



Reliable aggressive signalling in swamp sparrows

BARBARA BALLENTINE*†, WILLIAM A. SEARCY* & STEPHEN NOWICKI†

*Department of Biology, University of Miami

†Department of Biology, Duke University

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Whether aggressive displays are reliable predictors of attack is an important, unresolved issue in animal communication research. Here we test the extent to which vocal and visual displays predict subsequent attack in territorial male swamp sparrows, *Melospiza georgiana*. A brief playback of swamp sparrow song was used to provoke aggressive signalling from a territorial male, and the subject's displays were recorded for 5 min. A taxidermic mount of a male swamp sparrow was then revealed, coupled with additional playback, and the subject was given 14 min to attack while we continued to record its displays. Of 40 subjects, nine attacked the mount and 31 did not. For both the initial recording period and the 1 min before attack, attackers produced significantly more low-amplitude 'soft songs' and more bouts of wing waving than did nonattackers. Attackers and nonattackers did not differ significantly in song type-switching frequency or in numbers of broadcast songs, matching songs, wheezes or rasps. In discriminant function analyses, soft song was consistently the display that best predicted subsequent attack. Different acoustic forms of soft song were found, all of which appeared to be equally aggressive. Combinations of displays predicted attack better than did single displays. The overall reliability of swamp sparrow displays as predictors of aggression was impressively high.

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Although aggressive signals have been studied extensively, the reliability of such signals remains poorly understood. As is true for almost any category of signals, the evolution of reliability in aggressive signals presents an apparent paradox (Searcy & Nowicki 2005). If receivers respond to aggressive signals as if they are honest, then exaggeration of aggressive intentions should be favoured, and signalling should evolve towards dishonesty (Maynard Smith 1974, 1979; Caryl 1979). If dishonesty becomes sufficiently widespread, however, receivers should evolve to ignore the signals, and once the signals are ignored, signallers should cease to give them. Game theory models demonstrate that honest signalling can be evolutionarily stable under the right conditions, for example, if signals are costly and the costs fall more heavily on some

individuals than on others (Enquist 1985; Grafen 1990). Other models, however, allow a stable mixture of reliability and dishonesty (Adams & Mesterton-Gibbons 1995; Számadó 2000; Rowell et al. 2006). Valid empirical tests of the reliability of aggressive signalling are rare, making it difficult to determine how well theory accounts for actual levels of signal reliability. Here we present an experimental analysis of aggressive signalling in swamp sparrows, *Melospiza georgiana*, designed to determine how well several kinds of signals given in aggressive contexts actually predict attack.

Signals are often assumed to be aggressive, in the sense of threatening aggressive escalation, simply because they are given in agonistic contexts. For example, males of some species of songbirds increase their rate of switching between song types during simulated intrusions on their territories (D'Agincourt & Falls 1983; Kramer et al. 1985; Simpson 1985; Searcy et al. 2000), and this pattern is taken as evidence that rapid switching is an aggressive signal. Evidence of this kind is ambiguous, however, because agonistic displays may signal an intention to de-escalate or stay put rather than to escalate, and all such signals should increase in frequency in aggressive contexts. In

Correspondence and present address: W. A. Searcy, Department of Biology, University of Miami, Coral Gables, FL 33124, U.S.A. (email: wsearcy@miami.edu). B. Ballentine is now at the Smithsonian Migratory Bird Center, National Zoological Park, 3001 Connecticut Avenue, NW, Washington, D.C. 20008, U.S.A. S. Nowicki is at the Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338, U.S.A.

other cases, signals have been suggested to be aggressive because they are given in the same time periods as aggressive acts (Krebs et al. 1981). A signal cannot be said to predict behaviour, however, if that signal occurs at the same time or after the behaviour it is said to predict.

Another approach to assessing reliability has been to record natural sequences of behaviour in aggressive encounters and test whether aggressive escalation follows certain displays more often than expected by chance. This approach has been taken in studying vocal and postural displays in birds (Stokes 1962; Dunham 1966; Andersson 1976; Nelson 1984; Waas 1991a; Hurd & Enquist 2001), mammals (Lair 1990; Laidre 2005) and crustaceans (Dingle 1969). A problem with this approach is that the behaviour of a signaller following a display often depends on the receiver's response, which weakens associations between display and subsequent behaviour. This problem can be reduced by statistically controlling for receiver response (Nelson 1984; Popp 1987). Another way to circumvent this problem is to use an experimental stimulus to elicit display and subsequent aggression, so that the behaviour of the stimulus is under the researcher's control. This approach has been used in playback experiments with frogs (Burmeister et al. 2002) and birds (Krebs et al. 1981), but again these studies suffer the problems of measuring display and aggressive behaviour concurrently rather than sequentially.

