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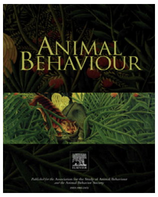

Special Issue: Whispered Communication

Quiet threats: soft song as an aggressive signal in birds

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Theory suggests that aggressive signals must be costly if they are to be reliable. Recent research in birds has shown, however, that in many species the best predictors of impending attack are low-amplitude vocal signals, soft songs or soft calls, that seem cheap to produce and easy to cheat. This observation leads to two related but separate questions: (1) why use low-amplitude signals to communicate aggressiveness and (2) what maintains the reliability of soft signals of aggression? We review potential answers to both questions and present evidence relevant to each. While some hypotheses are logically sound, others have logical flaws, and most of the hypotheses have yet to be critically tested. One exception is the hypothesis that the reliability of soft signals of aggressiveness is maintained by receiver retaliation, which has been supported by experimental evidence in multiple species. We emphasize the need for further research, particularly to answer the question of why soft song is soft, and outline future research directions.

How reliability, or ‘honesty’, is maintained in animal communication systems remains a major topic in evolutionary biology (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). Special attention has been paid to signalling in agonistic interactions, given that in these interactions signallers and receivers have directly opposing interests. Theoretical work indicates that aggressive signals can be reliable if they are difficult or impossible to cheat or too costly to bluff (Grafen, 1990; Nur & Hasson, 1984; Zahavi, 1975, 1977).

It is easy to see how aggressive threat signals emphasizing size or strength can be reliable, as in the case of fundamental frequency in the calls of frogs and toads (Davies & Halliday, 1978) and formant spacing in the roars of red deer, *Cervus elaphus* (Reby & McComb, 2003). In these cases, there is a direct physical link between the size of the animal and the characteristics of its display, making the salient display characteristics difficult or impossible to cheat (Maynard Smith & Harper, 2003). It is also well understood that signals that are intrinsically costly to produce can be reliable about signaller traits relevant to their costs (Grafen, 1990); thus, for example, the energetically costly drumming display of a spider is reliable about the physiological condition of the signaller (Kotiaho, 2000). Many of the signals used in aggressive interactions, however, seem to be both physically possible to cheat and relatively low in intrinsic production costs, raising the question of whether they are indeed reliable threat signals, and if so, how their reliability can be maintained.

In this paper, we focus on an example of a threat signal that has been shown to be a reliable predictor of aggression, but that on the surface appears to be both easy to produce and eminently cheatable: low-amplitude, or ‘soft’, songs and calls in birds. Soft song was first described as an aggressive signal by Margaret Morse Nice in her classic study of the behaviour of song sparrows, *Melospiza melodia* (Nice, 1943). Soft song has since been shown to occur in aggressive contexts in many other species of songbirds as well (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998). Soft vocalizations have also been found to occur during aggression in other taxa of birds (Reichard & Welklin, 2015; Ręk & Osiejuk, 2011), as well as in certain mammals (Brady, 1981; Gustison & Townsend, 2015).

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Interest in soft song as an aggressive signal picked up recently as a result of a study by Searcy and colleagues which found it to be the only signal that reliably predicted attack on a taxidermic mount in the song sparrow (Searcy, Anderson, & Nowicki, 2006), a finding that has since been replicated in a different population of this species (Akçay, Tom, Campbell, & Beecher, 2013; Akçay, Tom, Holmes, Campbell, & Beecher, 2011). Studies have also found low-amplitude vocalizations to be reliable predictors of aggressive escalation in several other bird species, including swamp sparrows, *Melospiza georgiana* (Ballentine, Searcy, & Nowicki, 2008), black-throated blue warblers, *Dendroica caerulescens* (Hof & Hazlett, 2010), corncrakes, *Crex crex* (Ręk & Osiejuk, 2011), and brownish-flanked bush warblers, *Cettia fortipes* (Xia, Liu, Alström, Wu, & Zhang, 2013).

