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## Is bird song a reliable signal of aggressive intent?

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### Abstract

In this commentary, we discuss recent experiments on the reliability of bird song as a signal of aggressive intent during territorial conflicts. We outline relevant theoretical views on honest signaling, highlighting the vulnerability handicap hypothesis as a possible explanation for soft song's reliability in predicting attack. We also sketch possible methods of testing whether soft song agrees with key predictions of the vulnerability handicap hypothesis. Finally, we suggest possible empirical refinements that may be useful in future studies of signals of intent, both in birds and in animals broadly. In particular, we argue that future studies of intent should strive to incorporate the following elements into their experimental design: (1) multi-modal signal components, (2) interaction dynamics, and (3) minimal time intervals. Simulated exchanges using dynamically-interactive models may provide a powerful means of incorporating all three of these design features simultaneously.

### Keywords

Animal communication; Honest signaling; Intentions; Soft song; Vulnerability

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Early ethologists largely took for granted that animal signals conveyed reliable information. Game-theoretical and gene-centered ways of thinking, however, identified a key problem with this tacit assumption of “honesty”: a mutant that produced signals outside of their appropriate contexts might accrue fitness gains, at a cost to its conspecifics, and could, consequently, spread through the population (Maynard Smith 1974; Dawkins and Krebs 1978). The stability of communication systems in the face of selective pressures favoring dishonesty was thus recognized as an important problem. Currently, this “honesty problem” is a vibrant area of research among biologists (reviewed in Maynard Smith and Harper 2003; Searcy and Nowicki 2005).

Signals of intent in conflicts provide a case in which honesty is especially problematical. These signals may convey information about a signaler's aggressive motivation or about what the signaler will do next, such as its likelihood of attacking (Hauser and Nelson 1991; Laidre 2005). Unlike signals that are somehow constrained or costly to produce, signals of intent appear highly susceptible to bluffing, and so their predicted level of reliability has been controversial. Indeed, John Maynard Smith (1982, p. 4) once argued that “natural selection will act on the sender to minimize the amount of information transmitted about intentions” (Maynard Smith 1982, p. 4).” Nevertheless, signals of intent could, theoretically, be stabilized by costs imposed by receivers, either through a receiver-retaliation rule or a vulnerability handicap (Vehrencamp 2000), or through individual recognition and targeted skepticism (van Rhijn and Vodegel 1980; Silk et al. 2000; Laidre 2005).

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Recent studies of bird song have provided support for some of these hypothetical stabilizing mechanisms, suggesting that some aspects of song may convey reliable information about a bird's aggressive intentions. Burt et al. (2001), Vehrencamp (2001), Molles and Vehrencamp (2001), and Vehrencamp et al. (2007), for instance, have provided evidence that song-type matching is associated with more aggressive behavior and that it is stabilized by receiver retaliation: playing back matching song types to territorial owners causes them to approach the playback speaker faster and more closely than in response to other song types. A shortcoming of these studies is that their measurement of reliability hinges on a proxy of aggressiveness: how near the bird comes to the speaker. Definitive evidence that bird song conveys information about aggressive intent would necessitate showing that these signals predict actual physical attack; yet, studies based solely on playback provide no opportunity for signalers to attack anything. Recent experiments by Searcy et al. (2006) have been designed to fill this gap. In a study with male song sparrows, these researchers provided opportunities for signalers to attack a model, and they examined whether any song parameters in fact predicted subsequent attack.

Searcy et al.'s experimental design used a taxidermic mount to control for variation in receiver response and to provide a constant stimulus for each bird they tested. The mount was revealed after first evoking a song reply from a live territorial male in response to playback. The researchers then evaluated if any parameters of the bird's song predicted outright attack of the model. One parameter, low amplitude "soft song", was a strong predictor: in the 1-min interval before an attack opportunity, the number of soft songs performed was significantly higher for birds that attacked compared to those that did not (their Fig 2a). Such a trend also existed for a lengthier, 5-min interval where it approached significance more closely than any other song parameter measured (their Fig 1a). Despite these results, Searcy et al. conclude that, in song sparrows, song "for the most part contained little or no information on the signaler's likelihood of attack" (p. 238). Nor; nor do they discuss possible reasons for the differential reliability of soft song compared to other kinds of song, like type-matching, which failed to reliably predict attack. In this commentary, we provide a potential explanation—based on the vulnerability handicap hypothesis—for why soft song, but not other song parameters, displayed robust reliability. We further identify potentially important design limitations in Searcy et al.'s experimental setup that might account for the poorer reliability that was found for song parameters other than soft song. Finally, we suggest how, with specific modifications in design, the reliability of signals of intent could be more rigorously tested, both for bird song and for other animal signals.