What is needed then are studies in which an experimental stimulus is used to elicit aggressive display and aggressive behaviour and in which a clear temporal separation is maintained between the displays that are measured and the aggressive behaviour that they predict. Waas (1991b) provides one such study with penguins. In a second example, Searcy et al. (2006) elicited aggressive display from territorial male song sparrows, *Melospiza melodia*, with song playback, recorded the subjects for 5 min, and then gave them the opportunity to attack a taxidermic mount of a conspecific male. One surprising result was that type matching and type switching, which had been proposed to be graded signals of aggression in songbirds (Krebs et al. 1981; Kramer & Lemon 1983), contained no information on attack likelihood. Instead, the only display behaviour to predict attack was low-amplitude 'soft song'. Low-amplitude singing has been observed in numerous species of songbirds (Dabelsteen et al. 1998; Morton 2000) and has been hypothesized to be an aggressive signal in some of these. Overall, the reliability of display in predicting attack was surprisingly low: among all the displays given, only soft song showed some predictive power, and combinations of displays were no better at predicting attack than were single displays.

This last result, that combinations of displays do not predict attack better than do single displays, raises the question of why song sparrows, like so many other species, use multiple aggressive displays rather than just one (Andersson 1980). Hypotheses originally proposed to explain the occurrence of multiple mating signals within a species (Møller & Pomiankowski 1993; Johnstone 1995) have been adapted to explain why multiple signals are used in aggressive signalling (Stuart-Fox et al. 2006). The 'multiple message hypothesis' suggests that each signal conveys a different kind of information; applied to

aggressive signalling, one signal might convey intention to attack, another might convey intention to retreat, a third, fighting ability, and so forth. The 'redundant signal hypothesis' suggests that several signals convey essentially the same information, but as there is some error in each signal, a signaller enhances the ability of receivers to assess him correctly by sending multiple signals. Finally, the 'unreliable signal hypothesis' proposes that many of the signals do not contain any valuable information. For aggressive signalling, this situation could arise through evolutionary cycles in which a series of new signals appear, each of which initially predicts escalated aggression, but which are all eventually corrupted by the spread of bluffing so that they become uninformative (Andersson 1980).

A primary goal of the present study was to use swamp sparrows to address these hypotheses on why animals have multiple aggressive displays. A second goal was to test the generality of some of the surprising results we found with song sparrows: that soft song is the most reliable aggressive signal and that matching and switching provide no information on attack likelihood. Given the paucity of studies that have experimentally measured the power of aggressive displays to predict attack, more such work is needed if we are to understand the evolution of signal reliability.

METHODS

The experiment was performed at Geneva Marsh in Crawford County, Pennsylvania, U.S.A. during May and June of 2006. Subjects were 40 territorial male swamp sparrows, 32 of which had been previously colour banded. Swamp sparrows have modest song repertoires, averaging 3.1 song types in this population (Ballentine et al. 2004). Males often share song types with neighbours, giving them the potential to interact via song type matching, but whether they match each other at above-chance frequencies has not been tested previously. During agonistic interactions, swamp sparrows produce two vocalizations in addition to song, which we term 'rasps' and 'wheezes' (Fig. 1). These may be the same as the 'zhrew' and 'buzz' notes, respectively, mentioned by Mowbray (1997). The most common postural display given by swamp sparrows in aggressive contexts is wing waving, a stereotyped movement in which a bird raises and vibrates one or both wings (Nelson & Marler 1989).

Experimental methods follow those used in Searcy et al. (2006), which can be consulted for additional details, including equipment specifications. Briefly, before a trial, we set a loudspeaker face-up on a portable support near the centre of the subject's territory. Trials were recorded on a stereo recorder, one channel of which was connected to a microphone attached to a 1.2-m pole that was fixed into the marsh next to the speaker. The other channel of the recorder was connected to a microphone in a parabola held by an observer who stood 15–20 m from the speaker. A second observer narrated the subject's behaviour, noting distance from the speaker (aided by flagging placed at 2, 4 and 8 m) as well as displays. This observer also noted whether songs were soft or normal in amplitude. In field tests with song sparrow song, this same observer

