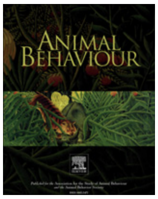
Animal Behaviour 82 (2011) 377–382

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Sing softly and carry a big stick: signals of aggressive intent in the song sparrow

Çağlar Akçay [a,*], Mari E. Tom [a], Dylan Holmes [b], S. Elizabeth Campbell [a], Michael D. Beecher [a,c]

[a] *Department of Psychology, University of Washington, Seattle, WA, U.S.A*
[b] *Department of Biology, Oberlin College, Oberlin, OH, U.S.A*
[c] *Department of Biology, University of Washington, Seattle, WA, U.S.A*

ARTICLE INFO

Article history:
Received 2 November 2010
Initial acceptance 25 January 2011
Final acceptance 3 May 2011
Available online 15 June 2011
MS. number: A10-00759R

Keywords:
eavesdropping
honest signalling
Melospiza melodia soft song
song sparrow
type matching

Reliability of signalling has been the focus of much research in behavioural ecology, yet few studies have been able to show that putative aggressive signals actually predict subsequent escalation (e.g. attack). This is partly because until recently researchers have usually used stimuli (e.g. song playback) that did not permit subsequent escalation in the form of attack. We presented male song sparrows, *Melospiza melodia*, with a traditional simulated intrusion that involved only playback of their own song (no-mount condition), or a simulated intrusion that coupled playback of their own song with a taxidermic mount. We hypothesized that aggressive signals that are predictive of attack should increase in frequency when there is a visible intruder present (i.e. in the mount trials). Our results showed that only low-amplitude song (soft song) and wing waves (the latter effect only approached significance) increased in frequency when there was a mount present, consistent with previous research. We discuss these results in the context of how reliability of such a low-cost signal can be maintained, and propose new hypotheses for future research.

Ever since animal behaviourists started taking the individual-level perspective to evolution in the 1970s (Otte 1974; Dawkins & Krebs 1978), the honesty of animal signals has been a central issue in behavioural ecology (Maynard Smith & Harper 2003; Searcy & Nowicki 2005). If sender and receiver have nonidentical interests, as is often the case, honest signalling is favoured only to the extent that it benefits both parties (i.e. it can help them resolve a conflict quickly and without costly actions such as fighting; Logue et al. 2010). At the same time, dishonest signalling is favoured if the signaller can get away with it (i.e. if a bluff causes a rival who would otherwise win a fight to back down). How signal honesty can be maintained has been one of the major questions in the modern study of animal behaviour (Maynard Smith & Harper 2003; Searcy & Nowicki 2005).

Theory suggests that the key to maintaining the honesty of a signal (i.e. for it to reveal the true level of the trait or state it is supposed to signal) is for the signal to be costly, and for that cost to be greater for lower-quality individuals (Zahavi 1975, 1977; Grafen 1990). While the literature is replete with examples of signals that conform to this expectation, recent research on vocal signalling in songbirds has produced an unexpected result, namely that a low-intensity signal, soft song, is the most reliable predictor of attack in several species (Searcy et al. 2006; Ballentine et al. 2008; Hof & Hazlett 2010). On the face of it, soft song would seem to be a low-cost signal, certainly a lower-cost signal that normal (loud) song.

In the first study showing that soft song is the most reliable predictor of attack, Searcy et al. (2006) used an experimental paradigm developed earlier by Waas (1991). The researchers staged a simulated intrusion on the subject's territory using the subject's (male song sparrows, *Melospiza melodia*) song broadcast from a speaker. Crucially, 5 min into the trial, a taxidermic mount of a song sparrow next to the playback speaker was revealed, and subjects were thus given an opportunity to further escalate to attack against the simulated intruder. The researchers then compared signals given by the birds that attacked during the 20 min trial with those of the birds that did not attack. Only number of soft songs (i.e. low-amplitude songs typically given from a close distance to the mount) reliably predicted subsequent attack. Since then, Ballentine et al. (2008) have replicated these findings in a closely related species, the swamp sparrow, *Melospiza georgiana*, where in addition to soft song, wing waves were also a reliable predictor. More recently, Hof & Hazlett (2010) also found that soft song was a reliable predictor of attack in the black-throated blue warbler, *Dendroica caerulescens*.

It is remarkable that of the vocal behaviours measured in these recent studies, none but soft song was a reliable predictor of subsequent attack. This is a surprising result as many of these

---

* Correspondence: Ç. Akçay, Department of Psychology, University of Washington, Box 351525, Seattle, WA 98195, U.S.A.
E-mail address: caglar@u.washington.edu (Ç. Akçay).

