broadcast song with a mixture of warbled and crystallized soft songs.

In the present study, we reexamined the question of whether receivers would respond to soft song as if it were a stronger threat signal than normal broadcast song. Using western song sparrows (*M. melodia morphna*) as our study species, we simulated an intrusion into the subject's territory using a taxidermic mount of a song sparrow and song playback. Once the subject approached, we switched either to soft song or continued playing loud song. We predicted that the subject would respond more strongly or be more likely to attack if the simulated intruder switched to soft song.

Methods

Study site and subjects

This research was conducted in Discovery Park, a large (534 acres), natural area park in Seattle, WA, USA (47°39' N, 122°24' W). Song sparrows are common throughout much of the park, and there are approximately 200 breeding pairs in our study area. Song sparrows have been studied intensively in the park since 1986, and most adults and many juveniles are banded each year. For this experiment, we selected adult males ($N=18$) located throughout the park. All subjects were banded with a unique combination of one numbered Fish and Wildlife Service aluminum band and three colored plastic bands. We recorded each subject's complete song repertoire and mapped his territory boundaries. The experiment was carried out during the breeding season, from 11 June to 17 July 2009.

Song stimuli

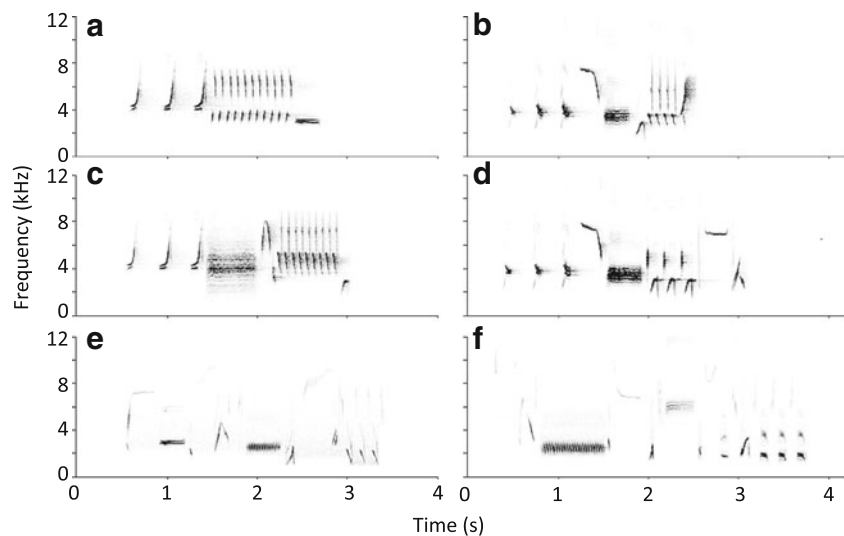
We constructed three different categories of playback stimuli for each subject: (1) lure song, (2) soft song stimuli, and (3) loud song stimuli. Each stimulus was selected from our highest-quality recordings (i.e., high signal-to-noise ratios), cleaned to remove any noise which was not part of the songs using the cursor filter tool in Syrinx (John Burt, www.syrinxpc.com), and saved as an uncompressed wave file.

We first constructed the lure stimulus for each subject. We used the subject's own song to equate the likely threat value of playback stimuli across birds. We selected a single song for each individual and created a 10-s recording (a 2- to 3-s song followed by 7–8 s of silence), which could be broadcast as a loop to stimulate each subject to approach the mount.

We then created treatment stimuli that were based on the subject's lure stimulus (Fig. 1). For the soft song treatment, we constructed stimuli of the same song type used to lure the bird but adjusted to 10 % of the amplitude of the lure song using the amplify function in Syrinx. This translates to a difference of approximately 20 dB, which is typical of loud vs. soft songs (Anderson et al. 2007). As noted above, soft song is generally sung as a mixture of soft crystallized song and soft warbled song. Therefore, to provide the most natural soft song treatment, we intermixed crystallized and warbled soft songs, using three soft crystallized songs followed by two warbled soft songs in each playback loop. Because warbled soft songs are highly stereotyped compared to repertoire songs and are difficult to record because of their low amplitude, we did not use self-song for the warbled soft song part of the playback stimuli. Instead, we used a total of six different exemplars taken from high-quality recordings of four different birds in the population.