## Soft song and the vulnerability handicap hypothesis

The vulnerability handicap hypothesis predicts that if signals differ in the level of performance risk they entail, then the riskiest signals will be the most effective (Enquist et al. 1985). Reliability is stabilized under these conditions since because only strongly motivated signalers that are prepared to attack will be willing to perform the riskiest displays, which make them susceptible to injury (Zahavi 1977). Empirical support for this model has derived from observational studies in birds (Popp 1987; Waas 1991a), where risk and effectiveness correlated strongly. Recent experimental manipulations in crustaceans (Laidre 2007/2007) have further shown that signalers display in accordance with their vulnerability to injury. These studies all concerned visual communication, but vulnerability handicaps might also exist in other modalities, like the acoustic domain.

Soft song in song sparrows appears to be a strong candidate as a vocal vulnerability handicap: due to its low amplitude and hence limited sound propagation, soft song should only be detectable at relatively close distances, where retaliation would be most likely. Moreover, it would seem difficult for birds to cheat using soft song: even if soft song is given from long distances, where a signaler could easily escape, the signal itself is so quiet that its effectiveness

would be much reduced. Interestingly, Searcy et al.'s results showed that mean distance to the speaker was a significant predictor of attack, with birds that eventually attacked exhibiting closer proximity. Also, more recent analyses in the same species (Anderson et al. 2007) found that playbacks of soft song repelled receivers more than playbacks of normal song [though the effect was not statistically significant ( $P = 0.08$ , Table 1) perhaps due to the sample size being smaller, only 15 birds compared to 95 in Searcy et al.'s study]. Together, these preliminary results are consistent with the vulnerability handicap's prediction that risky signals will be more effective. The reason for soft song's robust reliability may thus be that this signal unavoidably advertises how close a bird is willing to come to its rival and hence how likely it is to attack<sup>1</sup>.

Future experiments could further test the vulnerability handicap model by examining the limits on cheating, in which birds gave somewhat louder versions of soft song from far off positions where they could more readily escape attack. For instance, birds' behavior could be evaluated in response to two playback conditions (1) the loudest versions of soft song played back from afar versus (2) the softest versions of soft song played back from closer up, both playbacks arranged so that they attained the same amplitude upon reaching the target. If birds perceive the two conditions as different, perhaps using sound distortion cues, then this would suggest that potential cheaters could be hampered. In particular, the vulnerability handicap hypothesis would predict that condition (2) would elicit higher levels of both retreat and attack in receivers, such that the more effective signals would also be more costly in terms of retaliation.

Given that soft song appears, by necessity, to provide reliable information about aggressive intent, why were other parameters, like song-type matching, not indicative of a bird's intention to attack? These latter signals appear to be conventional signals (Vehrencamp 2001), not vulnerability handicap signals, and below, we discuss three features of Searcy et al.'s experimental setup that might have masked the relationship between these signals and the sender's subsequent attack behavior.

1. Postural displays and multi-modal signaling: The communicative salience of signals can reflect a mix of modalities, like visual and vocal. The importance of such multi-modal signaling has been shown across several taxa where the meaning of signals in one modality can change depending on whether components from another modality are present or not (Partan and Marler 1999). In little blue penguins, for instance, displays that are accompanied by calls are more effective in deterring opponents than the same displays performed silently (Waas 1991a). Many passerines possess rich postural repertoires alongside their diverse song repertoires (e.g., house sparrows: Summers-Smith 1963, Figs. 1–6), and these postural elements may accompany the acoustic ones during signaling. According to Nice (1943, p. 157) song sparrows, in particular, exhibit several threat postures or “methods of intimidation” prior to aggressive interactions and interposed in song bouts (e.g., the “puff–sing–wave”–wave” display). However, these potentially significant signal components were not integrated into Searcy et al.'s design.