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.05.016

behaviours, such as song type matching (Burt et al. 2001), or type switching (e.g. Searcy et al. 2000) have been proposed to be aggressive signals, and as mentioned, low-amplitude soft song would seem to be the least costly signal of all, owing to its amplitude. Indeed, these results led Searcy & Beecher (2009) to suggest that there is little evidence that many vocal signal features actually transmit aggressive intent.

Reviewing Searcy et al. (2006), Laidre & Vehrencamp (2008) questioned the validity of the conclusion that most of the behaviours examined were not aggressive signals because they failed to predict attack. They point out that the mount is not realistic in that it does not interact with the subject as a real intruder would. Thus, normal contingencies of behaviour do not materialize because of the noninteractive nature of the mount, which may mask the predictive value of the signals. Although this criticism is reasonable, the addition of the mount to the traditional playback experiment does make the simulation more realistic. In the conventional playback experiment, in wide use for some 50 years now (Weeden & Falls 1959), the subject is confronted with a paradoxical intruder: one that is loud but invisible. The mount makes the intruder visible. Reflection on the relative merits of the two paradigms led us to conduct the experiment described in this paper.

In this experiment, we manipulated whether or not an intruder was visually present by presenting subjects with two simulated intrusions on different days. One of the intrusions included a stationary taxidermic mount attached to the speaker, whereas the other intrusion merely consisted of song playback; all features of the two intrusions were identical except for the presence of the mount in one. The order of these two intrusions was counterbalanced across subjects. We reasoned that if a subject's signal functions to convey that he will escalate and, if necessary, eventually attack, then the subject should be more likely to give this signal when he sees as well as hears the intruder as opposed to when he only hears him (as in a conventional playback study). We used a within-subject design in our study, which affords more power as it controls for individual differences in signalling strategies and aggressiveness. We measured several putative aggressive signals: number of loud (normal) songs, number of soft songs, number of wing waves, number of song types sung, number of song type switches and number of matching song types. We also measured two other response variables that are not signals themselves but reflect intensity of response: number of flights and time spent within 1 m.

METHODS

Study Site and Subjects

The study was conducted in Discovery Park, Seattle, Washington, USA between June 17 and 22, 2010.This population of song sparrows has been studied since 1986 (Beecher et al. 1994), and consists of about 150 territories where the males are color-banded and the repertoires of most of them are recorded. We selected 18 male territory holders as subjects.

Stimuli and Apparatus

We recorded the song repertoires of males with Marantz PMD660 solid state recorders and Sennheiser ME66/K6 shotgun microphones and examined these repertoires in Syrinx (John Burt, www.syrinxpc.com, Seattle, WA). We selected two song types from each subject's repertoire as stimulus songs based on the quality of the recording. For each song type we created an audio file (.wav) that included the song and a period of silence (~12 s) such that the duration of the audio file was 15 s. These audio files were used during the playback in loop mode (using iTunes, Apple Inc.) so that the song rate of the playback was four songs/min.

The playbacks were carried out from a laptop (Dell Inspiron Mini 10, Dell Inc.), connected to a speaker (Pignose Model No. 7-100R) via a 20 m cable. On half of the trials, a taxidermic mount of a song sparrow, in singing posture, was attached to the speaker. The trials were recorded with two sets of the same type of recorders and microphones, as described above. One of the microphones was attached to a pole placed next to the speaker and was connected to a recorder that was held by an observer via a 20 m audio cable. The other microphone and recorder were held by a different observer, who recorded the trial along with a running commentary of each behaviour of the subject.

Procedure

For each trial, we placed the speaker, mounted on a tripod, roughly in the middle of the subject's territory. In the mount trials, the taxidermic mount was attached to the speaker. We placed the speaker such that there were a number of perches close by, giving the subject the opportunity to approach to a close distance during the trials. We also placed a Sennheiser ME66/K6 microphone (attached to a pole) next to the tripod with the aim of recording any soft songs subjects produced from close range. The playbacks consisted of loop playback of song from the subject's own repertoire, so that he could type-match it. In each trial we used two song types from the subject's repertoire. We presented one song type for 5 min and the second song type for another 5 min or until the subject attacked the mount in the mount trials. As we wanted to make sure that the subjects saw the mount during the mount trial, we counted only trials where the subject approached within 5 m of the mount. Five subjects failed to satisfy this criterion (these cases appeared to be birds that were heavily involved in parental activity) and those trials were discarded, leaving us with a sample size of 13. These 13 subjects all approached within 5 m of the speaker in both conditions. In the mount trials, if there was no attack during the playback period, we recorded the behaviour of the subject for another 5 min after the playback ended.