In their review of aggressive signalling through birdsong, Searcy and Beecher (2009) proposed three criteria for establishing that a signal used during aggressive interactions (an agonistic signal) is in fact a threat signal: (1) the context criterion: use of the signal must increase during aggressive interactions; (2) the response criterion: receivers should respond to the signal as if it is an aggressive signal; and (3) the predictive criterion: the signal should predict escalation of the interaction if the receiver does not back down. Soft song satisfies all three criteria (see reviews in Searcy, Akçay, Nowicki, & Beecher, 2014; Searcy & Beecher, 2009). Furthermore, of all the presumed vocal signalling behaviours reviewed by Searcy and Beecher (2009), soft song emerged as the only signal that satisfied all three of these criteria based on available evidence. Although a few other vocal signals, most notably song type matching in western (but not eastern) song sparrows, have since been shown to satisfy these criteria (Akçay et al., 2013; Searcy, DuBois, Rivera-Cáceres, & Nowicki, 2013), soft song remains the only aggressive vocal signal that has been shown to be reliable in several different species.

The striking association between soft vocalizations and reliable aggressive signalling in birds raises two related questions. The first is: why are aggressive signals often low amplitude? Is low amplitude an especially advantageous characteristic in a vocal threat, and if so, why? We refer to this as the ‘why soft’ question. The second question is: what maintains the reliability of soft signals of aggression? That is, how can soft vocalizations be evolutionarily stable as reliable threat signals, given that they are seemingly easy and cheap to produce? We refer to this as the ‘why reliable’ question. A series of hypotheses has been suggested to answer these questions, with considerable disagreement over which to favour (Akçay & Beecher, 2012; Laidre & Vehrencamp, 2008; Osiejuk, 2011; Searcy, Anderson, & Nowicki, 2008). Some hypotheses address both questions, but others address only one, so it is important to be clear on the conceptual distinction between the two. It is also important to note that many of these hypotheses are not mutually exclusive, even those that address the same question (Table 1).

Before we review the hypotheses on aggressive soft song below, we should note that the scope of our review is limited to aggressive soft songs and excludes soft vocalizations used in courtship. The latter are likely to be under different evolutionary pressures and most of the hypotheses we review below are simply not applicable to courtship soft song. The evolution of courtship soft song is reviewed elsewhere by Reichard and Anderson (2015).

AVOIDING UNWANTED ATTENTION

The first proposal we consider, the eavesdropping avoidance hypothesis (Dabelsteen et al., 1998), addresses only the ‘why soft’ question. It is now widely established that animals eavesdrop on interactions between other individuals, both conspecific and heterospecific (McGregor, 2005; Peake, 2005). If being eavesdropped upon is costly, then decreasing the likelihood of eavesdropping by singing at low amplitudes might be advantageous. Whether and how a signaller benefits from minimizing eavesdropping depends on the category of eavesdropper with which it is dealing. We consider two classes of potential eavesdroppers: predators and conspecifics.

Predators and other natural enemies have been shown to locate prey by their auditory signals in a number of systems, including bats feeding on frogs (Tuttle & Ryan, 1981), skuas preying on petrels (Mougeot & Bretagnolle, 2000) and parasitoid flies attacking crickets (Cade, 1975). For birds, it is generally presumed that producing loud vocal signals is dangerous (Hale, 2004; Krams, 2001; Lima, 2009; Mougeot & Bretagnolle, 2000; Schmidt & Belinsky, 2013). These signals may be particularly risky during aggressive interactions when the attention of the singer is occupied by the intruder. Decreasing the amplitude of the song would be a sensible way to decrease the risk of attracting the attention of a predator during an aggressive interaction.

Although this hypothesis has a rather straightforward logic, evidence for it is lacking. The only direct test of which we are aware is Searcy and Nowicki's (2006) study in which they presented song sparrows with two conditions that both involved territorial intrusions simulated using playback of conspecific songs. A simulated intrusion was accompanied in one condition by playback of song sparrow alarm calls, indicating the presence of predators, and in the other by playback of the songs of yellow warblers, *Dendroica petechia*, as a control. The eavesdropping avoidance hypothesis predicts that the birds should increase their use of soft song under increased risk of predation, but what the authors actually found was the opposite: the proportion of soft songs the subjects sang

Table 1
Hypotheses to explain the low amplitude and reliability of aggressive soft song