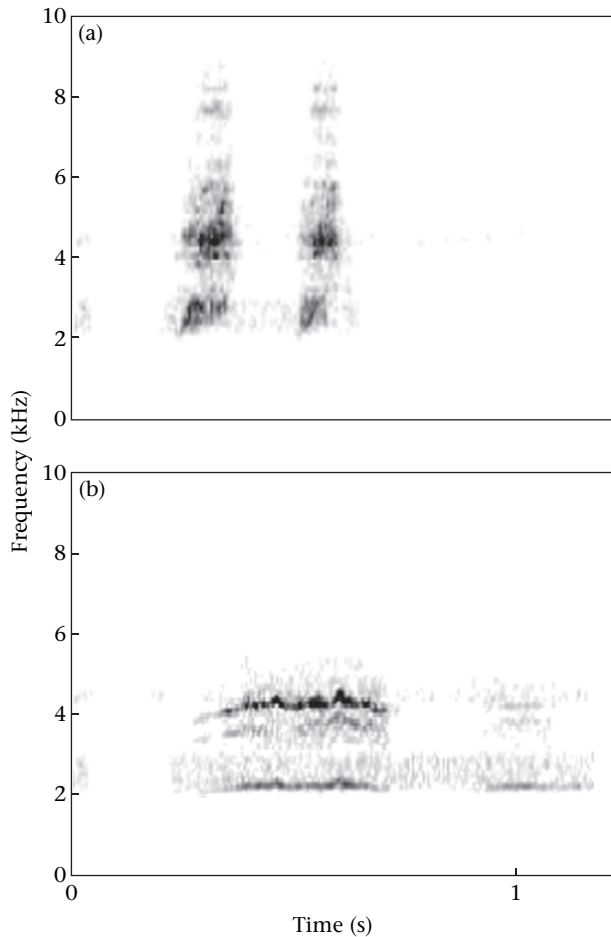


Figure 1. Spectrograms of two types of swamp sparrow aggressive vocalizations: (a) two rasps; (b) a wheeze.

(W.A.S.) is very accurate in discriminating songs of low and normal amplitude, whether produced naturally (Anderson 2006) or played back from a loudspeaker (Searcy et al. 2006). We did not perform parallel tests for swamp sparrow song, but note that the classification of songs as soft or normal was done before an attack occurred, and thus blind to whether the subject was an attacker or nonattacker (see below).

Figure 2 shows a timeline for a typical trial. A trial began with 1 min of playback of a swamp sparrow song chosen to match a song type in the subject's repertoire and recorded from a male distant enough in time and/or space to be unfamiliar to the subject. Songs were presented at approximately 85 dB SPL (measured at 1 m). At approximately 5 min 30 s, one observer moved forward to fix a taxidermic mount of a male swamp sparrow to the top of the 1.2-m pole that doubled as a microphone holder; this positioned the mount about 0.5 m above the speaker. The brief approach of this observer had little effect on the subjects. At 6 min, a second playback bout began with the same song type presented for 2 min at approximately 77 dB SPL. The trial ended at 20 min or when the subject attacked the mount. An attack was considered to occur when the subject either landed on the mount or flew directly at it, approaching within 1 m (a 'dive'). Nine subjects met one of these criteria ('attackers') and 31 did not

('nonattackers'). Although precisely estimating the approach distance during flight was difficult, ambiguous cases were rare: only one of the 31 nonattackers flew directly at the mount in a way that might have been classified as an attack (but in that case, approaching no closer than 5 m), whereas seven of the nine attackers either landed on the mount or dived at it multiple times.

Analysis concentrated on two time periods: (1) the 'initial recording period': the first 5 min of the trial, during which the mount was hidden so no attack was possible; (2) the '1 min before attack': defined for attackers as the 1-min interval before the 10-s interval in which the attack occurred. For nonattackers, we chose a 1-min period by pairing each of the nine attackers with three to four nonattackers drawn randomly without replacement, and analysing the same 1-min in the nonattacker as in the paired attacker. We obtained seven display measures for both time periods: (1) number of normal, broadcast songs; (2) number of soft songs; (3) number of bouts of wing waving; (4) type-switching frequency (number of song type switches divided by the number of opportunities to switch); (5) number of matches to the playback song (counting only broadcast songs); (6) number of wheezes; and (7) number of rasps. We also calculated a mean distance to the mount/speaker for each analysis period by averaging over 10-s blocks.

The statistical analysis compared attackers and nonattackers in an unpaired design, using each subject once in each comparison. Because some response variables were not normally distributed, we first used nonparametric Mann–Whitney *U* tests to compare attackers and nonattackers. We then used forward and backward stepwise discriminant function analyses to search for combinations of display variables that were superior to single variables in discriminating attackers from nonattackers (with the criteria for entering or removing variables set at $P = 0.15$). Although discriminant function analysis assumes that input variables follow a multivariate normal distribution, it is considered to be robust against departures from this assumption (Klecka 1975). We also ran discriminant function analyses containing distance in addition to the display measures. Switching frequency was not entered into the discriminant function analyses because of the large number of cases for which this variable could not be calculated (because the denominator was equal to 0). Spearman rank correlations (corrected for ties) were used to search for associations between display measures.

We also analysed song matching as a dichotomous variable. Males were classified as matching if the first song they produced after the first playback song matched the playback. The mean song repertoire size in this population is 3.1 song types (Ballentine et al. 2004), and the modal repertoire size is 3. We therefore considered the random chance of matching to be 1/3.

