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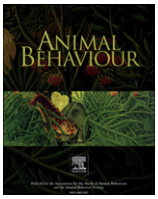

The receiver-dependent cost of soft song: a signal of aggressive intent in songbirds

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Social costs are one mechanism whereby reliability in signalling systems can be maintained. We measured the strength of aggressive response to territorial playback to ask whether the reliability of ‘soft song’, a strongly aggressive signal in the song sparrow, *Melospiza melodia*, is enforced by a social cost in the form of the receiver’s aggressive response. We also asked whether this cost is imposed by all receivers, or whether a differential response is found primarily or exclusively among the most aggressive subjects. We first measured the strength of each male’s aggressive response to playback on his territory, and then tested his responses to ‘warbled’ soft song and to broadcast song playbacks. While we found substantial variation in individual aggressiveness, nearly all males responded more strongly to warbled soft songs. Thus we provide evidence that warbled soft song imposes a social cost in the form of receiver retaliation, and provide a possible explanation for how the signal’s reliability is maintained. Questions about soft song remain, notably why selection should favour low amplitude in vocal signals of aggression in songbirds.

Reliable signalling is widespread in aggressive contexts. Signals produced in these contexts have been shown to convey information about a signaller’s resource-holding potential (Riede & Fitch 1999; Bee et al. 2000; Reby & McComb 2003; Tibbetts & Dale 2004) or aggressive intentions (Wagner 1989; Waas 1991; Hurd 2004; Laidre 2005; Searcy et al. 2006) in a wide range of animal groups. Several mechanisms exist that can maintain reliability in signals in general (Maynard Smith & Harper 2003; Searcy & Nowicki 2005), but some of these mechanisms seem less applicable to aggressive signals. In particular, intrinsic costs such as production and developmental costs can stabilize signals through a handicap mechanism (Zahavi 1975; Grafen 1990), but these types of costs often seem minor and unimportant for aggressive signals. It has been suggested, therefore, that aggressive signals are often stabilized instead by receiver-dependent costs (Enquist 1985; Vehrencamp 2000). Here the important costs, rather than being inherent in the development, production or maintenance of the signal, stem from how receivers interpret and respond to the signal (Guilford & Dawkins 1995). Aggressive-signalling models indicate that this type of cost can maintain reliability (Enquist 1985; Maynard Smith & Harper 1988; Hurd 1997), and empirical studies have found evidence in some aggressive-signalling systems for the predicted patterns of receiver response (Rohwer 1977; Popp 1987; Molles & Vehrencamp 2001; Vehrencamp 2001; Tibbetts 2008; Rek & Osiejuk 2011). In this study, we tested for receiver-dependent costs for warbled soft song, an aggressive signal in song sparrows, *Melospiza melodia*.

Soft song is produced by male songbirds in both aggressive and courtship contexts (Dabelsteen et al. 1998; Morton 2000). In several species of songbirds, soft song is the signalling behaviour that best predicts a physical attack by the singer, including song sparrows (Searcy et al. 2006; Akçay et al. 2011), swamp sparrows, *Melospiza georgiana* (Ballentine et al. 2008) and black-throated blue warblers, *Dendroica caerulescens* (Hof & Hazlett 2010). Soft song thus meets two of the three criteria of Searcy & Beecher’s (2009) definition of an aggressive signal: a signal that is associated with an aggressive context and that predicts attack or escalation towards attack. We addressed the third criterion, receiver response to the signal, by testing for a differential response to soft song compared to regular broadcast song.

Because soft song has been shown to signal aggression reliably, it follows that it should be costly in some way that enforces its reliability. Production and developmental costs seem unlikely to apply to soft song given its structural features (Anderson et al. 2007; Ballentine et al. 2008; Searcy et al. 2008). Soft song also seems unlikely to be a ‘performance’ or ‘index’ signal that only a subset of the population is capable of producing (Maynard Smith

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& Harper 2003; Hurd & Enquist 2005). Instead, it is logical to hypothesize that the reliability of soft song is maintained by a receiver-dependent social cost. In such a mechanism, use of soft song as a bluff by weak individuals is discouraged by the possibility that the signal will elicit a strong aggressive response from some receivers, a response that is particularly costly to weak signallers.