There were three observers in each trial. The observers placed themselves at different angles with respect to the speaker and, thus, at least one observer had the subject in view, should the subject be obscured by foliage from view of the other observers.

Subjects were tested with and without the mount using the same playback songs at least 3 days apart. The order of the first trial was determined randomly by a coin toss, and the order of the subsequent trials was alternated.

Response Measures

During the trial we recorded every flight the subject made along with the distance from the speaker, as well as every vocalization. Consistent with all previous studies on soft song, we classified every song as 'loud' or 'soft'. In-the-field classification of song as loud or soft by experienced field workers is reliable with respect to a single cutoff point on the amplitude continuum (Anderson et al. 2008). From the trial recordings we extracted the following as our response measures: number of loud songs, number of soft songs (classified as such in the field), number of wing waves, number of song types sung, number of song type switches, number of matching song types (given two playback types, the birds could match both types), number of flights and proportion of time spent within 1 m. The latter two measures were measures of aggression, commonly used in previous work with song sparrows: close approach is the best predictor of subsequent attack (Searcy et al. 2006) and number of flights has been used as a measure of aggressive response in all our previous playback studies as well as in many other studies of song sparrow aggression (Kroodsma 1976; Searcy et al. 1982; Wingfield & Hahn 1994; Wilson & Vehrencamp 2001). Although we continued to monitor the birds for 5 min after the end of mount trials (in case they attacked), we only used the responses during the playback period of these trials.

We converted the counts of each behaviour (loud song, soft song, wing waves and flights) to rates, as attacks occurred at different times during the trial (trial duration measured from first flight or vocal response to the end of the trial or attack). As a measure of type matching, we divided the number of matches during the trial by the total number of song types the subject sang (e.g. if the bird sang four song types during the full trial but matched only one of the two stimulus song types, the matching measure would be 0.25). This measure thus controls for the number of song types that the subjects produced. As a measure of song switching, we divided the total number of song types sung by the total (loud + soft) number of songs sung minus 1 to control for opportunity to switch (Searcy et al. 2006).

Data Analysis

We conducted Wilcoxon signed-ranks tests on the response measures listed above for the comparison between mount and no-mount trials. All tests were two tailed and were conducted in SPSS 14.0 (SPSS Inc., Chicago, IL, U.S.A.). The sample size for all tests was 13. We calculated repeatability of singing behaviour as suggested by Lessells & Boag (1987) from a one-way ANOVA (calculated in MS Excel).

RESULTS

Attackers versus Nonattackers

Three of the 13 subjects (23%) attacked during the mount trials. Two of these subjects attacked during the playback period, whereas one attacked in the 5 min postplayback period. Although rates of soft songs and of wing waves in attackers were twice those of nonattackers, the small number of attackers meant that we did not have sufficient statistical power to analyse the predictors of attack; we therefore simply report the means and standard deviations of our various measures in Table 1.

Mount versus No-mount

As predicted, subjects sang soft songs at a significantly higher rate in the mount trials than in the no-mount trials (mean ± SD, 2.05 ± 2.12 versus 0.37 ± 0.87; $Z = 3.06$, $P = 0.002$; Cohen's $d \pm \text{SE} = 0.89 \pm 0.24$; Fig. 1a). Subjects also sang loud songs at a significantly lower rate in the mount condition than the no-mount condition (2.21 ± 0.47 versus 3.86 ± 0.44; $Z = -3.18$, $P = 0.001$; Cohen's $d \pm \text{SE} = -1.05 \pm 0.26$; Fig. 1b). Subjects also gave wing waves at a higher rate in the mount condition, but the effect did not reach significance at $\alpha = 0.05$ (3.90 ± 4.25 versus 1.71 ± 2.17; $Z = 1.49$, $P = 0.14$; Cohen's $d \pm \text{SE} = 0.65 \pm 0.38$; Fig. 1c). Subjects did not differ in their song-switching rate between conditions (0.12 ± 0.08 versus 0.10 ± 0.03; $Z = -0.31$, $P = 0.75$; Cohen's $d \pm \text{SE} = 0.33 \pm 0.30$). The proportion of the song types that were type matches was similar in the mount trials and the no-mount trials (0.39 ± 0.32 versus 0.30 ± 0.23; $Z = 0.552$, $P = 0.58$; Cohen's $d \pm \text{SE} = 0.31 \pm 0.36$; Fig. 1d).