RESULTS

Initial Recording Period

The display measures for the initial recording period (before the mount was exposed) were largely independent

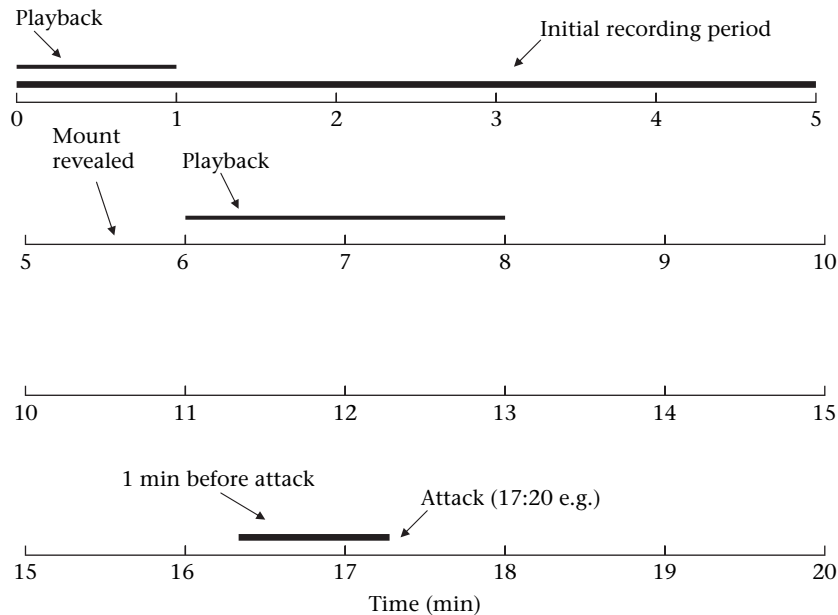


Figure 2. Timeline for an experimental trial. In this example, an attack occurs at 17 min 20 s into the trial.

of one another (Table 1). The only exception was that soft songs were positively associated with wing waves. These two displays were sometimes given simultaneously, but each was also often given alone.

The display that differed most dramatically between attackers and nonattackers during the initial recording period was soft song. The mean number of soft songs was roughly 10 times higher for the nine males that later attacked than for the 31 males that did not attack (Fig. 3), and this difference was highly significant (Mann–Whitney U test: $U = 29.5$, $N_1 = 9$, $N_2 = 31$, $P < 0.0001$). The number of wing-waving bouts was also significantly higher for attackers than nonattackers ($U = 54$, $P = 0.0002$; Fig. 3). Attackers and nonattackers did not differ in number of broadcast songs ($U = 109.5$, $P = 0.32$), number of matches ($U = 112$, $P = 0.32$), switching frequency ($U = 36$, $N_1 = 5$, $N_2 = 21$, $P = 0.12$), number of wheezes ($U = 134$, $P = 0.81$), or number of rasps ($U = 121.5$, $P = 0.44$). Mean distance to the mount/speaker was significantly lower during this period for attackers than nonattackers ($U = 36$, $P = 0.0008$).

In a forward stepwise discriminant function analysis with six display measures (songs, soft songs, wing waves,

matches, rasps and wheezes) as independent variables, soft songs entered first, followed by rasps. The discriminant function containing these two variables was a significant predictor of attack (Wilk's $\lambda = 0.647$, $F_{2,37} = 10.09$, $P = 0.0003$), and in a jackknifed procedure, correctly classified 56% of attackers and 90% of nonattackers (combined 83%). A backward stepwise discriminant function analysis with the same six display measures converged on the same model. In a forward discriminant function analysis with the six display measures plus distance, soft song entered first, followed by distance, and then rasps. The discriminant function containing these three variables was a significant predictor of attack (Wilk's $\lambda = 0.548$, $F_{3,36} = 8.544$, $P = 0.0002$), and in a jackknifed procedure, correctly classified 94% of nonattackers and 67% of attackers (88% total).

One Minute before Attack

Displays during the 1-min interval before attack were again mostly independent of one another (Table 1). There were three exceptions for this time period: soft songs were

Table 1. Spearman rank correlations between display measures for the 5-min initial recording period (above diagonal) and the 1 min before attack (below diagonal)

	Soft songs	Wing waves	Songs	Matches	Wheezes	Rasps	Switching
Soft songs		0.471**	0.006	-0.034	0.101	-0.178	0.139
Wing waves	0.783***		-0.235	0.108	0.230	0.101	-0.216
Songs	0.244	0.178		0.201	0.122	-0.277	0.137
Matches	-0.093	-0.173	0.609***		0.137	0.134	0.135
Wheezes	-0.079	-0.060	-0.131	-0.073		-0.001	-0.304
Rasps	-0.114	-0.086	-0.188	-0.105	0.698***		-0.304

Sample size is 40 for all correlations except those involving switching, for which $N = 25$. Switching is omitted for the 1 min before attack because of a high number of missing values. ** $P < 0.01$; *** $P < 0.0001$.