The loud song stimuli were constructed similarly to the soft song stimuli (Fig. 1). Again, we used the lure playback song as the basis for constructing our loud song stimulus loops. To parallel any anti-habituation effects of switching between crystallized and warbled songs in the soft song treatment, we varied the loud song playback stimuli in a similar fashion by incorporating major variations of the same song. Variations on a song type, e.g., substituting one trill for another, varying the number of repeats of a repeated note, or modifying the ending of a song (Fig. 1), are a major aspect of song sparrow song, and one hypothesized function is to prevent habituation on the part of the receiver (Stoddard et al. 1988; Podos et al. 1992; Searcy et al. 1995). For the few birds for which we did not have high-quality recordings of a single song type with more than one major variation, we synthetically created a variation by inserting a trill from another of the same bird's song types. Similar to the soft song playback, a loud song stimulus recording thus contained three identical songs, followed by two songs with the variation.

Fig. 1 Two representative sets of playback stimuli used in this study. Crystallized songs (**a, b**), major variations (**c, d**), and warbled songs (**e, f**) are shown for two different male subjects. Loud song playback sequences used a mixture of crystallized songs and variations (e.g., **a + c**), while soft song playback used the same crystallized songs mixed with low-amplitude warbled songs (e.g., **a + e**), played at a -20 -dB amplitude relative to the loud song stimuli



Playback trial procedure

We first set up a playback speaker (Pignose R100) and taxidermic mount in the approximate center of a subject's territory. The mount was constructed to resemble an aggressive intruder, with feathers puffed out, wings slightly drooped, and the bill open as if he were singing. We attached the mount to the top of a 1.5-m pole so that it could be quickly positioned in an appropriate location in each focal bird's territory. We carefully chose the location where the mount was positioned so that it would be in a highly visible location that also provided numerous perches at standardized distances ranging from very close (<15 cm) to far away (10 m). The loudspeaker was positioned on the ground directly below the mount (facing up) and connected by cable to an iPod (Apple Inc.), which we controlled from a hidden position approximately 15 m away.

We began each trial by broadcasting the lure stimulus every 10 s at a normal loud volume (approximately 80 dB sound pressure level (SPL) at 1 m re. 20 μ Pa, Radio Shack 33–2055 sound level meter, C-weighting fast response) until the subject approached the speaker/mount. Once a subject was observed within 4 m of the mount, and we could be sure he had seen it, we continued the playback for one additional minute (six songs) before switching to either the loud (80 dB SPL) or soft (60 dB SPL) song playback stimuli. These decibel levels correspond with the natural singing behavior of song sparrows (Anderson et al. 2008). Each subject received the other type of trial on a subsequent day (the two trials were separated by at least 2 days), with the order of the treatments counterbalanced across the subjects and the first treatment randomly determined. We continued each trial for 10 min beginning with the switch from lure to treatment stimuli, and continued the playback for the duration of the trial. If the subject attacked the mount before the end of this time, the trial was terminated to prevent excessive damage to the mounts.

Data collection and statistical analyses

We recorded the location of the subject relative to the mount at all times using distance categories of <0.5 m, 0.5–1 m, 1–3 m, 3–5 m, 5–7 m, 7–9 m, and >10 m. We also noted each occurrence of all conspicuous behaviors, including the number of flights, loud songs, soft songs, wing waves, and attacks. Each of these response variables predicts a different level of aggression. As discussed above, loud (normal broadcast) song is not generally correlated with aggression (Searcy and Beecher 2009); instead, song sparrows typically switch from loud to soft song when close-range interactions escalate (Searcy et al. 2006). Wing waves are visual signals that are also associated with close-range male agonistic interactions in song sparrows (Nice 1943; Searcy et al. 2006; Templeton et al. 2012). The number of flights and time spent in the closest distance category to the mount are standard indicators of aggression in song sparrows and other birds (Searcy and Beecher 2009).

