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Author(s): William A. Searcy, Rindy C. Anderson, Stephen Nowicki

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William A. Searcy · Rindy C. Anderson ·
Stephen Nowicki

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Abstract A central question in animal communication research concerns the reliability of animal signals. The question is particularly relevant to aggressive communication, where there often may be advantages to signaling an exaggerated likelihood of attack. We tested whether aggressive signals are indeed reliable signals of attack in song sparrows (*Melospiza melodia*). We elicited aggressive signaling using a 1-min playback on a male's territory, recorded the behavior of the male for 5 min, and then gave him the opportunity to attack a taxidermic mount of a song sparrow associated with further playback. Twenty subjects attacked the mount and 75 did not. Distance to the speaker was a significant predictor of attack for both the initial recording period and the 1 min before attack. For the initial recording period, none of the measures of singing behavior that we made was a significant predictor of attack, including song-type matching, type-switching frequency, and song rate. For the 1-min period immediately before attack, only the number of low amplitude "soft songs" was a significant predictor of attack. Although most aggressive signals contained little information on attack likelihood, as some models suggest should be the case, the unreliability of these signals was not caused by convergence of individuals on a single signaling strategy, as those models argue should occur.

Keywords Communication · Bird song · Aggressive signals · Reliability · *Melospiza melodia*

Introduction

The reliability of animal signals is a major issue in research on animal communication (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). The issue is particularly critical with respect to aggressive signaling. Honest signaling provides a cheap and efficient mechanism for settling aggressive encounters, but a signaling system that is honest about aggressiveness is vulnerable to a form of cheating in which individuals exaggerate their aggressiveness to win contests that they would otherwise lose (Maynard Smith 1974, 1979; Dawkins and Krebs 1978). Game theoretical models have shown that signals can be honest about aggressive intentions under certain conditions, for example if the most aggressive and effective signals are also the most costly (Enquist 1985; Grafen 1990). Even in such models, the power of an aggressive display to predict a signaler's behavior may be modest, for example because the behavior of the signaler after a signal is contingent on external factors such as the receiver's response (Enquist 1985). Moreover, other models have shown that aggressive signaling systems can be evolutionarily stable with a mix of honest and dishonest signals, with some individuals benefiting from producing signals that exaggerate their aggressive intentions (Adams and Mesterton-Gibbons 1995; Számadó 2000). Thus, theory allows a range of outcomes with respect to reliability in aggressive signals, and empirical investigation is needed to establish the true state of affairs with respect to a specific signaling system.

In this study, we describe an experimental investigation of the reliability of aggressive vocal signals in song sparrows (*Melospiza melodia*). Song sparrows exhibit a number of the singing behaviors that have been hypothesized to be aggressive signals. Among these is song-type matching, a behavior in which an individual replies to a rival with a song type that is identical (or highly similar) to the one a rival has just sung. Krebs et al. (1981) suggested that matching is a graded signal of aggressiveness, in the sense that "a territory holder signals the likelihood of attacking an intruder by the probability of matching the intruder's song." In support of this view, Krebs et al. (1981)

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W. A. Searcy (✉) · R. C. Anderson
Department of Biology, University of Miami,
Coral Gables, FL 33124, USA
e-mail: wsearcy@miami.edu
Fax: +1-305-2843039

S. Nowicki
Department of Biology, Duke University,
Durham, NC 27708, USA

demonstrated in great tits (*Parus major*) that a correlation exists between percent matching to playback and indirect measures of aggression such as latency to respond and close approach to the speaker. In song sparrows, Vehrencamp (2001) showed that males that matched a playback song spent more time close to the speaker than males that did not match; again, time spent close to a playback speaker is usually assumed to indicate aggressiveness. Beecher et al. (2000), however, found no difference in aggressiveness between male song sparrows that did or did not type match, with aggressiveness measured by a combination of approach and display. To our knowledge, no one previously has tested whether matching predicts actual attacks, as we do in this study.

Another signaling option available to songbirds with repertoires of song types is to vary the frequency of switching between types. The frequency of switching increases in aggressive contexts in a number of species of songbirds (Falls and D'Agincourt 1982; D'Agincourt and Falls 1983; Simpson 1985), including song sparrows (Kramer and Lemon 1983; Kramer et al. 1985; Searcy et al. 2000), suggesting that rapid switching is an aggressive signal. Type-switching frequencies did not, however, predict attack on a caged intruder in male bobolinks (*Dolichonyx oryzivorus*) (Capp and Searcy 1991). Song sparrows also possess another level of song variation, song-type variants, which are relatively minor variations of individual song types. Although the differences between song variants are small compared to the differences between song types (Podos et al. 1992), male song sparrows are responsive to this level of variation (Stoddard et al. 1988; Searcy et al. 1995). In aggressive contexts, song sparrows increase variant-switching frequencies even more consistently than they increase type-switching frequencies (Searcy et al. 2000). Thus, variant switching may also be an aggressive signal.