The two measures of aggressive response were higher in mount than in no-mount trials. Although this difference was not significant for the rate of flights (mount 6.28 ± 2.92 versus no mount: 5.77 ± 3.04; $Z = 0.80$, $P = 0.42$; Cohen's $d \pm \text{SE} = 0.16 \pm 0.19$), it was for the proportion of time spent within 1 m of the speaker during playback (mount 0.66 ± 0.29 versus no-mount: 0.33 ± 0.32; $Z = 3.108$, $P = 0.001$; Cohen's $d \pm \text{SE} = 1.08 \pm 0.30$).

The total number of songs subjects sang (loud + soft songs) was highly repeatable across the two conditions (intraclass coefficient: $r = 0.65$, $F_{12,25} = 4.73$, $P < 0.005$; mean total songs ± SE: no mount: 4.24 ± 0.41; mount: 4.17 ± 0.77; Fig. 2).

DISCUSSION

Song sparrows reacted to the presence of the taxidermic mount during playback by increasing their rate of soft songs and decreasing their rate of loud songs. That is, they stopped singing loud song and sang soft song instead. Although we could not analyse predictors of attack given that only three subjects attacked the mount, our results are consistent with Searcy et al.'s (2006) finding that soft song is the one strong predictor of attack on the mount in song sparrows (their observed rate of attack was essentially identical to ours, but their much larger sample size allowed them to conduct formal statistical analyses on predictors of attack). We also found a more than two-fold increase in wing waves in the mount condition compared to the no-mount condition, although the effect did not reach significance. This finding too is similar to Searcy et al.'s (2006) finding of a moderate association of wing waves with attacks, although their statistical test did not quite reach significance either. As more studies measuring various displays of aggression accumulate, we should be able to identify these smaller effects and estimate their magnitude through meta-analytic approaches (Nakagawa & Cuthill 2007). The overall increase in the other putative aggressive signals, namely type-switching rate and type matching, was small (effect sizes ~0.30), and individually variable (see Fig. 1d for type matching).

It is notable that many of the signals previously suggested to be important in aggressive interactions did not differ between the two conditions. In particular, it is surprising that type matching did not increase in the mount condition, given that it has been shown to be associated with subsequent approach by male song sparrows in at least one previous study (Vehrencamp 2001). Furthermore, in an interactive playback experiment, male song sparrows approached the speaker more readily when they were type-matched than when they were not type-matched (Burt et al. 2001). In Burt et al.'s experiment, playbacks were conducted from the boundary of a neighbour, and the playbacks were the shared songs of that neighbour, whereas in the present study and in Searcy et al.'s study, playbacks were conducted at the centre of the territory and were the bird's own song. It is possible that type matching, as a conventional signal, is predictive of approach (which signals willingness to escalate) only at shared boundaries between male neighbours, and not at the territory centre, where most birds will

Table 1

Behaviours (mean ± SD) given by male song sparrow attackers ($N = 3$) and nonattackers ($N = 10$) during the playback period

	Loud songs	Soft songs	Wing waves	Flights	Matches/no. of types sung	Proportion within 1 m
Attackers	1.15±0.91	3.25±4.14	6.18±6.60	6.50±1.44	0.52±0.41	0.90±0.05
Nonattackers	2.41±1.81	1.68±1.24	3.21±3.49	6.21±3.29	0.35±0.30	0.59±0.30