We previously tested for a social cost for soft song in song sparrows using aggressive response of territory owners to playback of different signal types to estimate the strength of receiver retaliation (Anderson et al. 2007). The design of this earlier study was complicated by the fact that song sparrows use two categories of soft song (Anderson et al. 2008): 'crystallized soft song', consisting of normal broadcast songs produced at low amplitudes, and 'warbled soft song', consisting of songs that are not part of the broadcast repertoire and having distinctive song structure and phonology, again sung at low amplitudes. In the earlier study (Anderson et al. 2007), we chose to use crystallized soft song to represent the general category of soft song. Thus in one experiment we tested for receiver retaliation to soft song by comparing the aggressive response of male song sparrows to broadcast song and crystallized soft song. In a second experiment, we compared responses to crystallized soft song and warbled soft song. In both experiments, we attracted territorial males by playback of an initial broadcast song type to within 4 m of the playback speaker to ensure that soft song playbacks would be heard, and we then switched the playback to one of the classes of test songs. In the first experiment, song sparrows showed no significant difference in their aggressive response to broadcast song and crystallized soft song; similarly, in the second experiment they showed no significant difference in their response to crystallized soft song and warbled soft song.

Although the results of Anderson et al. (2007) imply that male song sparrows do not respond more aggressively to warbled soft song than to broadcast song, no direct test of that hypothesis was made, that is, no experiment was conducted that allowed a within-experiment comparison of response to these two categories. Warbled soft song differs more from broadcast song in acoustic structure than does crystallized soft song (Anderson et al. 2008), so warbled soft song versus broadcast song may be an easier discrimination to make than crystallized soft song versus broadcast song. One goal of the present study was to make a direct, within-experiment comparison of aggressive response to warbled soft song and broadcast song.

In the present study, before testing male song sparrows for response to warbled soft song and broadcast song, we first assayed the aggressiveness of our subjects in separate playback trials. Previous work has shown that male song sparrows are individually consistent in the level of aggressiveness shown in such assays (Nowicki et al. 2002; Hyman et al. 2004). The rationale for performing these assays is that some models of socially enforced reliability of aggressive signals assume that aggressive retaliation is performed only by a subset of the receivers, those that are stronger or more aggressive than average (Enquist 1985). Empirically, some studies have found that only a subset of receivers show retaliation to aggressive signals (Osiejuk et al. 2007; Rek & Osiejuk 2011), whereas others have found evidence of retaliation across all receivers (Popp 1987; Molles & Vehrencamp 2001; Vehrencamp 2001). Therefore in this study we tested both whether aggressive response is stronger across all subjects to warbled soft song than to broadcast song, and whether a differential response is found primarily or exclusively among the most aggressive subjects.

METHODS

We tested 27 male song sparrows in the vicinity of Linesville and Hartstown, Crawford County, PA, U.S.A. Subjects were defending territories in edge habitat between deciduous forest and either old fields or mowed areas. Before testing began we noted the general size and shape of each subject's territory and the location of borders with other males. We captured each subject using nylon mist nests (Avinet, Inc., Dryden, New York, U.S.A.) and gave each a unique combination of three plastic colour bands and one U.S. Fish and Wildlife Service band. The study was approved by the Animal Care and Use Committee of Duke University (A090-08-04). We captured and banded birds under permissions from the United States Department of the Interior (bird banding permit no. 2153) and the Pennsylvania Game Commission (bird banding permit no. BBN-00168).

Testing occurred from 19 May to 18 June 2008. Nowicki et al. (2002) and Hyman et al. (2004), working in this same population, found considerable variation in how aggressively males respond to playbacks, and further found that individual differences in aggressive response remained significantly consistent across four rounds of trials that spanned the breeding season, from early May until late June. For each individual in our sample, we first performed an aggression assay playback to each male following the methods of Nowicki et al. (2002) and Hyman et al. (2004). We then performed two treatment playbacks, a warbled soft song playback and a broadcast song playback, with the order of these treatments balanced across the subjects. We waited an average of 12 days between the aggression assay and the first treatment playback, and we separated the treatment playbacks by 2 or 3 days.