The rate at which songs are sung is a third aspect of singing behavior that has been suggested to be a signal of attack likelihood (Falls 1969). Song rates depend on male condition in many songbirds (Davies and Lundberg 1984; Gottlander 1987), and we might expect aggressiveness also to covary with condition. Song rates have been shown to increase in aggressive situations in some songbird species (Falls 1969), but such an increase does not occur reliably in song sparrows (Peters et al. 1980).

A final singing behavior that might convey aggressiveness is the production of low amplitude "soft song." Low amplitude songs have been noted in several songbird species as occurring during aggressive encounters, courtship, or both (Dabelsteen et al. 1998). In song sparrows, soft song is typically observed only during aggressive encounters (Nice 1943).

The association of particular singing behaviors with aggressive situations suggests that these behaviors are signals that convey aggressive intent, but taken by itself, such an association is equally compatible with the displays having a submissive meaning. Submissive displays, like aggressive ones, are given during agonistic encounters rather than during foraging, resting, and so forth, and thus

their frequencies also can be expected to increase during encounters relative to their background frequencies. To support the interpretation that a signal conveys aggressive intent, it is necessary to demonstrate not merely that the signal is produced in an aggressive context, but that the signal actually predicts subsequent aggressive behavior by the signaler. Tests of this more stringent criterion must overcome several methodological challenges.

Much of the early work on the reliability of aggressive signals focused on avian postural displays given during contests over food. These studies concluded that some displays do predict aggression (Stokes 1962; Dunham 1966; Andersson 1976), but Caryl (1979) criticized the evidence on the grounds that the associations between displays and aggression were generally quite weak. One explanation for the weakness of the associations found in these studies is that all were observational studies of natural interactions, which looked at whether a signal was followed by a certain signaler behavior without controlling for the response of the receiver. One way around this problem is to use a statistical analysis that controls for receiver's response (Popp 1987); another is to replace the natural receiver with an experimental stimulus whose behavior can be controlled. This latter approach has been taken by experiments in which aggressive displays are elicited by playback of vocal signals, for example in frogs (Wagner 1992; Burmeister et al. 2002) and birds (Vehrencamp 2001). Playback studies typically introduce a new problem, however, in that outright attacks are no longer possible, so that one must examine associations between display and some weaker proxy of aggressive response, such as approach to the speaker. A final problem seen in some studies of aggressive communication is that the periods in which display and aggressive acts are measured may be partially or totally overlapping, so that some of the displays may be given after the aggression that they "predict" (e.g., Krebs et al. 1981; Husak 2004). In our work, we employed a design that obviates these problems: we used an artificial stimulus to remove the problem of contingencies based on receiver's response; we provided a taxidermic model as part of the stimulus so that outright attacks would be possible; and we maintained a temporal separation between signals and aggression so that displays we analyzed would always precede the behavior that they predicted.

Materials and Methods

Playback experiments

Playback trials were carried out in Crawford County, Pennsylvania, U.S.A. during May and June of 2000, 2001, and 2002, between the hours of 6:00 and 11:00 AM. Each subject was a territorial male song sparrow that had previously been recorded; no male was tested more than once. We used one of the subject's own song types in constructing each playback tape so that the subject could match the playback if he chose to do so. Recordings were made using a Realistic omnidirectional microphone in a

Sony PBR-330 parabola and either a Sony TCM 5000 or a Sony TC D5M tape recorder. Choice of the one song type to be used in playback for each subject was made on quality of recording. Playback songs were digitized at 25 kpts/s using 'SIGNAL' software (Engineering Design, Berkeley, CA, USA) and then dubbed onto a Sony TCM 5000 tape recorder.

Before a trial, we placed a Nagra DSM speaker face up on the ground well within the subject's territory. On top of the speaker, we placed a stand holding a taxidermic mount of a song sparrow, posed in a normal, perched posture. The mount was concealed by a cloth at the start of the trial. A microphone was positioned 10–15 cm from the mount and was connected via cable to one channel of a Sony TC D5M stereo tape recorder. This recorder was operated by one of two observers, who stood 15–20 m from the speaker/mount setup; this observer also held a Sony PBR-330 parabola with a Realistic omnidirectional microphone plugged into the second channel of the stereo recorder. The second observer narrated the behavior of the subject throughout the trial, and this commentary was recorded, along with the bird's vocal behavior. The narration included estimates of the subject's distance from the speaker, aided by markers at 0.5, 1 m, 4, and 8 m on either side of the speaker. The narration also noted bouts of wing waving, a stereotypic wing movement used as a postural display in aggressive contexts by song sparrows and other passerines (Nice 1943). Finally, the observer classified all songs produced by the subject as loud or soft. We subsequently tested the accuracy of the same observer (WAS) in making amplitude judgments, using playback of a variety of song sparrow song types at predetermined amplitudes that ranged in 3 dB intervals from 89 to 57 dB SPL (measured at 1 m with a GenRad 1565D sound level meter). The observer was tested in the field, in the same habitat used in the trials, and at the same observation distance. Seventy-eight percent of songs played at 78–80 dB and 100% of songs played at ≥ 80 dB were classified as loud, whereas 74% of songs played at 75–77 dB and 100% of songs played at ≤ 74 dB were classified as soft.