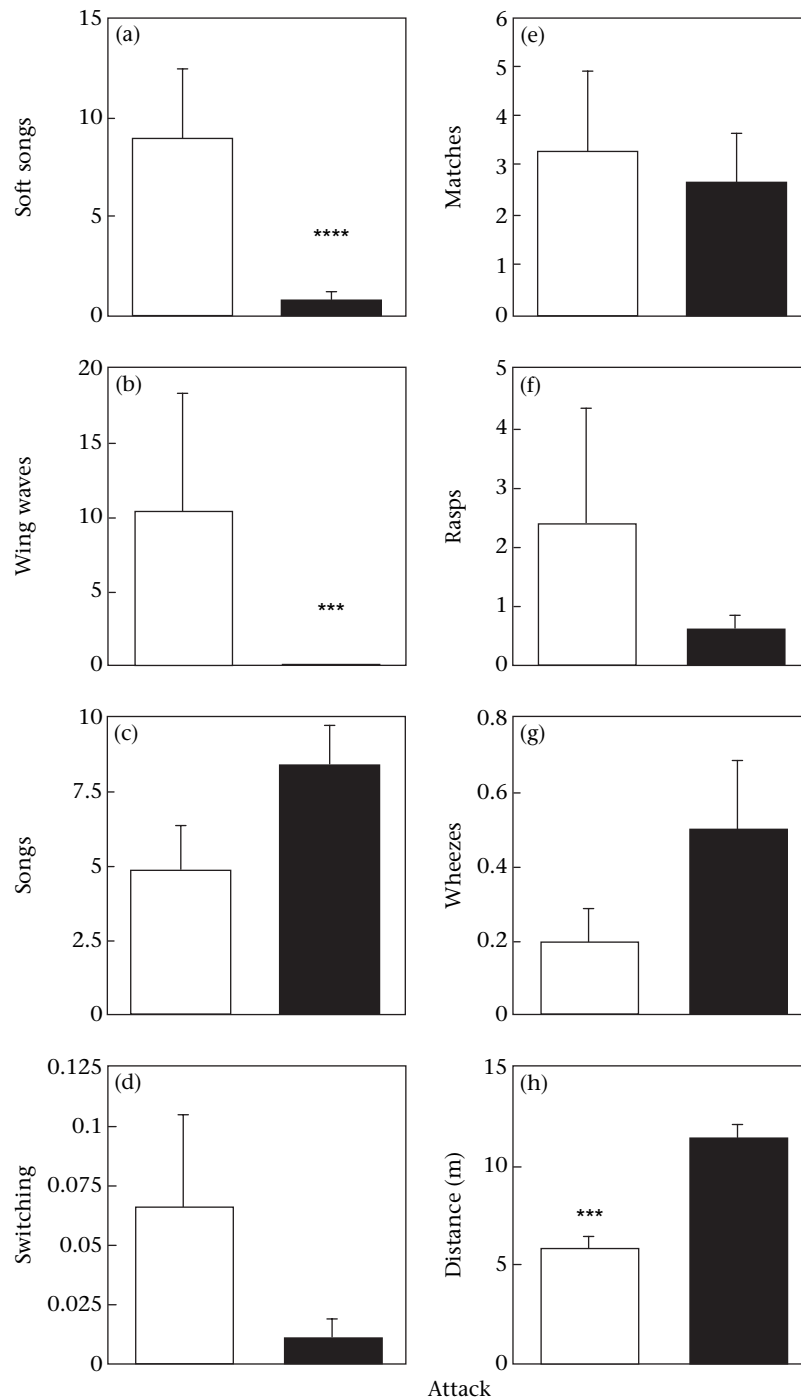


Figure 3. Behaviour during the initial 5-min recording period of males that did (□; $N = 9$) or did not (■; $N = 31$) later attack the mount. Means (\pm SE) for (a) numbers of soft songs, (b) number of bouts of wing waving, (c) number of songs, (d) switching frequency, (e) number of matching songs, (f) number of rasps, (g) number of wheezes and (h) distance to the speaker. *** $P < 0.001$; **** $P < 0.0001$.

again positively associated with wing waves, matches were positively associated with songs, and rasps were positively associated with wheezes.

The two displays that differed significantly between attackers and nonattackers were, as before, soft songs ($U = 55$, $N_1 = 9$, $N_2 = 31$, $P < 0.0001$) and wing waves ($U = 83$, $P = 0.0014$; Fig. 4). Attackers and nonattackers did not differ in broadcast songs ($U = 139$, $P = 0.99$),

matches ($U = 103.5$, $P = 0.12$), wheezes ($U = 135$, $P = 0.59$), or rasps ($U = 130.5$, $P = 0.44$). Switching frequency was dropped from this analysis because values were either missing or 0 for all but one subject. Attackers were significantly closer to the mount/speaker on average than were nonattackers ($U = 21.5$, $P = 0.0001$).

In a forward stepwise discriminant function analysis with the six display measures, soft songs entered the