Aggression Assay

Following Nowicki et al. (2002), we played song sparrow broadcast song from well within the subject's territory for 6 min at a rate of 1 song/10 s, using a Marantz PMD-660 digital recorder and an Advent AV570 speaker-amplifier placed face-up on the ground at the base of a hedgerow. Playbacks were calibrated at an amplitude of 85 dB SPL (at 1 m, B&K Precision 732A sound level meter, A-weighting). Each 6 min playback included two different song types recorded from the same source male presented in nine repetitions of each type and alternating twice between the two types (36 songs total). We used 27 different playback tracks, using 44 songs recorded from 15 different source males. Ten songs were used twice to make playbacks, but no male heard the same pair of songs. The songs were recorded using either a Sony TC-D5M or a Sony TCM 5000EV tape recorder with a Shure SM57 or Realistic 331070B microphone in a Sony PBR-330 parabola. Recordings were made 3–5 years prior to this study from males holding territories 12–30 km distant from our study area. Although test stimuli were local songs, it is highly unlikely that any of our subjects were familiar with the particular songs used as stimuli or with the individuals that sang them.

We measured the aggressive response to the playback using the male's distance to the playback loudspeaker averaged over the 6 min playback and a 3 min postplayback period. We did not consider other response measures, such as broadcast song rate, because the strongest test of the receiver retaliation hypothesis considers only responses that are associated with aggression. Distance to speaker is strongly associated with attack likelihood in song sparrows whereas broadcast song rate is not (Searcy et al. 2006).

The subject's distance to the speaker was sampled at 5 s intervals, binned into the categories 0–2 m, 2–4 m, 4–8 m, 8–16 m and >16 m. Estimation of distances was aided by placing markers at measured distances of 2, 4 and 8 m from the speaker before the trial. To calculate an average distance to the speaker, we considered a bird in the 0–2 m range for a given 5 s interval to be at 1 m from the speaker during that interval, a bird in the 2–4 m range at 3 m, in the 4–8 m range at 6 m, in the 8–16 m range at 12 m and in the >16 m range to be at 24 m, following the method of Peters et al. (1980).

The average distance was calculated from these 5 s interval estimates across the entire 9 min observation period.

For the 27 subjects tested, we used the median proximity measure to divide the subjects into two cohorts: the 13 birds that approached the speaker most closely during the aggression assay ('strong responders') and the 13 birds that approached least closely ('weak responders'). The bird with the median value of 3.8 m was excluded from analysis. We then compared each cohort's response to broadcast song playback and to soft song playback to test the hypothesis that the strong responders would respond more strongly to soft song (evidence of receiver retaliation), while the weak responders would not (no retaliation). Because this test involved small samples in each cohort ($N = 13$) we used the nonparametric Wilcoxon signed-ranks test for statistical comparison.

Broadcast and Soft Song Playbacks

The test protocol, with a few exceptions, followed the methods used in our earlier study of male response to soft song (Anderson et al. 2007). The playback stimuli were recorded as described above and were played using the same digital recorder and speaker used during the aggression assay. Playbacks were 3 min tracks of a single song exemplar played at 10 s intervals; this is a standard protocol based on the natural singing behaviour of male song sparrows (Marler & Peters 1988). Warbled soft song was used to represent the soft song category. We used 25 warbled soft song exemplars and 27 broadcast song exemplars (all different from those used during aggression assay playbacks), recorded from 18 different males (see Fig. 1 for examples). The speaker was placed in the same location as for the prior aggression assay for each male.

We began each test by presenting a single broadcast song exemplar played at 85 dB SPL to draw the subject to the vicinity of the speaker. These 27 'lure' songs were used in the aggression assay, but each male heard a different song from that used in his assay. The 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. On a few occasions (12 of 81 trials) the subject did not meet the 4 m criterion by the time the sixth song had been played. It appeared to observers that these males were off territory during the playback, because most responded immediately to a second round of playback after a 10 min time-out period. In only three of 81 trials did subjects not meet the 4 m criterion after two rounds of lure playback (all three subjects were not apparent on territory); in these few cases we stopped and completed the test with that subject on another day. Once the 4 m criterion was met, we began a 3 min playback of the experimental stimulus (broadcast song or soft song), with broadcast songs played at a mean amplitude of 85 dB SPL, and soft songs played at a mean of 65 dB SPL. These levels are within the natural range of variation in song sparrows for broadcast and soft song, respectively (Anderson et al. 2008). The treatment playbacks were counterbalanced among males as to whether broadcast or soft song playbacks were performed first. We measured the aggressive response to the different playback treatments as the subject's distance to the playback speaker averaged over the 3 min playback and 3 min postplayback periods. We compared distance measures between treatments using a paired *t* test. We tested the relationships of response between treatments using Pearson correlations. Because the distance measures did not conform to the normal distribution (Shapiro–Wilk test: $W > 0.70$, $P < 0.003$ in all cases) these data were log transformed before analysis with parametric tests. All analyses were performed using JMP software (SAS Institute Inc. Cary, NC, U.S.A.).