A trial began with 1 min of playback of the subject's chosen song type, presented at a rate of one song per 10 s and at an intensity of approximately 85 dB SPL measured at 1 m with a GenRad 1565-D sound level meter. The first playback song was used to mark the beginning of the trial; recording began some seconds before this. At 5 min and 45 s, the mount was revealed by removing the cloth cover remotely. At 6 min, a second playback bout began, using the same playback song, presented at the same rate but at a lower amplitude (approximately 79 dB SPL at 1 m). This second playback lasted 2 min. The subject was given until 20 min into the trial to attack the mount. An attack was considered to be any direct physical contact of the subject with the mount; sometimes, this contact consisted of a brief pounce, but more typically a subject landed on the mount and pecked vigorously at its head and body. Trials were ended at the point of attack. We continued recording until an attack occurred or 20 min was reached, whichever came first.

Analysis

The entire narration of each trial was transcribed onto a flow sheet divided into 10 s intervals. Subsequent analysis concentrated on two time periods: the initial recording period and the 1 min before attack. The initial recording period began with the first playback song and lasted for 5 min. For those subjects that attacked, the 1 min before attack was the 1 min preceding the 10 s interval in which the attack occurred. For those subjects that did not attack, a corresponding 1-min period was chosen by matching each of the 20 attackers to three to four of the 75 non-attackers drawn randomly without replacement, and analyzing the same 1-min period in the non-attacker as in the matched attacker. We compared the resulting 75 1-min periods for non-attackers to the 20 1-min periods for attackers in an unpaired analysis, thus using each subject once in the analysis. All songs recorded during the initial recording period and the 1 min before attack were digitized and viewed as spectrograms using Syrinx sound analysis software (J. M. Burt; <http://syrinxpc.com>). From the spectrograms, we determined for each song whether it (a) matched the playback song type, (b) represented a change in song type relative to the preceding song produced by the subject, and (c) represented a change in song-type variant relative to the preceding song. We also made spectrograms of enough songs produced by the subject after the onset of the second playback to determine whether the subject matched that playback with the first song he produced or the first song type to which he switched. The random expectation of matching was assumed to be 12.5%, the probability of meeting the matching criteria found in previous control trials with this population (Anderson et al. 2005).

From the spectrograms and narration, we abstracted six measures of display for both the initial recording period and the 1 min before attack. These measures were: (1) matches—the number of songs that matched the playback type; (2) soft songs—the number of soft songs produced by the subject; (3) total songs—the total number of songs, including matches and soft songs; (4) type-switching frequency—the number of type switches divided by the number of opportunities to switch types (Searcy et al. 2000); (5) variant-switching frequency—the number of variant switches divided by the number of opportunities to switch variants (Searcy et al. 2000); and (6) wing waves—the number of bouts of wing waving. Sample sizes are slightly smaller for results on the two switching variables, which could not be calculated in cases in which the denominator (opportunities to switch) was 0. Mean distance to the speaker during a period was estimated by first calculating the mean of the estimates made within each 10-s block and then averaging across all 10-s blocks.

Several of the response variables were not normally distributed and could not be normalized using standard transformations. We therefore first analyzed each variable by comparing attackers to non-attackers using a nonparametric procedure, the Mann Whitney *U* test. We also analyzed the response variables, separately and together, with discriminant function analysis, because this procedure

allows the possibility of discriminating between groups using combinations of variables. Discriminant function analysis assumes a multivariate normal distribution but is considered to be robust against departures from this assumption (Klecka 1975). We do not consider a result to be significant unless significance is supported by both the parametric and nonparametric tests. Because we use six different display measures to test the general hypothesis that display predicts attack, we use a Dunn–Sidák-corrected alpha level of 0.0085 for those tests.