Hypothesis	Description	Accounts for low amplitude?	Accounts for reliability in predicting attack?	Generalizes to all soft vocalizations?
Eavesdropping avoidance (predators)	Singing softly decreases the chances of the signaller being detected by a predator	Yes	No	Yes
Eavesdropping avoidance (conspecifics)	Singing softly decreases the chances of a conspecific competitor detecting the interaction	Yes	No	Yes
Readiness	Singing softly is a by-product of postures and visual demands necessary for getting ready to attack	Yes	No	No
Competing costs	Singing softly decreases the ability of the signaller to keep off intruders/attract females	Yes	Yes	No
Vulnerability handicap	Close-range song makes signallers more vulnerable because of the close distance of the signaller to the receiver	Yes	Yes	No
Receiver retaliation	Close-range song increases the likelihood of the receiver retaliating aggressively	No	Yes	No

was significantly lower in the predator condition than in the control condition.

Male and female conspecifics constitute a second class of potential eavesdroppers. Experimental evidence from a number of songbird species has confirmed that conspecific males do indeed eavesdrop on neighbouring singers (Akçay, Reed, Campbell, Templeton, & Beecher, 2010; Naguib, Fichtel, & Todt, 1999; Peake, 2005; Peake, Terry, McGregor, & Dabelsteen, 2001; Peake, Terry, McGregor, & Dabelsteen, 2002). Unlike eavesdropping by predators, which seems likely always to be disadvantageous to a signaller, eavesdropping by competitors may sometimes be beneficial. For example, if neighbouring males overhear a territory owner defeating an intruder, the eavesdroppers may subsequently be discouraged from confronting that owner themselves (Johnstone, 2001; Johnstone & Bshary, 2004). Territory owners thus might benefit from encouraging eavesdropping by using broadcast song, rather than soft song, when countering intruders. Conversely, it may be advantageous for intruders to use soft vocalizations when they trespass on territories of others. There is experimental evidence from song sparrows that territory owners that appear to intrude on a neighbour's territory pay a retaliation cost from other eavesdropping males (Akçay et al., 2010). If that is true, then intruders would benefit from limiting eavesdropping by competitors.

Another possible cost of being eavesdropped on by conspecific males is that neighbouring or floating males could take advantage of the challenge to the territory owner and intrude upon the territory to obtain extrapair copulations with the signaller's mate. In some species, extrapair copulations during the fertile period are most likely to happen on the female's own territory and therefore it is plausible that neighbouring males would time their intrusion to coincide with such challenges (Akçay et al., 2012; Hung, Tarof, & Stutchbury, 2009).

Evidence for eavesdropping costs imposed by conspecific males is again limited. In the single most direct test of this hypothesis, Searcy and Nowicki (2006) tested intrusion pressure during simulated aggressive interactions that did or did not incorporate soft song in song sparrows. After first removing the territorial male, they used playback to simulate an interaction in which an intruder singing broadcast song was countered by the resident male singing either at normal broadcast amplitudes or at low amplitudes characteristic of soft song. The results showed that the intrusion pressure (measured as duration of observed intrusions) was higher when the simulated resident male sang at low amplitudes. This result is in accord with the idea that territory owners dealing with intruders actually benefit when competitors eavesdrop, and thus provides no rationale for the use of soft song in such a context.

Conspecific females also are potential eavesdroppers. Evidence suggests that females of several species of songbirds eavesdrop on exchanges of broadcast song between conspecific males, and discriminate in favour of males that win such contests and against those that lose (Garcia-Fernandez, Amy, Lacroix, Malacarne, & Leboucher, 2010; Mennill, Ratcliffe, & Boag, 2002; Otter et al., 1999). Thus whether male songbirds would benefit from minimizing eavesdropping by females may again depend on whether males win or lose such contests. We know of no studies to date that have tested the possibility that eavesdropping by conspecific females has played a role in the evolution of soft song.

Future Directions

Although one experimental test of the predator version of the eavesdropping avoidance hypothesis has given negative results, this solitary result is not sufficient reason to discard this hypothesis. Further experiments should be done in additional species, using alternative methods of simulating predator presence such as playback of predator vocalizations or presentation of predator models or live predators. To test the conspecific version of the eavesdropping hypothesis, further experiments could be done using playback from multiple speakers to simulate interactions with and without soft vocalizations, and measuring response in additional categories of potential eavesdroppers, especially conspecific females.