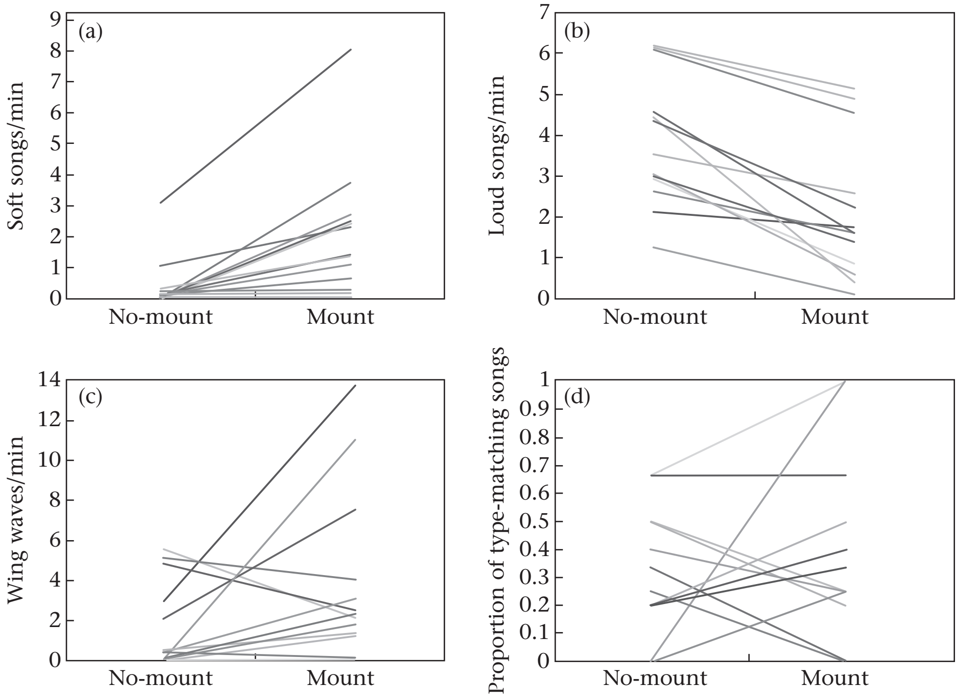


Figure 1. Signalling behaviour of individual male song sparrows during the trials: rates of (a) soft songs, (b) loud songs and (c) wing waves, and (d) proportion of song types that were type matches during the playback period. Each line represents a subject.

readily approach any intruder. If this is true, birds that type-match a playback from the boundary should be more likely to escalate further when the intruder moves into the territory (see Laidre 2009; for a similar design). We are currently testing this hypothesis.

Not very surprisingly we found that wing waves, a visual signal, also increased in the presence of a visual target. Visual signals are expected to transmit a relatively short distance in the visually dense habitat of song sparrows, and therefore should only be effective when the sender can be seen by the receiver. That is not to say that subjects failed to locate the source of the playback in the no-mount condition. It is well established that songbirds can locate the source of a playback relatively accurately, and recently it has been shown that birds of some species even direct singing towards a speaker during a staged intrusion (Brumm et al. 2011). Nevertheless, most subjects selectively increased their visual signalling effort only in the presence of an actual visual target.

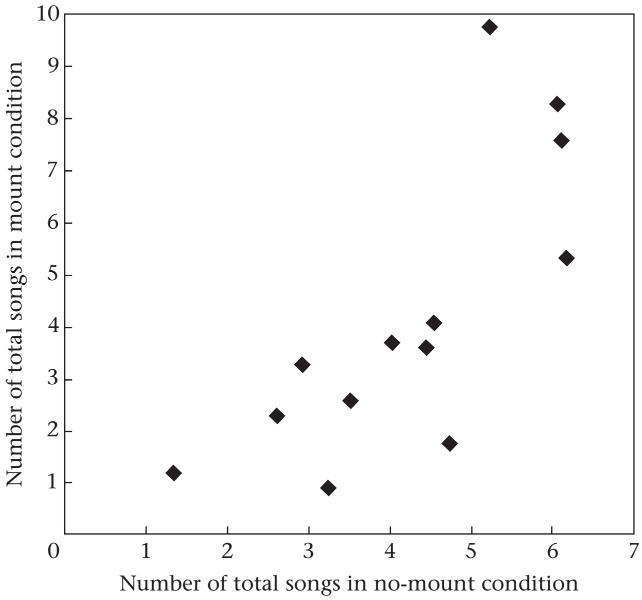


Figure 2. Number of total songs (loud + soft) sung by male song sparrows ($N = 13$) in the mount and no-mount conditions.

Perhaps the most interesting result of the current experiment and of other recent studies on signalling in songbirds as well (Searcy et al. 2006; Ballentine et al. 2008; Hof & Hazlett 2010) is that a low-cost signal such as soft song would be a reliable signal of aggression. It seems counter-intuitive to us humans that the animal should decrease signal amplitude as aggressive intensity increases, and there is a mystery from the theoretical perspective as well: soft song seems less costly, not more, than the obvious alternative, loud song. If anything, production costs should be lower for low-amplitude song. So how can a signal that is apparently not costly to produce be a reliable aggressive signal? Several hypotheses have been proposed to explain how soft song can be reliable in aggressive situations. Below we review these hypotheses, and then propose a new hypothesis. We should note that while we will focus on soft song in aggressive contexts, low-amplitude signals have been observed in the context of courtship as well (Dabelsteen et al. 1998). Some, although not all, of the ideas presented below may apply as well to soft courtship songs.