Results

Initial recording period

Of the 95 males that we tested, 20 attacked the mount within the allotted time and 75 did not. For the 5-min initial recording period, none of the six display measures differed significantly between attackers and non-attackers according to Mann–Whitney U tests (Fig. 1). When entered separately into discriminant function analyses with attack as the categorical variable, none of the display measures was a significant predictor of attack. The model with number of soft songs was the only display variable that significantly predicted attack (Wilks' lambda=0.951, $F=4.75$, $N=95$, $P=0.032$) but not lower than the Dunn–Sidák-corrected alpha value.

Mean distance to the speaker during the initial recording period was lower for attackers (4.3 ± 0.5) than non-attackers (8.4 ± 0.7), and this difference was significant by a Mann–Whitney U test ($P=0.005$). Mean distance to the speaker also was a significant predictor of attack in a discriminant function analysis (Wilks' lambda=0.907, $F=9.58$, $N=95$, $P=0.0026$). In the jack-knifed classification matrix, distance to speaker correctly predicted 16 of 20 attacks (80%) and 44 of 75 failures to attack (59%). In a forward stepwise discriminant function analysis, no display variable entered after distance, that is, none had additional predictive power once distance was taken into account.

One minute before attack

For the 1 min before attack, the number of soft songs was significantly higher for those males that attacked than for those that failed to attack (Fig. 2a), and this difference remained significant with the Dunn–Sidák correction. None of the other five display measures differed significantly between attackers and non-attackers (Fig. 2b–f). In single variable discriminant function analyses, the number of soft songs was the only display variable that significantly predicted attack (Wilks' lambda=0.912, $F=8.95$, $N=95$, $P=0.0035$). In the jack-knifed classification matrix, the number of soft songs correctly predicted 12 of 20 attacks

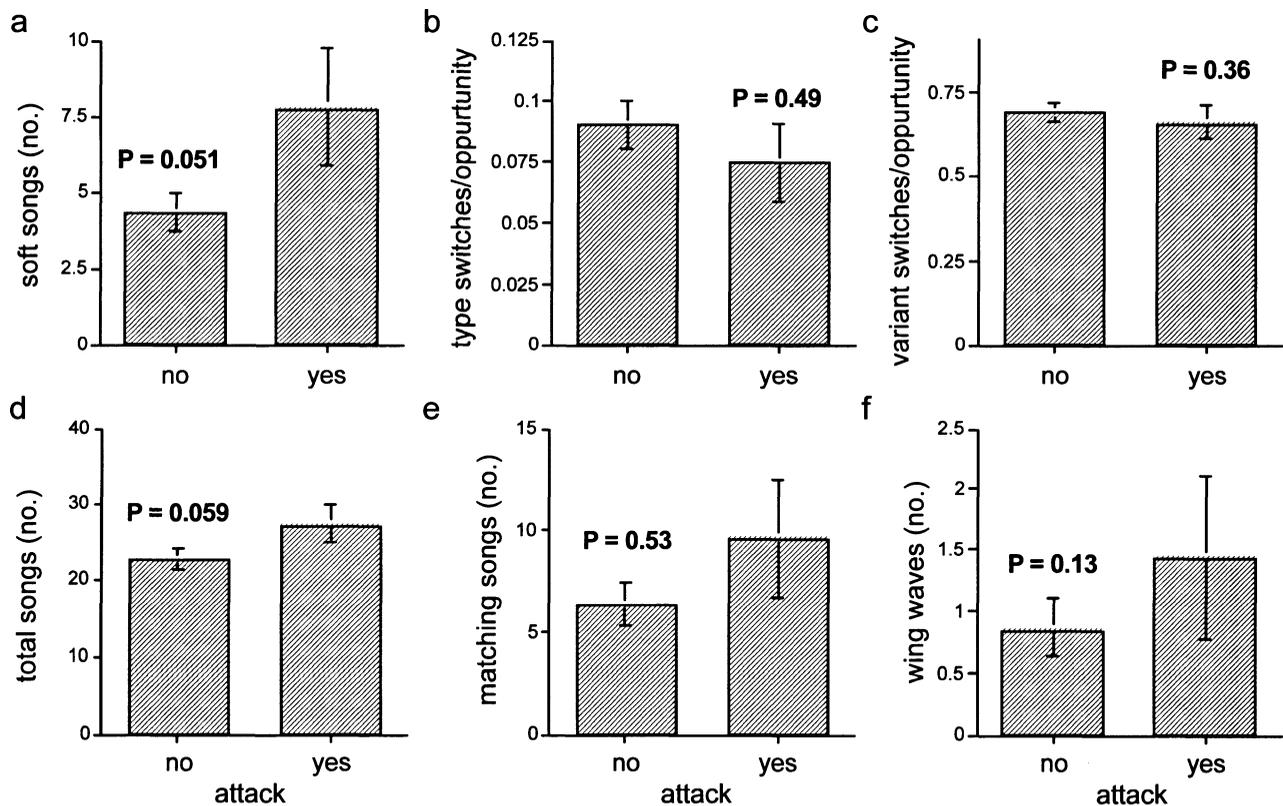


Fig. 1 Displays given during the initial 5-min recording period by those male song sparrows that subsequently did or did not attack the mount. **a** Low amplitude “soft songs” [Mann–Whitney $U=540.5$, N_1 (attackers)=20, N_2 (non-attackers)=75]. **b** Type-switching frequen-