Searcy et al.'s model was “posed in a normal, perched posture” (p. 236), not a threat pose. Birds that encountered the model might therefore have perceived an incongruity between its vocal and visual signals, the former signals advertising strong aggressiveness and the latter signals a lack thereof. Consequently, signalers may have reacted anomalously, which could account for the “enormous variability” that Searcy et al. observed and had difficulty explaining (p. 239). For example, birds that sang

<sup>1</sup>Even if birds ultimately use soft song to minimize eavesdropping (McGregor and Dabelsteen 1996), this ‘external constraint’ has a nontrivial effect: it enforces honesty. In other words, if birds are to prevent third parties from overhearing an interaction, they are compelled to use a signal whose form intrinsically precludes any advantage to bluffing.

with strong aggressiveness, but then failed to attack the model may have regarded the model's visually non-aggressive posture as no longer threatening enough to warrant attack. Conversely, birds that sang with weak aggressiveness, but then did attack the model may have experienced increased motivation to fight upon seeing that the intruder posed a less formidable challenge, having not even assumed a pre-fight posture.

2. Interaction dynamics: Although Searcy et al. emphasized the importance of receiver-response contingencies and the need to control them, their view that using a model "obviates these problems" (p. 235) may not be accurate from a bird's perspective. A stationary, non-interactive model does not contribute to the natural escalation process that occurs in conflicts between live animals. Such an escalation process, in which opponents proceed from lower- to higher- risk behavior, can be an essential prelude to actual attack (e.g., Waas 1991a). Indeed, one of the chief reasons observational studies of natural interactions are an important complement to experimental studies using models is that, in natural interactions, both participants can dynamically escalate and de-escalate, responding contingently to one another's moment-to-moment behavior. In Searcy et al.'s experiments, their model's unnatural lack of movement and engagement may have been perceived as submissive: the model failed to fly toward or even approach the bird it was supposedly threatening. Birds may have consequently reacted abnormally and inconsistently to the model, some attacking and some not, regardless of how they initially sang. It is even possible that the model was not universally perceived as the source of the original playback threat, since its immobile state would be more consistent with its being a peaceful roamer that happened to land in the same region where the playback originated.
3. Time intervals: The time intervals between signal production by live birds and Searcy et al.'s measurement of subsequent behavior was relatively long (either 1- min or from 5- up to 20- min). This temporal separation likely provided many opportunities for intervening distractions, as Searcy et al. acknowledge. Indeed, the significance of the soft song results only materialized in the shorter, 1-min interval. Prior studies attempting to measure intent have focused on the very next behavior a signaler performs, usually within seconds after the receiver has responded to its signal (e.g., Waas 1991b, Laidre 2005). This technique can help minimize the variability induced by external factors.

## Design modifications and conclusion

Based on the three issues raised above, specific experimental design improvements might be made as follows. With respect to multi-modal signaling, models could be placed in poses consistent with the song playbacks (e.g., an intense threat pose with type-matching playback). With respect to interaction dynamics, using a stationary, inanimate model may best be avoided. This is because natural selection has presumably molded animals to be exceedingly sensitive to subtle movements and behavioral changes exhibited by their conspecifics. As such, animal communication researchers attempting "experimental dialogues" may need to employ models that can be finely controlled and moved in coordinated sequences that are contingent upon their subjects' behavior (e.g., Patricelli et al. 2006 with an avian robot). Future experiments on intent could therefore try attaching a model to a simple pulley system. Then, after a live bird arrived in the vicinity and produced its song, the model could either be propelled a set distance toward the bird, simulating further escalation, or pulled backwards the same distance, simulating retreat. The former condition would be expected to facilitate detecting a tighter relationship between certain signal parameters and the sender's subsequent attack of the model (see e.g., Waas 1991b). Finally, with respect to time intervals, the aforementioned interactive-model experiments might permit a more straightforward measure of intent than using time windows

of predetermined length: researchers could quantify the sender's very next act after they had moved their model in response to the sender's signal.

We conclude by re-iterating the intention behind this commentary, less it be misinterpreted: we do not wish to detract from Searcy et al.'s interesting study, which is a useful contribution to the field of animal communication. More studies like Searcy et al.'s that employ novel experimental designs to examine the information content of signals are vital to furthering our understanding of communicative complexity. Moreover, Searcy et al.'s results on soft song merit more follow-up work, especially innovative attempts at investigating a possible vocal vulnerability handicap. The main conclusion of Searcy et al.'s study, however—that song does not reliably signal birds' intent to attack—is, at best, premature. Future studies will be better tailored to decipher the information about intent that bird song potentially encodes if they (1) control for multi-modal signal components, like postural displays, (2) combine a dynamically-moveable avian model with interactive song playback, and (3) measure intent as the very next act that the sender performs after a model has been moved towards it. No doubt, further work will identify yet more crucial factors that researchers must be sensitive in controlling if we are to fully decode the myriad subtle meanings of bird song and other animal signals.

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