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A test of a hierarchical signalling model in song sparrows

William A. Searcy [a,*], Adrienne L. DuBois [a], Karla Rivera-Cáceres [a], Stephen Nowicki [b]

[a] Department of Biology, University of Miami, Coral Gables, FL, U.S.A.
[b] Department of Biology, Duke University, Durham, NC, U.S.A.

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Hierarchical signalling may be a common adaptation for aggressive signalling. In this strategy an animal progresses through a series of discretely different signals of escalating level of threat before eventually proceeding to physical aggression. A model of such hierarchical aggressive signalling has been proposed for song sparrows, *Melospiza melodia*, in which a core part of the sequence is: song type match → soft song → attack. The model predicts that song type matching is a strong predictor of soft song, but only a weak predictor of attack. We used a two-part playback design to test these predictions, with an initial edge playback from just off the subject's territory using a song type that the subject could match, followed by a centre playback from a speaker placed well within the territory. Each male was tested twice with this design. We found that matching the edge playback did not predict soft song production at the centre. A second strong threat, wing waving, was actually negatively associated with matching. Matching the edge playback also was not associated with physical measures of aggression such as approach and latency to approach. Thus, this particular model of hierarchical aggressive signalling was not supported for our study population. Song type matching in our study population may have some function not associated with aggressive signalling to the matched individual, or no function at all.

Many animals possess multiple aggressive displays (Hazlett & Bossert 1965; Andersson 1980; Waas 1990; Bradbury & Vehrencamp 2011). A logical explanation for the evolution of multiple, seemingly redundant threat displays is that each communicates a different level of aggressive intention, so that the repertoire as a whole allows for a graded series of threats. A simple extension of this hypothesis is that animals tend to progress upwards through such a graded series as an aggressive encounter continues, successively switching to displays that are more and more reliable as predictors of attack. A functionally similar outcome can be accomplished by varying properties of a single display, as cricket frogs, *Acris crepitans*, do by lengthening their calls (Wagner 1989). We reserve the term 'hierarchical signalling' for cases in which animals escalate aggressive signalling using a progression of discretely different signals. Here we test a specific model of hierarchical signalling proposed for song sparrows, *Melospiza melodia*, by Beecher and colleagues (Beecher & Campbell 2005; Searcy & Beecher 2009; Akçay et al. 2013).

Various animals have been suggested to employ a hierarchy of aggressive signals, including mammals (Clutton-Brock & Albon 1979; Bartos et al. 2007), birds (Popp 1987; Waas 1991a, b), insects (Chen et al. 2002; Egge et al. 2011) and spiders (Fowler-Finn & Hebets 2006). Red deer, *Cervus elaphus*, provide a classic example. Two displays are especially prominent during aggressive contests between red deer stags: roars and parallel walks. Typically, roars lead into parallel walks, and parallel walks lead into fights (Clutton-Brock & Albon 1979). A similar system has been described for fallow deer, *Dama dama*, with groans substituted for roars, and here it has been explicitly shown that both displays predict aggression, with one (parallel walks) being a stronger predictor than the other (Bartos et al. 2007). Another classic example involves little blue penguins, *Eudyptula minor*. Among a large variety of agonistic displays given by these birds (Waas 1990, 1991b), two vocalizations, growls and hisses, appear to form a hierarchy of threat. When confronted with a model penguin at their burrows, lone males that give growls are more likely to attack than males that remain silent, and males that give hisses are more likely to attack than those that growl (Waas 1991a). Thus hisses are a more reliable threat than growls.

The model of hierarchical aggressive signalling in song sparrows emerged from work by Beecher and colleagues on matching behaviours. In song type matching, one individual replies to another

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* Correspondence: W. A. Searcy, Department of Biology, University of Miami, Coral Gables, FL 33124, U.S.A.
E-mail address: wsearcy@miami.edu (W. A. Searcy).

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with the song type that the latter has just sung. Matching at above chance levels has been demonstrated for a number of species of songbirds (Hinde 1958; Falls 1985; Rogers 2004; Burt & Vehrencamp 2005; Gammon et al. 2008; Price & Yuan 2011) and has been suggested to be an aggressive signal (Krebs et al. 1981). Stoddard et al. (1992) found that western song sparrows matched playback of self song types and shared stranger song types at frequencies far above chance levels. Sharing of whole song types is more frequent in western populations of song sparrows (Hill et al. 1999; Wilson et al. 2000) than in eastern ones (Hughes et al. 1998; Stewart & MacDougall-Shackleton 2008), but eastern individuals are nevertheless able to interact through matching by using partially shared song types (Hughes et al. 1998; Burt et al. 2002; Anderson et al. 2005). Some evidence suggests that type matching is an aggressive signal in song sparrows: males are more likely to match stranger than neighbour songs (Stoddard et al. 1992) and are in general more aggressive towards strangers than neighbours (Stoddard et al. 1990); males are more likely to match neighbours early in the breeding season when relationships are more aggressive than later when relationships are more relaxed (Beecher et al. 2000); and males that stay on a type match in response to playback show stronger aggressive reactions than males who switch to a different song type or stop singing (Burt et al. 2001; Akçay et al. 2013).