cy ($U=814.5$, $N_1=20$, $N_2=74$). **c** Variant-switching frequency ($U=840$, $N_1=20$, $N_2=74$). **d** Total songs ($U=543$, $N_1=20$, $N_2=75$). **e** Matching songs ($U=687$, $N_1=20$, $N_2=75$). **f** Bouts of wing waving ($U=610.5$, $N_1=20$, $N_2=75$). Histograms show means \pm SE

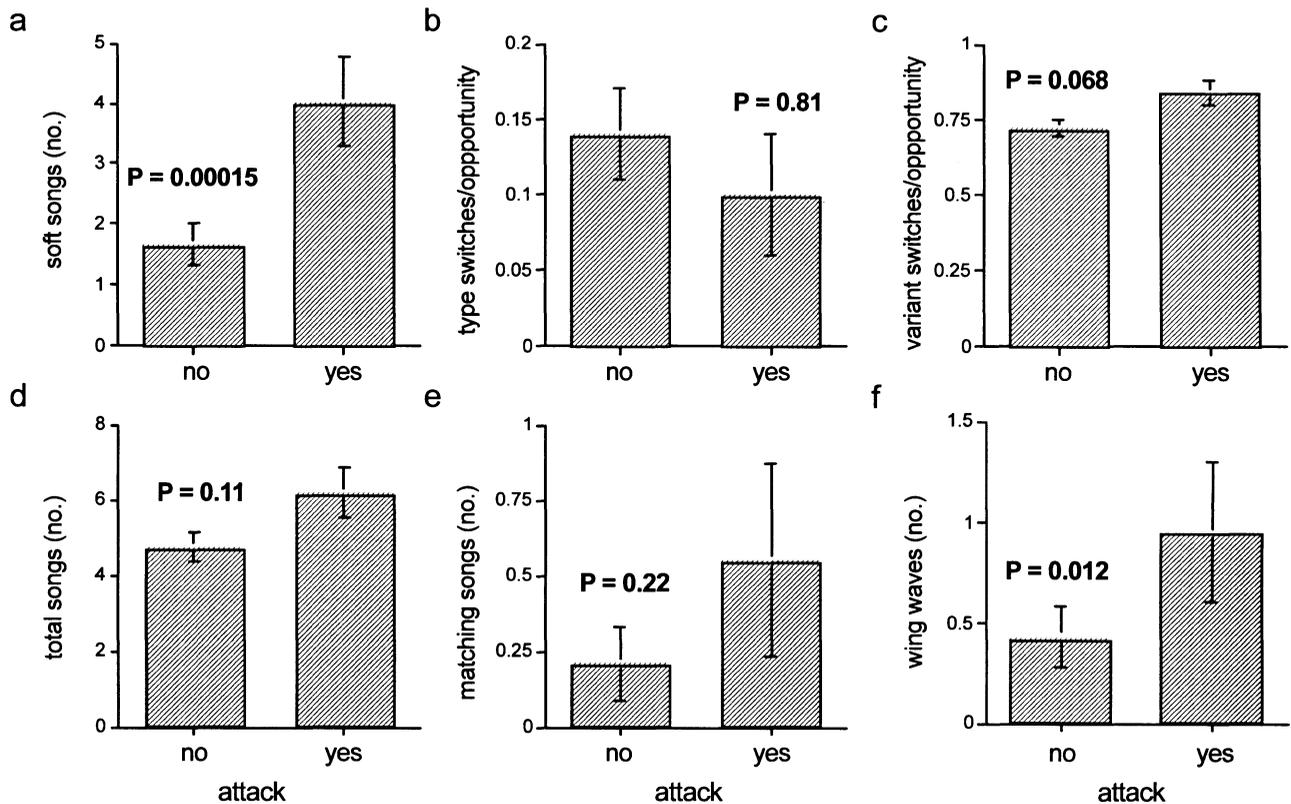


Fig. 2 Displays given during 1-min period before attack by those male song sparrows that subsequently did or did not attack the mount. **a** Low amplitude “soft songs” [Mann Whitney $U=370.5$, $N_1(\text{attackers})=20$, $N_2(\text{non-attackers})=75$]. **b** Type-switching frequen-

cy ($U=619$, $N_1=20$, $N_2=60$). **c** Variant-switching frequency ($U=416$, $N_1=20$, $N_2=57$). **d** Total songs ($U=574$, $N_1=20$, $N_2=75$). **e** Matching songs ($U=685$, $N_1=20$, $N_2=75$). **f** Bouts of wing waving ($U=561$, $N_1=20$, $N_2=75$). Histograms show means \pm SE

(60%) and 58 of 75 failures to attack (77%). None of the other display measures was a significant predictor of attack when entered alone, nor did any of these measures provide significant additional predictive power when entered in a forward discriminant function analysis together with the number of soft songs.