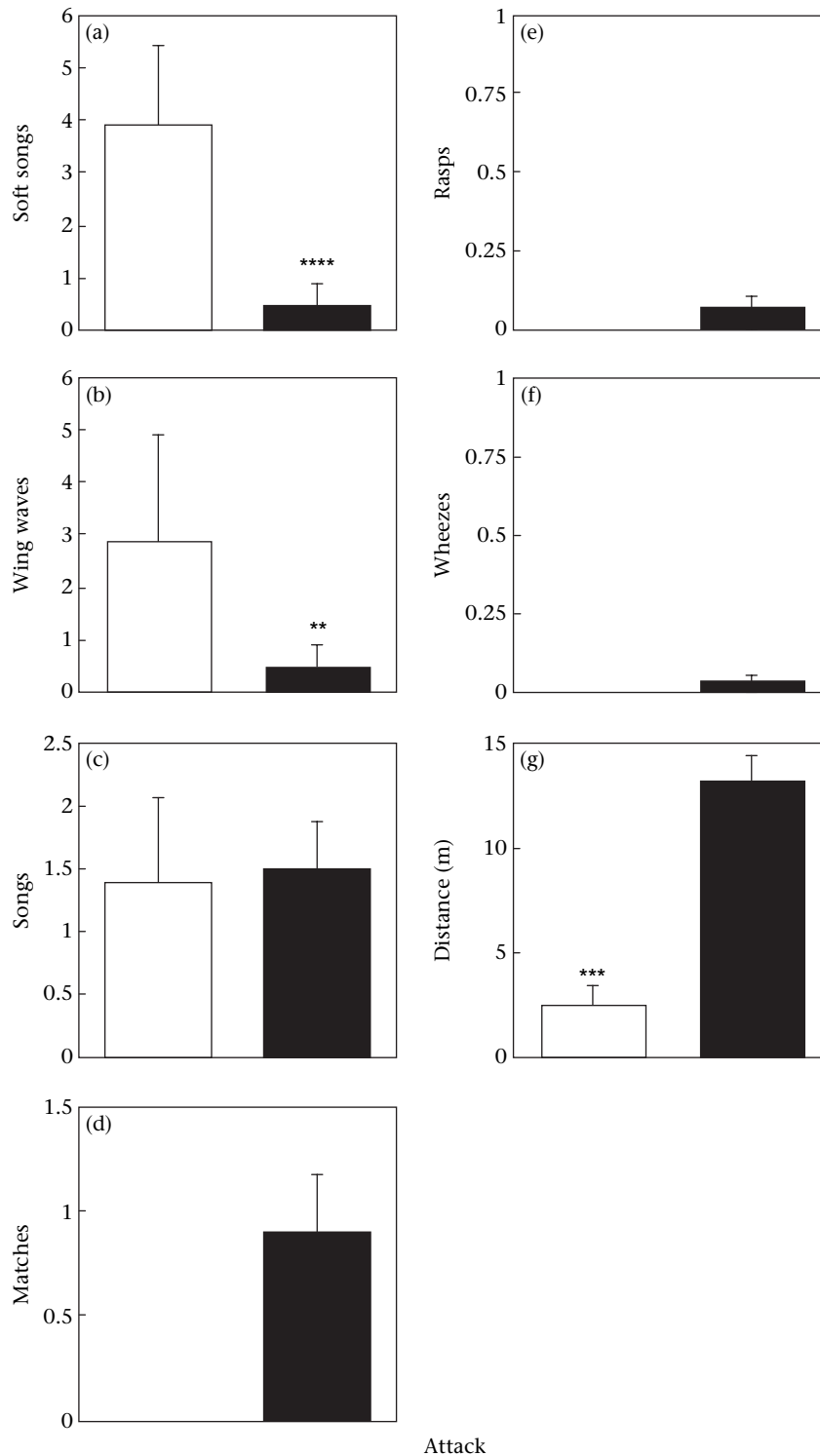


Figure 4. Behaviour during the 1 min before attack for males that did (□; $N = 9$) or did not (■; $N = 31$) attack the mount. Means (\pm SE) for (a) numbers of soft songs, (b) number of bouts of wing waving, (c) number of songs, (d) number of matching songs, (e) number of rasps, (f) number of wheezes and (g) distance to the speaker. ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

model first, followed by wing waves. The discriminant function was a significant predictor of attack (Wilk's $\lambda = 0.692$, $F_{2,37} = 8.220$, $P = 0.0011$), and in a jackknifed procedure, correctly classified 97% of nonattackers and 44% of attackers (85% total). A backwards stepwise

discriminant function analysis converged on the identical model. In a forward stepwise discriminant function analysis with distance as well as the six display measures, distance was the first variable to enter, followed by soft songs and wing waves. The resulting discriminant function was

a significant predictor of attack (Wilk's $\lambda = 0.560$, $F_{3,36} = 9.42$, $P = 0.0001$). A jackknifed procedure showed that the discriminant function containing these three variables correctly classified 56% of attackers and 90% of nonattackers (83% overall).

Matching

Of 40 subjects, including both attackers and nonattackers, 37 sang at least one song during the initial recording period and thus had an opportunity to match. Of the 37, 15 (40.5%) matched the playback song type, which was not significantly greater than the random expectation of 33% ($\chi^2_1 = 0.87$, $P = 0.35$). The percentage of attackers that matched (50%) did not differ significantly from the percentage of nonattackers that matched (38%) ($\chi^2_1 = 0.38$, $P = 0.54$).