GETTING READY TO FIGHT

A second answer to the why soft question is the readiness hypothesis (Akçay & Beecher, 2012; Akçay et al., 2011). This hypothesis proposes that preparing for a fight is incompatible with producing loud vocalizations, so that birds about to fight are constrained to produce vocalizations at low amplitude if they choose to sing (Akçay & Beecher, 2012; Akçay et al., 2011). Getting ready to fight requires tracking the opponent visually. In loud singing, birds often open their bills and throw their heads back so that they are looking upwards, which would usually mean that the opponent cannot be tracked. Experimental research indicates that bill gape is correlated with song amplitude, such that songs are sung with lower amplitude when the bill is closed (Goller, Mallinckrodt, & Torti, 2004; Hoese, Podos, Boetticher, & Nowicki, 2000; Williams, 2001). It seems reasonable to expect visual tracking of the opponent to take precedence over singing loudly during aggressive interactions, especially if the bird has the intention to attack or is in danger of being attacked by its opponent, and given that the bird does not need to sing loudly to be heard by his opponent when the two are already in close proximity. If readiness to attack is compatible with soft vocalizations but not with loud vocalizations, then that provides a sufficient explanation for why soft vocalizations are associated with aggression.

Future Directions

Although this hypothesis also makes intuitive sense, it has not yet been subjected to critical tests. Two types of functional morphology analyses would seem particularly relevant. One would be to test the assumption of a trade-off between the head and bill movements associated with loud song and visual perception of a target such as a competitor (Akçay & Beecher, 2012). A second would be to test the importance of head movements to the production of loud songs, to see whether and how head posture affects song amplitude.

COMPETING FUNCTIONS OF SINGING

The competing functions hypothesis proposes that singing softly rather than loudly is costly because soft song cannot accomplish the advertisement functions of song as effectively as loud songs due to its limited transmission distance (Searcy et al., 2008; Searcy & Nowicki, 2006). The advertisement functions of songs include proclamation of territory ownership as well as mate attraction. Following the logic of the handicap hypothesis (Zahavi, 1975, 1977), paying the cost is only of net benefit to signallers that are either highly motivated or of especially high quality. Because this hypothesis proposes a cost to low-amplitude signalling that might enforce honesty, the hypothesis addresses the ‘why reliable’ question. Because the competing functions cost is a direct result of low amplitude, the hypothesis also addresses the ‘why soft’ question. That is, low amplitude might be favoured in vocal signals of aggressive intent because this characteristic ensures their honesty.

The competing functions hypothesis has some empirical support. There is evidence that soft song in simulated interactions (with an opponent that sings loudly) is a less effective deterrent than is loud song, as reviewed above (Searcy & Nowicki, 2006). Soft song has also been found to be ineffective in stimulating courtship in one songbird species in which soft song is an aggressive signal (Anderson, Nowicki, & Searcy, 2007). In other species such as red-winged blackbirds, *Agelaius phoeniceus*, and zebra finches, *Taeniopygia guttata*, females also show preference for louder songs over softer songs (Ritschard, Riebel, & Brumm, 2010; Searcy, 1996). Although competing costs have some empirical backing in experimental situations, it is not clear to what extent these costs apply in natural interactions. First, unlike the situations that have been simulated in male removal experiments (Searcy & Nowicki, 2006) and female response tests (Anderson et al., 2007), songbirds often intermix loud and soft songs in a singing bout. In principle, singing some loud song may be enough to keep off other intruders and to attract or stimulate mates (Anderson, Searcy, Peters, & Nowicki, 2008; Nice, 1943). Furthermore, the periods of time owners spend in soft song may be short enough to have rather negligible effects on success in warding off distant intruders and attracting and courting females. Thus, even if competing functions costs exist, they may be too minor to play a role in enforcing signal honesty.

Future Directions

Further observational studies of the use of soft song, how often and in what circumstances would be important for evaluating this hypothesis. If soft song is indeed rarely given, and if, when given, is usually intermixed with louder signals, then this hypothesis would not be supported.