Mean distance to the speaker during the 1 min before attack was lower for attackers (1.8 ± 0.8) than for non-attackers (8.0 ± 1.1), and this difference was significant by a Mann Whitney U test ($P=0.00021$). Distance during the 1-min periods was also a significant predictor of attack in a discriminant function analysis (Wilks' lambda=0.916, $F=8.58$, $N=95$, $P=0.0043$). The P value, however, was not as low as for soft songs, and when both distance and soft songs were entered in a forward stepwise discriminant function analysis, only the soft song variable was retained in the model.

Matching

Song-type matching is often treated as a categorical variable (males match or do not match), rather than as a continuous variable as above. The criterion usually applied in a categorical analysis is that a subject is considered to have matched if the first song type he produces after the playback starts, or the first song type he switches to

matches the playback. Using these criteria, 41 of 95 subjects (43%) matched the first playback, significantly more than expected by chance ($\chi^2=81.4$, $df=1$, $P<0.0001$). However, the percentage of matchers attacking (19.5%) was not higher than the percentage of nonmatchers attacking (22.2%). Only 11.6% (11 of 95) of the subjects matched the second playback, quite close to the random expectation of 12.5%. The percentage of matchers attacking (18.2%) was again not higher than the percentage of nonmatchers attacking (21.4%).

Discussion

The vocal and visual displays produced by song sparrows during an aggressive encounter for the most part contained little or no information on the signaler's likelihood of attack, even though each of the displays has been labeled at one time or another as an aggressive signal. Proximity to the stimulus did consistently predict attack across both recording periods; this result has methodological implications, as it supports the widespread practice of using distance to a loudspeaker or other stimulus as a proxy for aggressiveness. Proximity cannot, however, be considered a signal if signals are defined as “characteristics fashioned or maintained by natural selection because they convey information to other organisms” (Otte 1974). In other

words, position of one individual relative to a second may convey information to the second, but position is not a characteristic that has evolved to convey that information.

The conclusion that most signals, given in an aggressive context, do not contain information about attack seems particularly surprising with respect to type matching, given that song-type matching has been shown to be associated with correlates of aggression such as time of season and approach to a perceived intruder in both song sparrows (Beecher et al. 2000; Vehrencamp 2001) and other species (Krebs et al. 1981). The explanation may be that type matching is a signal of attention rather than aggression, as originally suggested by Bremond (1968), and is predictive of milder forms of escalation than attack (Burt et al. 2001).

The one display that we found to contain reliable information about attack likelihood is low amplitude soft song. Soft song was not only a better predictor of attack than any of the other displays we observed, but it was also a better predictor than proximity during periods immediately before attack. Soft song was in general associated with close proximity, but we also observed soft song produced as far as 30 m from the mount; conversely some males gave broadcast song from within 0.25 m of the mount, or approached the mount closely while not singing at all. Thus, soft song production does provide information independent of proximity.

Soft song may seem an odd signal to use to convey the highest level of aggressive intent, in that the signal's form (i.e., its low amplitude) appears to be antithetical to its function (intimidating rivals). One explanation for the use of soft song in aggressive encounters is that the low intensity of the signal may benefit the signaler by minimizing eavesdropping (McGregor and Dabelsteen 1996). McGregor (1993) defines eavesdropping as occurring when "individuals not directly involved in a signaling interaction... none the less gather information from it." Recent studies demonstrate that eavesdropping in this sense occurs in territorial birds and other animals (Oliveira et al. 1998; Otter et al. 1999; Peake et al. 2001). Territorial males that use low amplitude songs when confronting intruders might benefit through concealing such interactions from eavesdropping females, who might lower their assessment of males that have difficulties with intruders, and from eavesdropping males, who might be tempted to trespass on territories whose owners appear to be preoccupied already with an intruder. We have recently shown, however, that neighboring males do not trespass less when we simulate an interaction between a soft owner and a loud intruder than when we simulate a loud owner/loud intruder interaction (Searcy and Nowicki unpublished).