Soft Songs

Male swamp sparrows produced three categories of soft song. First, some soft songs were normal broadcast song types produced at low amplitudes (Fig. 5a). In some cases, males sang broadcast and soft songs of the same song type intermixed; in other cases, males sang a soft song of one normal song type intermixed with broadcast songs of a different song type. Second, some soft songs were of a unique song type that we have not recorded in the broadcast repertoires of these males, but which resembles broadcast song types in consisting of a single syllable repeated in

a steady rate trill (Fig. 5b). We have designated this vocalization song type Z. Eight of 14 males that produced soft song during at least one analysis period also produced at least one Z song type. Third, some soft songs did not have the pattern of a normal song type, but instead consisted of short (<1 s) groups of unrepeated notes (Fig. 5c). We termed these vocalizations gargles. Gargles were sometimes appended either before or after one of the other soft song types, and sometimes were given alone.

To test whether one of the three categories of soft song was especially predictive of aggression, we compared the frequency of the categories in attackers and nonattackers (Table 2). For this analysis, we combined the two analysis periods (to maximize the sample available), and considered only the six nonattackers and eight attackers that gave at least one soft song. When a male gave a gargle appended to another soft song category (e.g. a gargle-Z), we counted this as one exemplar of each category (e.g. one gargle and one Z). The mean proportion of gargles was higher in attackers than in nonattackers, and the mean proportion of song type Z was lower, but neither of these differences was significant (Mann–Whitney *U* tests: $U = 14.5$, $P = 0.21$ and $U = 20.5$, $P = 0.64$, respectively).

DISCUSSION

The results of this experiment with swamp sparrows were in some ways similar to those of our previous experiment with song sparrows (Searcy et al. 2006) and in some ways quite different. The biggest difference was in the reliability of signals in predicting attack: displays gave more information on whether attack would occur in swamp sparrows than they did in song sparrows, multiple displays contained information on attack likelihood instead of just a single display, and displays in the initial recording period predicted attack as well as displays in the 1-min interval before attack. The most notable similarity was that the one display that best predicted attack in swamp sparrows, as in song sparrows, was soft song. In swamp sparrows the number of soft songs was significantly higher for attackers than for nonattackers during both time periods that we analysed, and soft song was also the first display measure to the enter forward stepwise discriminant functions discriminating attackers from nonattackers for both time periods. For the initial recording period, soft song was an even better predictor of attack than was distance to the speaker/mount assembly.

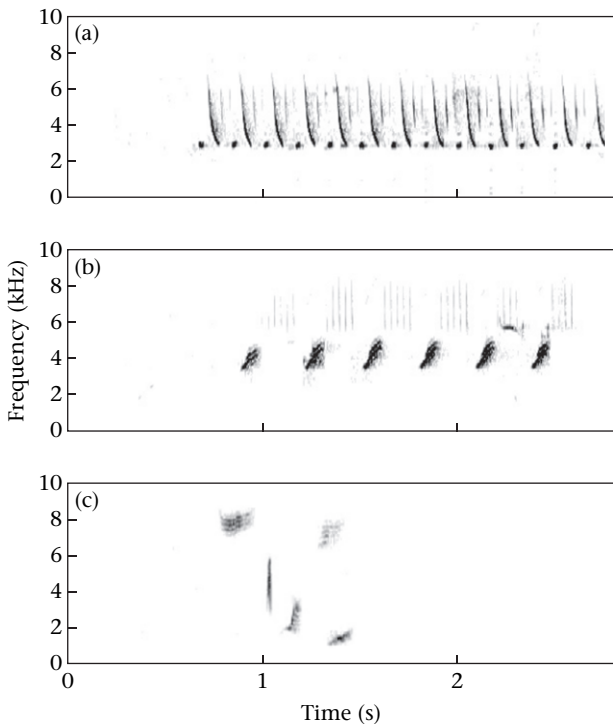


Figure 5. Spectrograms of three categories of soft song produced by male swamp sparrows during aggressive signalling: (a) a song type from the normal broadcast repertoire; (b) song type Z; (c) a gargle.

Table 2. Use of the three classes of soft songs by attackers and nonattackers

	Gargles	Broadcast song type	Z song type
Attackers (<i>N</i> =8)	0.54±0.11	0.31±0.12	0.16±0.07
Nonattackers (<i>N</i> =6)	0.24±0.11	0.35±0.17	0.42±0.20

Values are means ± SE.

We found that swamp sparrows produce multiple forms of soft song, some of which had not been previously described. Some soft songs are simply songs from the individual's normal, broadcast repertoire produced at exceptionally low amplitude; this form of soft song has been termed 'crystallized soft song' in song sparrows (Anderson 2006). The second form of soft song in swamp sparrows, which we have termed 'gargles', resembles the introductory segments of swamp sparrow flight songs (Nowicki et al. 1991), both in the overall temporal pattern and in the structure of individual notes. Finally, swamp sparrows sing a third form of soft song that we have termed song type Z. Song type Z resembles broadcast song types in its acoustic pattern, but it has not been recorded in the broadcast repertoires of males in our study population. Although more evidence is needed to confirm this, our present data suggest that the three forms of swamp sparrow soft song are interchangeable, with none having a more aggressive or less aggressive message than the others.