RESULTS

During aggression assays, the subjects' average proximity to the playback speaker (combined 6 min playback and 3 min postplayback periods) ranged from 1.3 to 11.5 m. The median proximity measure (3.8 m) divided the subjects into two cohorts, strong responders (mean ± SE = 2.5 ± 0.2 m) and weak responders (7.1 ± 0.7 m). We then asked whether the strong cohort and weak cohort responded differently to soft song relative to broadcast song playbacks; specifically, our prediction was that the strong cohort would respond more strongly to soft song than to broadcast song, while the weak cohort would show the reverse pattern. In fact, we found that both cohorts approached the speaker more closely during soft song playbacks compared to broadcast song playbacks (Wilcoxon signed-ranks test: strong cohort: $W = 11$, $N = 12$ nontied

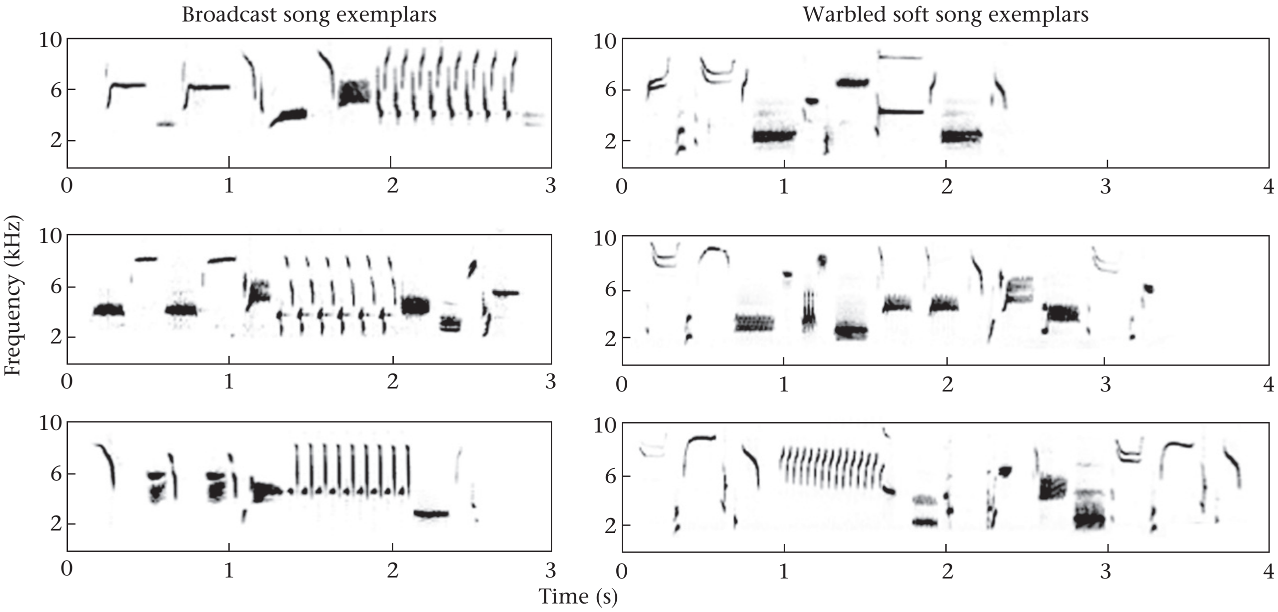

Figure 1. Examples of song exemplars used as stimuli in broadcast song and 'warbled' soft song treatment playbacks.

ranks, $P = 0.027$; weak cohort: $W = 6$, $N = 12$ nontied ranks, $P = 0.007$; Fig. 2).

Since both cohorts of birds responded more strongly to soft song playbacks, we treated all subjects as a single group for further analysis. The majority of subjects (19 of 27) were closer to the playback speaker (averaged over the playback) during soft song playbacks compared to broadcast song playbacks (paired t test, two-tailed: $t_{26} = 4.29$, $P = 0.0002$; Fig. 2). The aggressiveness of the response measured during the aggression assay was highly positively correlated with the aggressive response during broadcast playbacks (Pearson correlation coefficient: $r = 0.53$, $P = 0.005$). Response during the assay was also positively correlated with response during soft song playbacks ($r = 0.44$, $P = 0.02$), although this relationship was weaker. Responses to broadcast song and to soft song playbacks were highly correlated ($r = 0.63$, $P = 0.0004$). Thus, we found that the aggression assay was predictive of responses during both the broadcast song and soft song playbacks, and that individuals were highly consistent in the strength of their responses to the two song categories.