Despite our finding that soft song predicts attack, the overall impression from our results is that display behavior in song sparrows provides surprisingly little information on attack likelihood. This conclusion is consistent with theoretical predictions made by Maynard Smith (1974, 1979) and Caryl (1979), but our results do not necessarily support their reasoning. These authors suggested that signals would contain little information on attack likelihood because most or all signalers would converge on the

most aggressive signaling pattern, which would be the most effective behavior in terms of winning encounters. Our observations provide little evidence for such convergence. What we observed instead was enormous variability in the signals given among the males that attacked as well as among those that did not. Variability in display by those that do not attack can be explained by the hypothesis that some individuals follow a dishonest signaling strategy of exaggerating their aggressiveness; variability in display by those that do attack requires a different explanation.

Another explanation for why signals produced in an aggressive context are poor predictors of attack invokes the role of contingency. By contingency, we mean the dependence of the signaler's behavior on events that occur in the time interval between the signal and the subsequent behavior. Effects of contingency are built into many signaling models; for example, in the first model of Enquist (1985), a signal that is completely honest about the intention to attack is followed by attack in only half the instances it is given, because in the other half, the receiver submits immediately, making an attack unnecessary. In our experiments, we minimized the influence of this type of contingency by employing an inanimate opponent whose behavior did not vary between trials. Other types of contingencies are still possible, however; for example, a signaler might give an aggressive signal and then, before it can attack, be distracted by the behavior of its mate, a territorial neighbor, a predator, and so forth. The fact that in our results attack was better predicted by signals given in the 1 min just before attack than by signals given earlier (in the initial recording period) is consistent with the contingency hypothesis, as the shorter the interval between signal and subsequent behavior, the less opportunity there is for contingency to intervene. As with the dishonest signaling hypothesis, however, contingency seems a better explanation for why some individuals give aggressive signals and then fail to attack, than of why some individuals attack without giving aggressive signals beforehand.

In previous work, we have found that territorial male song sparrows show considerable variation in aggressive and singing rates in response to intrusions, and that individuals are consistent from trial to trial in these behaviors (Nowicki et al. 2002; Hyman et al. 2004). Individuals are also consistent between trials in the proportion of soft songs that they produce (Searcy and Nowicki unpublished). Individual behavior is consistent across trials despite the contingencies that arise in successive trials, implying that contingencies cannot be blamed entirely for the weakness of the associations between signaling and subsequent aggression. Individual strategies seem to include all possible combinations of weak signaling/weak aggression, strong signaling/weak aggression, weak signaling/strong aggression, and strong signaling/strong aggression. Despite the variability in individual strategies, almost all males are able to maintain their territories, which suggests that the fitness payoffs of the different strategies are similar. We suggest that multiple strategies of equal overall fitness exist for both signaling and aggression, and that the equivalence of these strategies is one major reason that the

relationship between signals and subsequent aggression is inherently weak.