Audio recorders (Marantz PMD-660 with Sennheiser K6/ME67 microphone) were used to note the occurrence of all behaviors during the trial, and these data were later coded in the laboratory using JWatcher Software (DT Blumstein, JC Daniel, and CS Evans, www.jwatcher.ucla.edu). With JWatcher, we calculated the proportion of time each bird spent in each distance category and the number of occurrences of each behavior. Because some trials were cut short when the bird attacked the mount, all counts were converted into rates per minute. We statistically compared the subjects' behavioral responses to the loud and soft song treatments using non-parametric Wilcoxon signed-rank tests, and we used a McNemar test to examine the number of trials ending in an attack (a dichotomous variable). We examined whether any of the approach variables (average distance, time spent <0.5 m, and time spent <1 m) separated the attacking vs. non-attacking individuals with a forward-stepwise

discriminant function analysis (DFA). All statistics were conducted in JMP v8.0 (SAS Institute Inc.) using two-tailed tests. In addition to p values, we report effect sizes and 95 % confidence intervals following the recent calls for changes in statistical practices (Nakagawa and Cuthill 2007).

Results

All response measures were in the direction predicted by the hypothesis that soft song is a more aggressive signal than normal broadcast song (Table 1). Three of these measures—proportion of time the subject spent within 0.5 m of the mount, proportion of songs that were soft songs, and rate of wing waving—were statistically significant. Note that the difference in the singing behavior between treatments was due at least as much to a decrease in loud song rate (means \pm SE: loud=1.28 \pm 0.34 songs/min, soft=0.48 \pm 0.70; Cohen's $d \pm$ SE, 0.34 \pm 0.24) as to an increase in soft song rate (loud=1.89 \pm 0.43, soft=2.35 \pm 0.50; Cohen's d , 0.23 \pm 0.22) during the soft song treatment relative to the loud song treatment. Two additional measures—rate of flights and average distance from the mount—were in the predicted direction but showed a clear ceiling effect: subjects were always close and flying at a very high rate. Presumably because of this ceiling effect, no distance measures greater than 0.5 m from the mount varied between treatments, and in fact, the time spent <0.5 m was the only approach variable to enter into the DFA (Wilks' lambda=0.50, $F(1,16)=16.0$, $p=0.001$). The proportion of the trial spent <0.5 m classified 77.8 % of the subjects correctly in the DFA (80 % of non-attackers and 75 % of attackers), indicating that the time spent in close proximity of the mount predicted attack behavior. Attacks on the mount were not common, but the trend was again in the direction predicted, with attacks more likely in the soft song condition. The tendency to attack varied more

by individual than by experimental condition: ten birds attacked in neither trial, four birds attacked in both trials, and four birds attacked in the soft song trial, but not the loud song trial (no birds attacked in the loud trial that did not attack in the soft trial).

Discussion

Our data indicate that song sparrows indeed responded more aggressively to soft song compared to loud song, providing evidence for receiver retaliation as a mechanism for maintaining the reliability of this otherwise cheap signal. As discussed above, three criteria need to be met to fully establish that a given signal is aggressive (Searcy and Beecher 2009). For soft song, there is considerable evidence that this signal meets the context criterion (Nice 1943; Anderson et al. 2007; Akçay et al. 2011; Templeton et al. 2012). Searcy et al. (2006) further demonstrated that soft song also meets the predictive criterion. Although earlier studies have failed to find that soft song meets the response criterion, the data we report in this study clearly show that song sparrows respond differentially to loud and soft song playback. Thus, soft song meets all three criteria established by Searcy and Beecher (2009) and should be considered as an honest signal of aggressive intent in song sparrows.

Our results differ from those reported in a similar, earlier experiment by Anderson et al. (2007). One possible explanation for this difference is that the Anderson et al. study was on the eastern subspecies of song sparrows (*M. melodia melodia*): many population differences are known between the eastern and western subspecies (Arcese et al. 2002), including some which are related to songs and singing behavior (Peters et al. 2000). However, the structure and context in which soft song is produced are very similar in the eastern and western populations, so this explanation seems unlikely.