DISCUSSION

Searcy & Beecher (2009) outlined three criteria for determining whether a signal should be classified as aggressive: (1) whether the signal increases in aggressive contexts (the context criterion); (2) whether the signal predicts aggressive escalation by the signaller (the predictive criterion); and (3) whether receivers show differential responses to the signal and a control stimulus (the response criterion). Soft song in the song sparrow has been shown to meet the context criterion as this behaviour is observed predominantly during aggressive interactions (Nice 1943; Searcy et al. 2006) and does not serve a courtship function (Anderson et al. 2007). Soft song was shown to meet the predictive criterion by Searcy et al. (2006), who conducted playbacks to provoke aggressive signalling from territorial males. After the subjects' displays were recorded, a stuffed male conspecific was revealed and the subjects were given an opportunity to attack it. Of a variety of displays, only numbers of soft songs differed significantly between the males that attacked and those that did not. The results of the present study provide evidence for the response criterion: subjects responded more aggressively to soft song playbacks than broadcast song playbacks, demonstrating that the difference between the two signal categories is salient to receivers in the context of male–male aggressive signalling.

The result that males responded more aggressively to soft song than to broadcast song supports the hypothesis that a receiver-dependent cost maintains the reliability of soft song in conveying aggressive intentions. We found a stronger response to soft song both in subjects that were of above-average aggressiveness and in subjects that were of below-average aggressiveness. This pattern of across the board greater response to an aggressive signal is what has been found in most previous studies of aggressive retaliation, including the studies of Popp (1987) on postural displays in American goldfinches, *Carduelis tristis*, Molles & Vehrencamp (2001) on song matching in banded wrens, *Thryothorus pleurostictus*, and Vehrencamp (2001) on song matching in song sparrows. In all these cases, a pattern of stronger response to more escalated signals was found for all subjects combined, without dividing subjects into stronger and weaker sets. Receiver retaliation towards an aggressive signal has been found to be confined to a subset of signallers in two cases, a study of immediate variety singing in ortolan buntings, *Emberiza hortulana* (Osiejuk et al. 2007) and a study of soft calls in corncrakes, *Crex crex* (Rek & Osiejuk 2011). In the former case, those retaliating were older, more experienced individuals, whereas in the latter case it is unknown whether retaliating individuals differed systematically in any way from those intimidated by the aggressive signal.

The theoretical problem raised by evidence that all individuals retaliate against an aggressive signal is that such evidence suggests there is no benefit to giving the aggressive signal. To stabilize an aggressive signalling system, a benefit of giving the aggressive signal is just as necessary as is a cost. In the model of Enquist (1985), for example, stability is achieved as follows: strong individuals give a signal of strength, and weak individuals give a signal of weakness. The benefit of giving the signal of strength is that it intimidates weak receivers, causing them to submit without a fight. The cost of giving the signal of strength is that it provokes an attack from strong signallers. If we add the reasonable assumption that experiencing an attack by a strong receiver is more costly for a weak signaller than for a strong one, reliable signalling can be favoured for both weak and strong signallers (Enquist 1985). Receiver retaliation is essential in stabilizing the system, in that it prevents the aggressive signal from spreading to all signallers and thus becoming meaningless. The intimidating effect of the strong signal on weak opponents is also essential, however, because without this benefit there is no reason for anyone to give the aggressive signal. In this respect, then, the result that all our subjects responded