To explain the reliability of soft song, Laidre & Vehrencamp (2008) proposed a vulnerability handicap hypothesis. Their argument is that soft song requires close proximity to function as a signal, since receivers can only hear it when they are close to the signaller. This means that the signaller has to put himself at a higher risk to sing soft song and to make sure the opponent hears him, making soft song costly for bluffers. This explanation as proposed, however, has the serious flaw that loud song would signal proximity of the signaller to the receiver just as unambiguously as would soft song; indeed, Searcy et al. (2008) suggested that loud song might be a more reliable signal. That soft song can be perceived only from close range but not from long range, as proponents of this hypothesis have emphasized, is irrelevant because loud song can be perceived as coming from close range just as well as soft song can. Therefore, there seems to be no logical basis for hypothesizing a special role for low amplitude in creating a handicap mechanism. Furthermore, soft song is very commonly given even when birds are close and in full visual contact, presumably signalling very reliably the risk they are willing to take.

A second hypothesis suggests that singing song softly seriously curtails the active space of the signal and thus reduces the ability of a singer to keep intruders away (Searcy et al. 2008). Under this 'competing cost' hypothesis, intrusion pressures should be positively correlated with the relative amount of soft song (compared to loud song) that is used to counter an intruder. While there is some evidence for this hypothesis (Searcy & Nowicki 2006), we have never observed an intrusion by another bird, let alone a challenge to the territory owner (Ç. Akçay, C. N. Templeton, S. E. Campbell & M. D. Beecher, personal observations) during any of our mount experiments despite the fact that territory owners differed greatly in their soft song output. We believe this is because soft song and loud song often are given together in a bout of singing (Nice 1943; Anderson et al. 2008), as for instance, when two birds split up for a few seconds to sing loudly from high perches.

A third hypothesis is that the reliability of soft song can be ensured via a receiver-retaliation rule where motivated or high-quality receivers are more likely to escalate against opponents that use soft song (Laidre & Vehrencamp 2008). Therefore, only highly motivated or high-quality individuals can pay the potential cost of further escalation as a result of singing soft song. While we believe this last hypothesis is the most promising, the evidence for a receiver-retaliation rule has been hard to come by so far. For instance, in a playback experiment, Anderson et al. (2007) were not able to detect a differential response by male song sparrows to playbacks of loud versus soft song. Furthermore, there is evidence in at least some species that higher-amplitude song elicits a stronger response from territory owners, and hence, presumably greater retaliation (Brumm & Ritschard 2011).

Another set of hypotheses has proposed that soft song reduces eavesdropping by third parties, thereby explaining the low-amplitude aspect of the signal if not its reliability (Dabelsteen et al. 1998). Individuals might be under pressure to keep disputes private either from eavesdropping predators or conspecifics. Eavesdropping indeed can be an important factor in animal societies (McGregor 1993, 2005; Peake 2005; Akçay et al. 2010). So far, we are aware of only one study that has tested the hypothesis that soft song serves to minimize eavesdropping by predators, and that study failed to find an effect in the predicted direction (Searcy & Nowicki 2006), although further tests are warranted. There is also very little evidence that eavesdropping from conspecifics can actually drive evolution of private aggressive signals that are also reliable; if anything, the evidence suggests that territory owners should be selected to sing more loudly, not less (Searcy & Nowicki 2006). Finally, in models of eavesdropping in animal contests, aggressive individuals are predicted to enhance their reputation as such, to further discourage eavesdroppers from challenging them (Zahavi 1979; Johnstone 2001; Johnstone & Bshary 2004). Thus, we believe, minimizing eavesdropping from conspecifics is unlikely to explain a reliable signal of aggressive intent.