VULNERABLE BUT HONEST

The vulnerability handicap hypothesis is a general explanation for the honesty of aggressive signals that has been applied to soft vocalizations (Laidre & Vehrencamp, 2008). The logic of the general hypothesis is that if performing a particular display makes a signaller more vulnerable to attack, a cost is imposed on the display that only the most strongly motivated signallers will be willing to pay (Enquist, Plane, & Röed, 1985; Zahavi, 1977). Applied specifically to soft vocalizations, the argument is that low-amplitude signals are costly because they can only be perceived when the signaller is in close proximity to the receiver, where the signaller's vulnerability to attack is high (Laidre & Vehrencamp, 2008). Thus soft sounds signal proximity, and by doing so demonstrate the signaller's willingness to pay the resulting vulnerability cost. Because this hypothesis specifies a cost of soft signals that is directly tied to their low amplitude, it addresses both the ‘why soft’ and ‘why reliable’ questions.

A logical difficulty for this hypothesis is that the amplitude of an auditory signal always decreases with increasing distance from the source; consequently, high amplitude, not low amplitude, indicates close proximity (Searcy et al., 2008). Experiments with birds (and humans) have shown that signals with lower amplitude are indeed interpreted as having originated at a greater distance, rather than a closer one (Naguib, 1997; Naguib & Wiley, 2001; Nelson, 2000). If amplitude is the only attribute of a signal that both changes with distance and is available to a receiver, then clearly the receiver must interpret a high-amplitude version as having been produced closer than a low-amplitude version. If, instead, the receiver also has available other acoustic cues that change with distance, such as signal degradation and reverberation, then the more important these other cues are to judging distance the less important is amplitude, but to the extent that the receiver does rely on amplitude as a distance cue, lower amplitude will still suggest greater distance. If the receiver also has a visual fix on the signaller, which is often the case in the contexts in which soft signals of aggression are used, then presumably acoustic cues to distance will not be used at all.

Future Directions

Further experiments on how amplitude affects estimation of distance to source could be done with birds, with amplitude manipulated independently of other cues. The signalling proximity hypothesis predicts that low-amplitude playback will be interpreted as being closer, whereas the logic given above predicts the opposite.

RECEIVER RETALIATION

The receiver retaliation hypothesis proposes that bluffing is disadvantageous in aggressive signalling because of the danger that a dishonest signal of aggressive intent will provoke a costly attack from a stronger opponent (Enquist, 1985; Vehrencamp, 2000). This hypothesis is related to the vulnerability handicap hypothesis in that under both it is the response of receivers to aggressive signals that imposes a cost that maintains signal reliability. Under the vulnerability handicap hypothesis, however, the cost is a direct consequence of physical attributes of the signal, whereas under the receiver retaliation hypothesis the aggressive signal can be conventional, with meaning and costs that are arbitrary with respect to the signal's physical form (Guilford & Dawkins, 1995). Game theory models have supported the general idea that the cost of provoking attacks from opponents can be sufficient to stabilize the reliability of conventional signals of aggressive intent (Enquist, 1985; Számadó, 2008). Under the receiver retaliation hypothesis, then, the meaning of a soft signal is arbitrary with respect to its principal auditory feature, its low amplitude; therefore the hypothesis does not address the ‘why soft’ question, only the ‘why reliable’ question.