Table 1 Song sparrows responded more strongly to soft song than loud song playback

Variable	Treatment	Mean	SE	Cohen's $d \pm$ SE	W	p
Average distance from mount (m)	Loud	1.58	0.52	0.23 \pm 0.30	0.72	0.472
	Soft	1.16	0.32			
Proportion time within 0.5 m	Loud	0.35	0.09	0.48 \pm 0.19	41.0	0.032
	Soft	0.54	0.10			
Proportion time within 1.0 m	Loud	0.68	0.08	0.05 \pm 0.16	0.34	0.733
	Soft	0.70	0.09			
Flights (per min)	Loud	6.72	0.85	0.20 \pm 0.21	26.5	0.265
	Soft	7.45	0.89			
Proportion of soft songs	Loud	0.63	0.09	0.51 \pm 0.29	2.12	0.034
	Soft	0.79	0.08			
Wing waves (per min)	Loud	0.31	0.10	0.62 \pm 0.16	33.5	0.017
	Soft	1.37	0.56			
Attacks (% trials)	Loud	22 %			$\chi^2=2.25$	0.125
	Soft	44 %				

Means and standard errors (SE), along with effect size estimates (Cohen's $d \pm$ SE), are shown for all response variables. Test statistics and associated two-tailed p values for Wilcoxon signed-rank (W) and McNemar (χ^2) tests are also shown

A more likely explanation of the different results relates to the differences in the design and methodology of the two studies. First, our experiment used a taxidermic mount in addition to song playback. The mount increases the realism of the aggressive encounter, may allow a more accurate assessment of playback source levels by the subjects, and provides a target for a subject's aggression. Recent studies indicate that song sparrows respond differently in the presence of a mount compared with merely using song playback (Akçay et al. 2011). Second, we used a mixture of warbled and crystallized songs for playback, whereas Anderson et al. (2007) compared loud song only with soft crystallized song (and subsequently compared warbled and crystallized soft songs). Because we used a mix of warbled and crystallized soft songs, we cannot say for certain what the relative importance or signal strength of the two types of soft songs are compared with loud song. However, if this is the critical methodological difference between these two studies, it suggests that the presence of warbled soft song (either by itself or intermixed with soft crystallized song) might be the key to signaling aggression. A final difference between the current study and the Anderson et al. (2007) study was in how aggressive response was measured. Anderson et al. took distance from the playback speaker as their sole response variable and did not consider the signaling behavior of the subjects. Some of the strongest effects we observed between the loud and soft song treatments were on how subjects modulated their own aggressive signals (soft songs and wing waves). Furthermore, as their measure of subject approach, Anderson et al. calculated the average distance of each subject to the playback speaker and the proportion of time within 2 m of the speaker. Like Anderson et al., our data indicate no difference between the loud and soft song treatments for either of these variables, with the only difference observed among subjects being limited to distances that were very close to the mount (<0.5m). Thus, although our data indicate that the approach distance differed between the two treatments, this difference is a subtle one. Because aggression studies can suffer from a ceiling effect—a territory intruder is such a strong stimulus that birds frequently display near maximal responses, regardless of other manipulations such as the specific types of songs the intruder sings—the specific distance used as response measures may determine the power to differentiate subject responses.

Our results and interpretation are confirmed by a study just published by Anderson et al. (2012). They redesigned their earlier study and found that playback of soft song did elicit heightened aggression in test subjects relative to loud song playback. A key methodological change in their new study was the direct comparison of warbled soft song with loud song playbacks. Such a comparison was lacking in the 2007 study (which compared loud song with soft crystallized song, and then soft crystallized song with soft warbled

song). These results, taken with those of the experiment we have reported here, suggest that the presence of warbled soft song is the critical signal of aggressive intent in this species.