In summary, there is little consistent support at present for any of the hypotheses proposed so far to explain why soft song is soft and reliable. Here we propose a new hypothesis that we term the 'readiness hypothesis' that specifically addresses why song at close range is given at low amplitude. We propose that the low amplitude of soft song may be explained by the fact that it is given at close range by birds that are on the brink of a physical fight. This means that the bird needs to keep track of his opponent, be ready to attack him or evade an attack from him. Now, singing loudly in songbirds is a head-back, whole-body affair and the posture required for singing loudly decreases the ability of the singer to visually keep track of the opponent, puts him at a higher risk of injury, and makes it harder for him to evade an incoming attacker. Thus, a bird may be better off singing with beak closed, maintaining an eyes-ahead, ready posture. Beak opening is correlated with song amplitude (Hoese et al. 2000; Williams 2001; Goller et al. 2004), so singing with a closed beak means singing at low amplitude. In other words, the low-amplitude of soft song may be a by-product of bodily posture needed to minimize vulnerability during an aggressive interaction with an intruder, to minimize the risk of losing track of the intruder or being subjected to an attack while singing loudly. The fact that song need not be loud when the two birds are within centimetres of one another of course means the birds are not paying a transmission cost by singing softly. Consistent with this hypothesis, subjects actually did not increase their total output of song, but simply started singing softly in the visual presence of an intruder.

Note that the readiness hypothesis is explicitly about explaining the low-amplitude feature of soft song, and not necessarily its signal value. In other words, the readiness hypothesis makes no claim that soft song is a reliable signal. Indeed, if it is true that the low amplitude of soft song is a by-product of the postures taken by birds during a close encounter, soft song is no different than loud song in its signal value. In other words, under this view the act of singing at close range is a signal (sensu Otte 1974), but the low amplitude of soft song has not evolved for its signal value.

The readiness hypothesis might also explain why bobolinks in Capp & Searcy's (1991) experiment sang shorter songs before attacking a decoy. Here too, the subjects that subsequently attacked seemed to have decreased the cost of their signals by singing shorter songs. It is conceivable that longer songs interfere with posturing and/or make the singer vulnerable to an attack for a longer period of time. We believe that decreasing signal intensity when animals are getting ready to escalate to a physical fight might be a common phenomenon in animal communication.

Acknowledgments

This research was supported by a National Science Foundation (NSF) grant IOS-0733991 to M.D.B., an NSF REU Supplement to M.D.B. and an NSF Doctoral Dissertation Improvement Grant to Ç.A. The research reported here was described in Animal Research Protocol 2207-03 approved on 23 April 2009 by the University of Washington IACUC. We thank William A. Searcy for comments on the manuscript. We also thank Discovery Park, Seattle for hosting our field research.

References

Akçay, Ç., Reed, V. A., Campbell, S. E., Templeton, C. N. & Beecher, M. D. 2010. Indirect reciprocity: song sparrows distrust aggressive neighbours based on eavesdropping. *Animal Behaviour*, **80**, 1041–1047, doi:10.1016/j.anbehav.2010.09.009.

Anderson, R. C., Nowicki, S. & Searcy, W. A. 2007. Soft song in song sparrows: response of males and females to an enigmatic signal. *Behavioral Ecology and Sociobiology*, **61**, 1267–1274.

Anderson, R. C., Searcy, W. A., Peters, S. & Nowicki, S. 2008. Soft song in song sparrows: acoustic structure and implications for signal function. *Ethology*, **114**, 662–676.

Ballentine, B., Searcy, W. A. & Nowicki, S. 2008. Reliable aggressive signalling in swamp sparrows. *Animal Behaviour*, **75**, 693–703.

Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of National Academy of Sciences, U.S.A.*, **91**, 1450–1454.

Brumm, H. & Ritschard, M. 2011. Song amplitude affects territorial aggression of male receivers in chaffinches. *Behavioral Ecology*, published online 20 January 2011, doi:10.1093/beheco/arq205.

Brumm, H., Robertson, K. A. & Nemeth, E. 2011. Singing direction as a tool to investigate the function of birdsong: an experiment on sedge warblers. *Animal Behaviour*, **81**, 653–659, doi:10.1016/j.anbehav.2010.12.015.

Burt, J. M., Campbell, S. E. & Beecher, M. D. 2001. Song type matching as threat: a test using interactive playback. *Animal Behaviour*, **62**, 1163–1170.

Capp, M. S. & Searcy, W. A. 1991. Acoustical communication of aggressive intentions by territorial male bobolinks. *Behavioral Ecology*, **2**, 319–326.

Dabelsteen, T., McGregor, P. K., Lampe, H. M., Langmore, N. E. & Holland, J. 1998. Quiet song in birds: an overlooked phenomenon. *Bioacoustics*, **9**, 80–105.

Dawkins, R. & Krebs, J. R. 1978. Animal signals: information or manipulation? In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 282–309. Oxford: Blackwell.