The principal prediction of the receiver retaliation hypothesis is that conspecific receivers will respond more aggressively to soft vocalizations than to loud vocalizations. Two early studies found negative results on this prediction. Dabelsteen and Pedersen (1990) tested European blackbirds, *Turdus merula*, with low-amplitude ‘strangled’ song and two types of loud song, high intensity and low intensity. Aggressive response was higher to high-intensity than to low-intensity loud songs, but no difference was found in response to high-intensity song and strangled song. Anderson et al. (2007) compared the response of male song sparrows to loud song and one of the two forms of soft song found in this species, crystallized soft song (Fig. 1). Males responded just as aggressively to the loud songs as to the soft songs. Although these first two studies gave negative results, several more recent studies have supported the prediction. Anderson, Searcy, Hughes, and Nowicki (2012) compared response of male song sparrows to loud song and the species' second form of soft song, warbled soft song (Fig. 1), and in this case found stronger aggressive response to the soft song than to the loud song. In a third experiment with song sparrows, Templeton, Akçay, Campbell, and Beecher (2012) compared response to loud song and to a mixture of crystallized and warbled soft songs; such a mixture is a common mode of soft song production in this species. Again, stronger aggressive response was found for the soft songs than for the loud songs. The prediction of stronger aggressive response to soft song has also been supported in an experimental study with brownish-flanked bush warblers (Xia et al., 2013). Finally, Ręk and Osiejuk (2011) found for corncrakes that soft calls elicited more attacks than loud calls, but also elicited more retreats. This pattern is exactly what is predicted by receiver retaliation models, as long as the attackers are the stronger

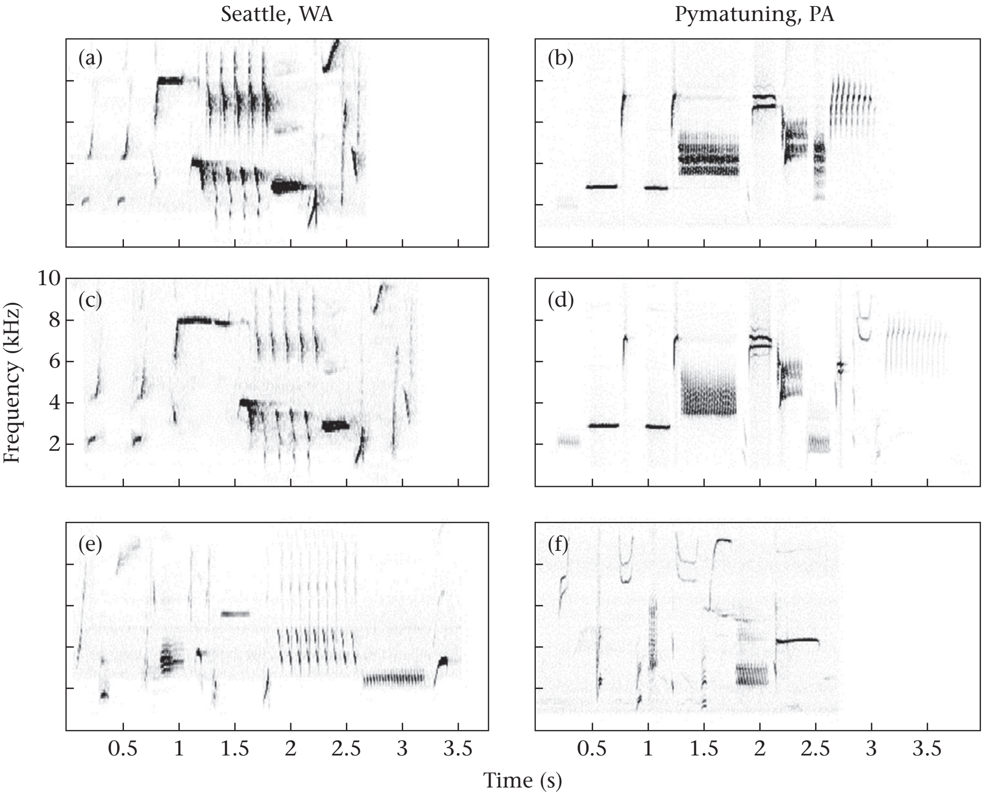

Figure 1. Examples of (a, b) broadcast song, (c, d) crystallized soft song and (e, f) warbled soft song from our two populations of song sparrows. Sonograms of the soft songs are darkened for clarity.

individuals and retreaters are the weaker, but this last part of the prediction was not tested.