In a second matching behaviour, termed ‘repertoire matching’ by Beecher et al. (1996), one male replies to another not with the song type that the other has just sung, but with another shared song type. Beecher et al. (1996) found that male song sparrows reply to playback of neighbour song with a shared song type at much higher than expected frequencies, regardless of whether the playback song is itself shared. Male song sparrows respond less aggressively to playback of a repertoire match than to playback of a song type match (Burt et al. 2001), suggesting that a repertoire match is a lower level of threat than is a type match. Beecher & Campbell (2005) showed that song sparrows de-escalate more quickly in response to playback of unshared songs than to a repertoire match, implying that singing an unshared song is an even lower level of threat than is repertoire matching. Together these results suggest a hierarchical system with three levels of threat (Beecher & Campbell 2005): unshared song → repertoire match → song type match.

One problem with this model is that evidence is equivocal on whether even the highest level of threat in the hierarchy actually predicts physical aggression. Although type matching has been positively correlated with aggressive measures such as approach to a playback speaker in some studies (Burt et al. 2001; Vehrencamp 2001), in others no such correlations were found (Beecher et al. 2000; Anderson et al. 2005). In a study of eastern song sparrows, Searcy et al. (2006) found that type matching did not predict attack on a taxidermic mount: 19.5% of 41 males that matched attacked the mount, compared with 22.2% of 54 males that did not match. In contrast, production of low-amplitude soft songs proved to be a strong predictor of attack, as has since been found in other songbirds as well (Ballentine et al. 2008; Hof & Hazlett 2010).

The confluence of the soft song and matching results led to an expanded model of hierarchical signalling in song sparrows (Searcy & Beecher 2009). Here the basic progression of escalation is hypothesized to be: unshared song → repertoire match → type match → soft song → attack. The full progression could only be used in signalling to others whose repertoires are known by the subject; strangers would have to be dealt with using the latter part of the progression: type match → soft song → attack. Under this hypothesis, type matching is an aggressive signal, in that it predicts aggressive escalation, but it is only a weak predictor of attack, weaker in particular than soft song. Matching should instead be a strong predictor of an escalation in aggressive signalling, and specifically of soft song production.

Here we test the hierarchical signalling hypothesis using a two-part playback design. The first part consists of playback of a shared song type from just outside a subject’s territory. This ‘edge playback’ gives the subject an opportunity to type match, but does not allow close approach to the speaker. Once the subject has replied to the edge playback, playback switches to a second speaker placed well within the subject’s territory. This ‘centre playback’ gives the subject the opportunity to approach the speaker and produce soft songs. The hierarchical signalling model predicts that type matching of the edge playback should be associated with higher soft song production for the centre playback.

METHODS

The experiment was carried out in Crawford County, Pennsylvania, U.S.A., during May and June of 2011 and 2012. The study was approved by the Institutional Animal Care and Use Committee of the University of Miami (Protocol 11-073). Subjects were 40 male song sparrows holding territories on the edges of old fields in state gamelands and mown lawns in parks. Prior to playback trials we mapped territories and recorded partial repertoires from each subject (with a Marantz 660 digital recorder and a Realistic omnidirectional microphone in a Sony Parabolic Reflector-330). Males were identified during playback trials using previously applied colour bands ($N = 10$), or by using spectrograms to determine whether whole songs given during trials were found in our prior recordings ($N = 27$). A small subset ($N = 3$) did not have identities confirmed by either method, but in this population territories remain stable during the height of the breeding season (Hughes & Hyman 2011), so territorial males can also reliably be identified by location.

We tested males with a two-part playback design in which they were first presented with a short bout of song playback at the edge of their territories, providing an opportunity to song type match, followed by playback at the centre of the territory, providing an opportunity to produce soft song and other aggressive behaviours. The design simulated an intrusion by one male onto another’s territory; such intrusions are fairly common in song sparrows (Akçay et al. 2012) and often involve the intruder singing both before and during the intrusion (Kramer & Lemon 1983; Bower 2000). The first part of the playback trial consisted of a single song type from the male’s own repertoire broadcast repeatedly from just outside the subject’s territory: the ‘edge playback’. Male song sparrows typically sing with ‘eventual variety’, repeating one song type many times before switching to another (Nowicki et al. 1994). The playback stimulus was recorded from the subject male to guarantee that the subject could potentially type match the edge playback. Response to self songs in song sparrows is similar to response to stranger song both in terms of matching (Stoddard et al. 1992) and aggression (Searcy et al. 1981), and self songs have been used extensively in prior experiments on matching in song sparrows (Stoddard et al. 1992; Anderson et al. 2005; Akçay et al. 2011, 2013). Playback songs were stored as WAV files and broadcast at a rate of six songs/min at 83–87 dB SPL (measured with a B&K Precision 32A sound level meter) using an iPod Touch and an iMainGo X portable speaker. During playback the speaker was housed in an open box lined with polyurethane composite foam (Acoustical Surfaces, Inc., Chaska, MN, U.S.A.), with the open end directed towards the subject’s territory. This set-up reduced the amplitude of the playback behind and to the sides of the speaker, lowering responses by males other than the subject. If the subject did not