The percentage of trials ending in an attack during our study were considerably higher than those found during the previous studies using mounts with song playback in song sparrows. Searcy et al. (2006) reported attack rates of about 20 % of trials, and Templeton et al. (2012) reported attacks in 30 % of trials with an adult mount. In the soft song trials in the current study, 44 % of the birds attacked the mount. Although not statistically different from the 22 % of attacks during our loud song trials, this pattern suggests that individuals are more likely to attack intruders that sing soft song, indicating that intruders will be punished for producing this signal. This type of receiver retaliation can be an effective mechanism for maintaining signal reliability and may establish how soft song is maintained as a reliable signal of aggression.

From a comparative perspective, the role of song amplitude in mediating aggressive interactions is intriguing. While song sparrows, and a number of other species (reviewed in Searcy and Beecher 2009), employ soft song as a reliable threat signal, it appears that increased song amplitude has a similar function in other species. Specifically, playback of a higher-amplitude song evokes heightened aggression in some species, suggesting a similar retaliation cost to these loud signals (Lampe et al. 2010; Brumm and Ritschard 2011; Ritschard et al. 2012). Why some species employ a higher-amplitude song while others use a low-amplitude soft song as aggressive signals remains an evolutionary puzzle.

Acknowledgments This research was funded by the National Science Foundation. Sievert Rohwer, Kevin Epperly, Rob Faucett, Dan Froehlich, Annie Kidder, Eugene Makela, and the UW Burke Museum of Natural History and Culture helped with the mounts. This manuscript benefited from the comments from Henrik Brumm and an anonymous reviewer. We thank Discovery Park and its staff for hosting our research.

Ethical standards All work conforms to the ABS/ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching and was approved by the University of Washington Institutional Animal Care and Use Committee (Animal Research Protocol 2207-03, approved on 23 April 2009).

Conflict of interest The authors declare that they have no conflict of interest.

References

- Akçay Ç, Tom M, Holmes D, Campbell SE, Beecher MD (2011) Sing softly and carry a big stick: Soft song as an aggressive signal in song sparrows. *Anim Behav* 82:377–382