ADDITIONAL EVIDENCE

Specialized Acoustic Structure

In some of the bird species with low-amplitude aggressive signals, soft vocalizations have a specialized acoustic structure, very different from that of loud songs and calls; this is true, for example, in corncrakes (Ręk, 2013; Ręk & Osiejuk, 2011) and brownish-flanked bush warblers (Xia et al., 2013). In other species, such as song sparrows, swamp sparrows, black-throated blue warblers and dark-eyed juncos, *Junco hyemalis*, some soft songs have specialized acoustic structure, whereas others are basically low-amplitude versions of broadcast songs (Fig. 1; Anderson et al., 2008; Ballentine et al., 2008; Hof & Hazlett, 2010; Titus, 1998). The similarities and differences in acoustic structure between loud and soft vocalizations can provide additional evidence relevant to the why soft and why reliable questions.

If selection has favoured low amplitude in aggressive signals to limit eavesdropping, then other adaptations to limit the active space of these vocalizations should also have been favoured. Thus the eavesdropping hypothesis predicts that soft vocalizations will show specialized acoustic features, and that these features will be ones that limit transmission distance. A test of this prediction was carried out by Ręk (2013) in corncrakes. When Ręk (2013) played soft calls and loud calls from a loudspeaker at equal amplitudes and re-recorded them at a distance of 40 m, the re-recorded soft calls had lower signal-to-noise ratios than did the re-recorded loud calls. Thus soft calls degraded more rapidly than loud calls with distance, as predicted by the eavesdropping hypothesis. As illustrated by this study, transmission studies provide another method for testing the eavesdropping avoidance hypothesis; the test has the disadvantage of being somewhat indirect, but the advantage that it tests a prediction that is not specific to a particular class of potential eavesdroppers. More studies of this type, with additional species, would be valuable.

Imperfect Reliability and Individual Consistency

Another significant finding from studies of reliable aggressive signalling in song sparrows is that the reliability of signals is imperfect (Searcy, Anderson, Ballentine, & Nowicki, 2013). Theory suggests that signals should be reliable on average, which means some level of imperfection is expected. However, usually the variation in reliability is in the form of deception, or overstating the aggressive signal (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). The surprising result that has emerged from multiple studies on song sparrows is the opposite of this expectation: undersignalling, an aggressive individual failing to signal reliably, is much more prevalent than the more typical form of deception, which is oversignalling (Akçay et al., 2013; Searcy, Anderson, et al., 2013). A few theoretical models have incorporated the possibility of undersignalling (sometimes called the 'modest' strategy) and found that it may be evolutionarily stable (Botero, Pen, Komdeur, & Weissing, 2010; Johnstone & Norris, 1993; Searcy, Anderson, et al., 2013), but these models have yet to be tested in the field.

The prevalence of the undersignalling phenomenon may also be partially explained by the eavesdropping avoidance hypothesis. Under this hypothesis, conspicuous signals are costly because of eavesdropping by other individuals which should lead to the evolution of inconspicuous signals such as soft song. If the costs of being eavesdropped upon are high enough and if the detection risk is still marginally higher when singing soft song than when not singing at all, then would-be honest signallers may be selected to forego singing and become undersignallers.

Another interesting finding is that both aggressive signalling and aggressive behaviours are individually consistent in song sparrows (Akçay, Campbell, & Beecher, 2014; Anderson et al., 2012; Hyman, Hughes, Searcy, & Nowicki, 2004; Nowicki, Searcy, Krueger, & Hughes, 2002). Furthermore, a recent study in song sparrows suggests that at least some of the variation in reliable signalling (via soft song and wing waves) reflects consistent differences between individuals: in repeated trials over several months some individuals consistently undersignalled while others consistently oversignalled relative to their aggression levels (Akçay et al., 2014). Whether these consistent individual differences in signalling strategies reflect adaptive variation is an open question.

Seasonal Variation in Soft Song Production

A final finding worth considering is that use of soft song may vary seasonally in a systematic pattern (Maddison, Anderson, Prior, Taves, & Soma, 2012). Seasonal variation was first revealed in a study of a song sparrow population from British Columbia, Canada, where Maddison et al. (2012) found that song sparrows use significantly more soft songs in response to intrusions during the nonbreeding season (December) than during the breeding season (June–July). Maddison and colleagues reasoned that soft song production may be higher in December because of decreased leaf cover at that time compared to June and July, making the birds potentially more visible to aerial predators. This possibility would be consistent with the predator version of the eavesdropping avoidance hypothesis. We evaluated this idea further by taking a closer look at soft song rates in the data set reported by Akçay et al. (2014) that also shows a seasonal effect. In this data set, however, the proportion of soft songs within the total amount of singing was highest in September, October and January, intermediate in February and lowest in May, during the breeding season (Fig. 2). Because leaf cover is highest in September and October and lowest in January and February, these results suggest that the increased risk of predation does not completely explain the seasonal variation in soft song.