Goller, F., Mallinckrodt, M. J. & Torti, S. D. 2004. Beak gape dynamics during song in zebra finch. *Journal of Neurobiology*, **59**, 289–303.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Hoese, W. J., Podos, J., Boetticher, N. C. & Nowicki, S. 2000. Vocal tract function in birdsong production: experimental manipulation of beak movements. *Journal of Experimental Biology*, **203**, 1845–1855.

Hof, D. & Hazlett, N. 2010. Low amplitude song predicts attack in a North American wood warbler. *Animal Behaviour*, **80**, 821–828, doi:10.1016/j.anbehav.2010.07.017.

Johnstone, R. A. 2001. Eavesdropping and animal conflict. *Proceedings of National Academy of Sciences, U.S.A.*, **98**, 9177–9180.

Johnstone, R. A. & Bshary, R. 2004. Evolution of spite through indirect reciprocity. *Proceedings of the Royal Society B*, **271**, 1917–1922.

Kroodsma, D. E. 1976. The effect of large song repertoires on neighbor 'recognition' in male song sparrows. *Condor*, **78**, 97–99.

Laidre, M. E. 2009. How often do animals lie about their intentions? An experimental test. *American Naturalist*, **173**, 337–346.

Laidre, M. E. & Vehrencamp, S. L. 2008. Is bird song a reliable signal of aggressive intent? *Behavioral Ecology and Sociobiology*, **62**, 1207–1211.

Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.

Logue, D. M., Abiola, I. O., Rains, D., Bailey, N. W., Zuk, M. & Cade, W. H. 2010. Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song. *Proceedings of Royal Society B*, **27**, 2571–2575, doi:10.1098/rspb.2010.0421.

McGregor, P. K. 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 237–244.

McGregor, P. K. 2005. *Animal Communication Networks*. Cambridge: Cambridge University Press.

Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. Oxford: Oxford University Press.

Nakagawa, S. & Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591–605.

Nice, M. M. 1943. Studies in the life history of the song sparrow II. The behavior of the song sparrow and other passerines. *Transactions of the Linnean Society of New York*, **6**, 1–328.

Otte, D. 1974. Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics*, **5**, 385–417.

Peake, T. M. 2005. Eavesdropping in communication networks. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 13–37. Cambridge: Cambridge University Press.

Searcy, W. A. & Beecher, M. D. 2009. Song as an aggressive signal in songbirds. *Animal Behaviour*, **78**, 1281–1292.

Searcy, W. A. & Nowicki, S. 2005. *The Evolution of Animal Communication*. Princeton, New Jersey: Princeton University Press.

Searcy, W. A. & Nowicki, S. 2006. Signal interception and the use of soft song in aggressive interactions. *Ethology*, **112**, 865–872.

Searcy, W. A., Nowicki, S. & Hogan, C. 2000. Song type variants and aggressive context. *Behavioral Ecology and Sociobiology*, **48**, 358–363.

Searcy, W. A., McArthur, P. D., Peters, S. S. & Marler, P. 1982. Response of male song and swamp sparrows to neighbour, stranger, and self songs. *Behaviour*, **77**, 152–163.

Searcy, W. A., Anderson, R. C. & Nowicki, S. 2006. Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology*, **60**, 234–241.

Searcy, W. A., Anderson, R. C. & Nowicki, S. 2008. Is bird song a reliable signal of aggressive intent? A reply. *Behavioral Ecology and Sociobiology*, **62**, 1213–1216.

Vehrencamp, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions? *Proceedings of the Royal Society B*, **268**, 1637–1642.

Waas, J. R. 1991. Do little blue penguins signal their intentions during aggressive interactions with strangers. *Animal Behaviour*, **41**, 375–382.

Weeden, J. S. & Falls, J. B. 1959. Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals. *Auk*, **76**, 343–351.

Williams, H. 2001. Choreography of song, dance and beak movements in the zebra finch. *Journal of Experimental Biology*, **204**, 3497–3506.

Wilson, P. L. & Vehrencamp, S. L. 2001. A test of the deceptive mimicry hypothesis in song-sharing song sparrows. *Animal Behaviour*, **62**, 1197–1205.

Wingfield, J. C. & Hahn, T. P. 1994. Testosterone and territorial behaviour in sedentary and migratory sparrows. *Animal Behaviour*, **47**, 77–89.

Zahavi, A. 1975. Mate selection: a selection for handicap. *Journal of Theoretical Biology*, **53**, 205–214.

Zahavi, A. 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, **67**, 603–605.

Zahavi, A. 1979. Why shouting? *American Naturalist*, **113**, 155–156.