- Anderson RC, Nowicki S, Searcy WA (2007) Soft song in song sparrows: Response of males and females to an enigmatic signal. *Behav Ecol Sociobiol* 61:1267–1274
- Anderson RC, Searcy WA, Hughes M, Nowicki S (2012) The receiver-dependent cost of soft song: A signal of aggressive intent in songbirds. *Anim Behav* 83:1443–1448
- Anderson RC, Searcy WA, Peters S, Nowicki S (2008) Soft song in song sparrows: Acoustic structure and implications for signal function. *Ethology* 114:662–676
- Arcese P, Sogge MK, Marr AB, Patten MA (2002) Song sparrow (*Melospiza melodia*). The Birds of North America Online database: <http://bna.birds.cornell.edu/bna/species/704>. Accessed 14 Oct 2011
- Ballentine B, Searcy WA, Nowicki S (2008) Reliable aggressive signalling in swamp sparrows. *Anim Behav* 75:693–703
- Beecher MD (2008) Function and mechanisms of song learning in song sparrows. *Adv Stud Behav* 38:167–225
- Brumm H (2009) Song amplitude and body size in birds. *Behav Ecol Sociobiol* 63:1157–1165
- Brumm H, Ritschard M (2011) Song amplitude affects territorial aggression of male receivers in chaffinches. *Behav Ecol* 22:310–316
- Brumm H, Todt D (2004) Male–male vocal interactions and the adjustment of song amplitude in a territorial bird. *Anim Behav* 67:281–286
- Catchpole CK, Slater PJB (2008) Bird song: biological themes and variations, 2nd edn. Cambridge University Press, Cambridge
- Clutton-Brock TH, Albon SD (1979) Roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–170
- Dabelsteen T, McGregor PK, Lampe HM, Langmore NE, Holland J (1998) Quiet song in song birds: An overlooked phenomenon. *Bioacoustics* 9:89–105
- Dabelsteen T, Pedersen SB (1990) Song and information about aggressive responses of blackbirds, *Turdus merula*: Evidence from interactive playback experiments with territory owners. *Anim Behav* 40:1158–1168
- Davies NB, Halliday TR (1978) Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274:683–685
- Gil D, Gahr M (2002) The honesty of bird song: Multiple constraints for multiple traits. *Trends Ecol Evol* 17:133–141
- Grafen A (1990) Biological signals as handicaps. *J Theor Biol* 144:517–546
- Hof D, Hazlett N (2010) Low-amplitude song predicts attack in a North American wood warbler. *Anim Behav* 80:821–828
- Krebs J, Ashcroft R, Webber M (1978) Song repertoires and territory defence in great tit. *Nature* 271:539–542
- Lack D (1965) The life of the robin. Witherby, London
- Lampe HM, Balsby TJS, Espmark YO, Dabelsteen T (2010) Does twitter song amplitude signal male arousal in redwings (*Turdus iliacus*)? *Behaviour* 147:353–365
- Maynard Smith J (1974) Theory of games and evolution of animal conflicts. *J Theor Biol* 47:209–221
- Maynard Smith J (1979) Game theory and the evolution of behavior. *Proc Roy Soc Lond B* 205:475–488
- Maynard Smith J, Harper D (2003) Animal signals. Oxford University Press, Oxford
- McDonald MV (1989) Function of song in Scott's seaside sparrow, *Ammodramus maritimus peninsulae*. *Anim Behav* 38:468–485
- Molles LE, Vehrencamp SL (2001) Songbird cheaters pay a retaliation cost: Evidence for auditory conventional signals. *Proc Roy Soc Lond B* 268:2013–2019
- Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biol Rev* 82:591–605
- Nice MM (1943) Studies in the life history of the song sparrow. II The behavior of the song sparrow and other passerine birds *Trans Linn Soc NY* 6:1–329
- Nowicki S, Searcy WA, Hughes M (1998) The territory defense function of song in song sparrows: A test with the speaker occupation design. *Behaviour* 135:615–628
- Peters S, Searcy WA, Beecher MD, Nowicki S (2000) Geographic variation in the organization of song sparrow repertoires. *Auk* 117:936–942
- Podos J, Peters S, Rudnicki T, Marler P, Nowicki S (1992) The organization of song repertoires in song sparrows: Themes and variations. *Ethology* 90:89–106
- Reichard DG, Rice RJ, Vanderbilt CC, Ketterson ED (2011) Deciphering information encoded in birdsong: Male songbirds with fertile mates respond most strongly to complex, low-amplitude songs used in courtship. *Am Nat* 178:478–487
- Rek P, Osiejuk TS (2011) Nonpasserine bird produces soft calls and pays retaliation cost. *Behav Ecol* 22:657–662
- Ritschard M, van Oers K, Naguib M, Brumm H (2012) Song amplitude of rival males modulates the territorial behaviour of great tits during the fertile period of their mates. *Ethology* 118:197–202
- Rohwer S, Rohwer FC (1978) Status signaling in harris sparrows: Experimental deceptions achieved. *Anim Behav* 26:1012–1016
- Searcy WA, Anderson RC, Nowicki S (2006) Bird song as a signal of aggressive intent. *Behav Ecol Sociobiol* 60:234–241
- Searcy WA, Beecher MD (2009) Song as an aggressive signal in songbirds. *Anim Behav* 78:1281–1292
- Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton
- Searcy WA, Podos J, Nowicki S, Peters S (1995) Discrimination of song types and variants in song sparrows. *Anim Behav* 49:1219–1226
- Stoddard PK, Beecher MD, Willis MS (1988) Response of territorial male song sparrows to song types and variations. *Behav Ecol Sociobiol* 22:125–130
- Templeton CN, Campbell SE, Beecher MD (2012) Territorial song sparrows tolerate juveniles during the early song-learning phase. *Behav Ecol* 23:916–923
- Tibbetts EA, Dale J (2004) A socially enforced signal of quality in a paper wasp. *Nature* 432:218–222
- Titus RC (1998) Short-range and long-range songs: Use of two acoustically distinct song classes by dark-eyed juncos. *Auk* 115:386–393
- Zahavi A (1975) Mate selection—a selection for a handicap. *J Theor Biol* 53:205–214
- Zahavi A (1977) The cost of honesty (further remarks on handicap principle). *J Theor Biol* 67:603–605