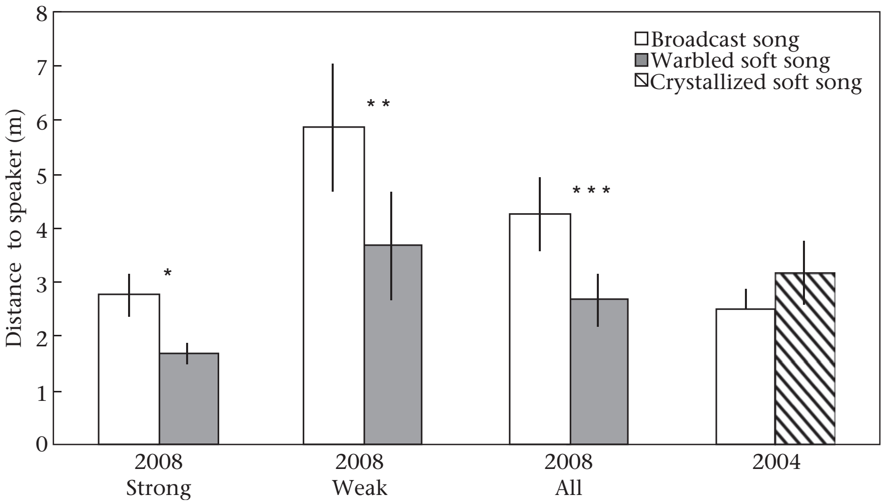

Figure 2. Aggressive response as measured by distance to the playback speaker (mean ± SE). The 2004 data are from Anderson et al. (2007). Asterisks indicate significantly different responses: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Smaller bars indicate closer proximity to the speaker and thus a stronger aggressive response. $N = 27$ in 2008, $N = 15$ in 2004.

aggressively to warbled soft song is puzzling. We suggest as a possible answer to this puzzle that the weak individuals intimidated by soft song may be younger, nonterritorial males, and that the benefit of the display is that it can ward off such individuals when they intrude on the territory of an older, more experienced male. Under this hypothesis, the subjects of our experiment, as territory owners, would all fall in the category of strong receivers, explaining why they all showed retaliation. These ideas might be tested by provoking take-overs of territories by floater males through short-term removal of territory owners. The intimidating effects of soft songs could then be studied during interactions between new and old owners after release of the latter.

Anderson et al. (2007) performed two playback experiments measuring aggressive response by male song sparrows to soft song, using methods very similar to the ones used here. In one experiment, they found no significant difference in aggressive response to warbled soft song and crystallized soft song; in the second they found no significant difference in response to crystallized soft song and broadcast song. A logical inference from those results is that aggressive response ought to be equal to warbled soft song and broadcast song, but Anderson et al. (2007) did not perform an experiment to test that inference directly. Here we performed such a direct experimental test, and found significantly stronger response to warbled soft song than to broadcast song. The difference in results of the two studies can be attributed in part to the provisional nature of any conclusion of no difference, and in part to the fact that we used considerably larger sample sizes in the present study (27 subjects) than in the Anderson et al. (2007) study (15 subjects). The larger sample sizes presumably allow more accurate estimates of response strength, and certainly provide greater statistical power to discern differences.

The results of the present study support aggressive retaliation to warbled soft song, whereas the results of Anderson et al. (2007) suggest no aggressive retaliation to crystallized soft song. Why one form of soft song would be subject to receiver retaliation and not the other is puzzling. At one level, an answer to this puzzle is apparent: warbled soft song should be much easier to discriminate from broadcast song than is crystallized soft song. Crystallized soft song consists of the same song types as broadcast song, whereas warbled soft song consists of songs that are never sung at high amplitude (Anderson et al. 2008). Consequently, the differences between broadcast song and warbled soft song are much greater than those between broadcast song and crystallized soft song in acoustic properties such as duration, maximum frequency, frequency range and note composition (Anderson et al. 2008). Therefore it is understandable why subjects might discriminate warbled soft song from broadcast song, while failing to discriminate crystallized soft song from broadcast song. What this proximate explanation leaves unanswered is the question of how it could be that warbled soft song is stabilized as an aggressive signal by receiver retaliation when crystallized soft song is not. As far as our previous work can show, both forms of soft song are equally reliable as predictors of attack. Thus a signal cost to stabilize reliability is equally necessary for crystallized soft song as for warbled soft song, so it is puzzling why receiver retaliation provides such a cost for one but not the other.

Low-amplitude songs or 'soft songs' are used in both mate attraction and aggressive signalling contexts in birds (Dabelsteen et al. 1998; Morton 2000). Since Dabelsteen et al.'s (1998) review of this 'overlooked phenomenon', we still know relatively little about this class of vocal signal. Soft song is particularly intriguing because it has been shown to be an exceptionally reliable signal of aggressive intent in several species of birds (Searcy et al. 2006; Ballentine et al. 2008; Hof & Hazlett 2010), and yet appears to lack intrinsic costs that might enforce its reliability (Anderson et al. 2008). Here we provide evidence for a songbird that low-amplitude song imposes a social cost in the form of receiver retaliation, although puzzlingly this cost applies to only one of the two forms of soft song in this species. Other questions remain, notably why selection has so often favoured low amplitude as a defining acoustic feature in vocal signals of aggression in songbirds.

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