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References

- Adams ES, Mesterton-Gibbons M (1995) The cost of threat displays and the stability of deceptive communication. *J Theor Biol* 175:405–421
- Anderson RC, Searcy WA, Nowicki S (2005) Partial song matching in an eastern population of song sparrows, *Melospiza melodia*. *Anim Behav* 69:189–196
- Andersson M (1976) Social behaviour and communication in the great skua. *Behaviour* 58:40–77
- Beecher MD, Campbell SE, Burt JM, Hill CE, Nordby JC (2000) Song-type matching between neighbouring song sparrows. *Anim Behav* 59:21–27
- Bremond JC (1968) Recherches sur la semmatique et les elements vecteurs d'information dans les signaux acoustiques du rouge-gorge (*Eriothacus rebecula* L.). *Terre Vie* 2:109–220
- Burmeister SS, Ophir AG, Ryan MJ, Wilczynski W (2002) Information transfer during cricket frog contests. *Anim Behav* 64:715–725
- Burt JM, Campbell SE, Beecher MD (2001) Song type matching as threat: a test using interactive playback. *Anim Behav* 62:1163–1170
- Capp MS, Searcy WA (1991) Acoustical communication of aggressive intentions by territorial male bobolinks. *Behav Ecol* 2:319–326
- Caryl PG (1979) Communication by agonistic displays: what can games theory contribute to ethology? *Behaviour* 68:136–169
- D'Agincourt LG, Falls JB (1983) Variation of repertoire use in the eastern meadowlark, *Sturnella magna*. *Can J Zool* 61:1086–1093
- Dabelsteen T, McGregor PK, Lampe HM, Langmore NE, Holland J (1998) Quiet song in birds: an overlooked phenomenon. *Bioacoustics* 9:80–105
- Davies NB, Lundberg A (1984) Food distribution and a variable mating system in the dunnoek, *Prunella modularis*. *J Anim Ecol* 53:895–912
- Dawkins R, Krebs JR (1978) Animal signals: information or manipulation? In: Krebs JR, Davies NB (eds) *Behavioural ecology*. Blackwell, Oxford, pp 282–309
- Dunham DW (1966) Agonistic behavior in captive rose-breasted grosbeaks, *Pheucticus ludovicianus* (L.). *Behaviour* 27:160–173
- Enquist M (1985) Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Anim Behav* 33:1152–1161
- Falls JB (1969) Functions of territorial song in the white-throated sparrow. In: Hinde RA (ed) *Bird vocalizations*. Cambridge Univ. Press, Cambridge, pp 207–232
- Falls JB, D'Agincourt LG (1982) Why do meadowlarks switch song types? *Can J Zool* 60:3400–3408
- Gottlander K (1987) Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca*: causes and consequences. *Anim Behav* 35:1037–1043
- Grafen A (1990) Biological signals as handicaps. *J Theor Biol* 144:517–546
- Husak JF (2004) Signal use by collared lizards, *Crotaphytus collaris*: the effects of familiarity and threat. *Behav Ecol Sociobiol* 55:602–607
- Hyman J, Hughes M, Searcy WA, Nowicki S (2004) Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour* 141:15–27
- Klecka WR (1975) Discriminant analysis. In: Nie NH, Hull CH, Jenkins JG, Steinbrenner K, Bent DH (eds) *SPSS: Statistical Package for the Social Sciences*. McGraw-Hill, New York, pp 434–467
- Kramer HG, Lemon RE (1983) Dynamics of territorial singing between neighboring song sparrows (*Melospiza melodia*). *Behaviour* 85:198–223
- Kramer HG, Lemon RE, Morris MJ (1985) Song switching and agonistic stimulation in the song sparrow (*Melospiza melodia*): five tests. *Anim Behav* 33:135–149
- Krebs JR, Ashcroft R, Van Orsdol K (1981) Song matching in the great tit *Parus major* L. *Anim Behav* 29:918–923
- Maynard Smith J (1974) The theory of games and the evolution of animal conflicts. *J Theor Biol* 47:209–221
- Maynard Smith J (1979) Game theory and the evolution of behaviour. *Proc R Soc Lond B* 205:475–488
- Maynard Smith J, Harper D (2003) *Animal signals*. Oxford Univ. Press, Oxford
- McGregor PK (1993) Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Phil Trans R Soc Lond B* 340:237–244
- McGregor PK, Dabelsteen T (1996) Communication networks. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell Univ. Press, Ithaca, New York, pp 409–425
- Nice MM (1943) Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerines. *Trans Linn Soc NY* 6:1–328
- Nowicki S, Searcy WA, Krueger T, Hughes M (2002) Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *J Avian Biol* 33:253–259
- Oliveira RF, McGregor PK, Latruffe C (1998) Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc R Soc Lond B* 265:1045–1049
- Otte D (1974) Effects and functions in the evolution of signaling systems. *Ann Rev Ecol Syst* 5:385–417
- Otter K, McGregor PK, Terry AMR, Burford FRL, Peake TM, Dabelsteen T (1999) Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proc R Soc Lond B* 266:1305–1309
- Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2001) Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proc R Soc Lond B* 268:1183–1187
- Peters SS, Searcy WA, Marler P (1980) Species song discrimination in choice experiments with territorial male swamp and song sparrows. *Anim Behav* 28:393–404
- Podos J, Peters S, Rudnicki T, Marler P, Nowicki S (1992) The organization of song repertoires in song sparrows: themes and variations. *Ethology* 90:89–106
- Popp JW (1987) Risk and effectiveness in the use of agonistic displays by American goldfinches. *Behaviour* 103:141–156
- Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton Univ. Press, Princeton, NJ
- Searcy WA, Podos J, Peters S, Nowicki S (1995) Discrimination of song types and variants in song sparrows. *Anim Behav* 49:1219–1226
- Searcy WA, Nowicki S, Hogan C (2000) Song type variants and aggressive context. *Behav Ecol Sociobiol* 48:358–363

- Simpson BS (1985) Effects of location in territory and distance from neighbours on the use of song repertoires by Carolina wrens. *Anim Behav* 33:793–804
- Stoddard PK, Beecher MD, Willis MS (1988) Response of territorial male song sparrows to song types and variations. *Behav Ecol Sociobiol* 22:125–130
- Stokes AW (1962) Agonistic behaviour among blue tits at a winter feeding station. *Behaviour* 19:118–138
- Számádó S (2000) Cheating as a mixed strategy in a simple model of aggressive communication. *Anim Behav* 59:221–230
- Vehrencamp SL (2001) Is song-type matching a conventional signal of aggressive intentions? *Proc R Soc Lond B* 268: 1637–1642
- Wagner WE (1992) Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Anim Behav* 44:449–462