The proportionally increased levels of soft songs may instead be explained by the fact that during the nonbreeding season, males are under relaxed pressure to sing for females, leading to increased rates of soft song compared to loud song in the nonbreeding season. This idea is consistent with the competing functions hypothesis, which posits that loud song is better adapted as a mating signal. Related to this fact is that during the nonbreeding season, the songs of song sparrows show structural changes and individual notes show reduced stereotypy (Smith, Brenowitz, Beecher, & Wingfield, 1997), which may lead to the songs losing some of their appeal as a mating signal.

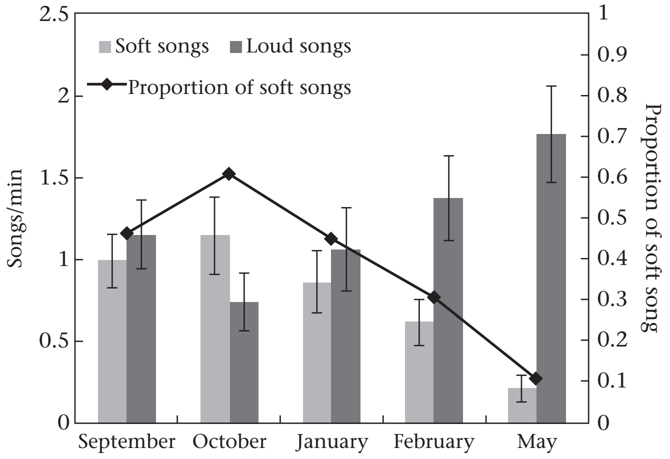

Figure 2. Soft and loud songs in response to simulated territorial intrusions (without a taxidermic mount) throughout autumn, winter and spring in the Seattle, WA population. Values are means ± SE.

CONCLUSIONS

We have reviewed a series of hypotheses proposed to answer two questions concerning reliable soft signals of aggressive intent. The first, why soft, question does not appear to have a convincing answer as of yet. Of the potential answers to the question of why low amplitude is so often a characteristic of aggressive signals in birds, none is supported by direct evidence, and two of the hypotheses (competing costs and vulnerability handicap) have logical difficulties. We believe further attention is warranted, however, for the remaining two, the eavesdropping avoidance and readiness hypotheses. Two experimental tests of the eavesdropping avoidance hypothesis gave negative results, addressing the possibilities that soft vocalizations are adapted to avoid eavesdropping by (1) predators and (2) conspecifics (Searcy & Nowicki, 2006). Weighing against this negative evidence are the findings on signal transmission of calls in corncrakes, showing that soft calls are adapted for lower transmission in features additional to low amplitude (Ręk, 2013). Given this new positive evidence, and the attractive logic of the hypothesis, further tests of this hypothesis are in order. In particular, the predator version of the eavesdropping avoidance hypothesis would benefit from stronger tests of whether use of soft song changes in response to predator presence (for instance with a taxidermic mount of a predator or a live decoy). The only empirical evidence thus far available on the conspecifics version of the eavesdropping avoidance hypothesis is negative on the proposed benefit, but that evidence is specific to the case in which a territory owner attempts to conceal from other males that he is interacting with an intruder. Different answers might be obtained with respect to owners concealing interactions from females, or intruders concealing interactions from neighbouring territory owners, and so forth.

The second, why reliable, question seems to have a more solid answer in the form of a receiver retaliation cost: although early tests of this hypothesis failed to find evidence for higher levels of aggression to soft calls compared to loud calls, later experimental tests for the most part support the predicted pattern of receiver response (Anderson et al., 2012; Ręk & Osiejuk, 2011; Templeton et al., 2012; Xia et al., 2013). More studies in taxa other than songbirds are still needed to test whether aggressive soft vocalizations are also maintained by receiver retaliation costs in other species.

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