The use of low-intensity soft song as the most aggressive, most threatening display in a species' display repertoire seems counterintuitive, but it is possible to explain its use as an aggressive signal in terms of the costs and benefits of this display. Theory suggests that a signal can be a reliable signal of aggression if it has a cost that falls more heavily on less aggressive individuals. A more precise way of stating this criterion is that the ratio of marginal cost of the signal to its marginal benefit must decrease with increasing aggressiveness (Grafen 1990). Thus, soft song may be the most aggressive display in swamp sparrows because the costs and benefits of this display fit this criterion better than do the costs and benefits of the other displays in the species' repertoire. A problem with this idea is that it is not immediately apparent that soft song should have any cost at all. Production costs in terms of energy consumption are unlikely, since song in general has low energy costs in songbirds (Oberweger & Goller 2001; Ward et al. 2003), and low-intensity song would be expected to be particularly inexpensive. Production costs in terms of exposure to predation risk also seem unlikely, as a low-amplitude display must be especially unlikely to attract the attention of a predator. Some aspects of song have considerable developmental costs (Nowicki et al. 2002; Spencer et al. 2004, 2005), but developmental costs are more likely to explain the reliability of signals of quality than of signals of intention (Searcy & Nowicki 2005). The costs most likely to apply to aggressive signals in general are receiver-dependent ones, especially receiver retaliation and vulnerability costs (Vehrencamp 2000).

Receiver-retaliation costs occur when a highly aggressive signal is especially likely to provoke attack from a high-quality opponent; game theory models demonstrate that this form of cost can maintain reliability in aggressive signalling (Enquist 1985). A receiver-retaliation cost is possible for soft song in swamp sparrows, but an initial test for such a cost in song sparrows proved negative (Anderson et al. 2007). A vulnerability cost is incurred when production of the display puts the signaller in a position that increases its vulnerability to attack. Vehrencamp (2000) has argued that low-amplitude vocal displays have

a vulnerability cost because a signaller must be close to a receiver if the receiver is to perceive the display; the low-amplitude display thus unambiguously communicates that the signaller is close. We find this idea unconvincing, however. Because of the way that sound attenuates with distance, a song that is of low amplitude when it reaches the receiver may be a soft song produced nearby or a broadcast song produced at a greater distance, whereas a song that is of high amplitude when it reaches the receiver is unambiguously a song produced in close proximity.

We propose that soft song may be reliable because it is an unambiguous and costly signal of attention. Soft song cannot be perceived at a distance, and therefore a lone male near the singer can be sure that a soft song is intended for him, whereas a broadcast song might be intended for a distant receiver. The signal is costly to the singer because by lowering the intensity of his signal he is sacrificing his ability to signal to other individuals, either male or female. Searcy & Nowicki (2006) have shown, by simulating vocal interactions between song sparrows using playback, that territory owners that use soft song to counter an intruder suffer more intrusion by third-party males than do males that use broadcast song; presumably this effect occurs because the third-party males cannot perceive the owner's soft song from off his territory and so cannot tell that he is contesting the intrusion. Soft song, then, signals to an intruder that the owner is attending to him and only to him. Brémond (1968) made a similar suggestion for song type matching: matching is an unambiguous signal of attention to another singer because only a male that has listened to the other's most recent song can match him. Matching, however, is not costly in the same way as is soft song, because third-party individuals can perceive the matching song type, and it is presumably as effective with them as a song type chosen randomly from the singer's repertoire.

Again, theory requires not only that a reliable signal of aggression have a cost, but also that the ratio of marginal cost to marginal benefit decreases with increasing aggressiveness. Here we suggest one way that this criterion might be met for soft song. Assume that aggressiveness depends primarily on value asymmetries, and that different males put different values on being able to eject a particular intruder from their territory. Soft song has a cost, in that it communicates only to the particular intruder that is being confronted, and ignores other receivers, such as additional males that also might intrude on the territory. The more a male values ejecting this one intruder, the more willing he is to escalate his level of aggression towards that intruder, and the more he is willing to pay the cost of using soft song. Singers then choose a level of use of soft song that accurately conveys their aggressiveness.

Other Vocal Signals

Our results give provisional support for the idea that rasps are aggressive signals. Although rasps did not differ significantly between attackers and nonattackers in either

time period, rasps did enter the discriminant function predicting attack for the initial recording period after soft songs had entered, suggesting that rasps are positively associated with attack if soft songs are controlled. We found no evidence that wheezes in either time period were associated with attack. Further work needs to be done to clarify the function of both these vocalizations.

We found no evidence that swamp sparrows use song type matching as an aggressive signal. Our subjects did not match an apparent intruder more often than expected by chance. The method we used, assessing matching to playback on a subject's territory, has been used to demonstrate song type matching at above-chance levels in a number of songbird species (Falls et al. 1982, 1988) including song sparrows (Stoddard et al. 1992). Demonstrating above-random matching is more difficult when repertoires are small because the random level of matching is high; for example, the random expectation of matching is 33% in swamp sparrows with a mean repertoire of three songs compared to 12.5% in song sparrows with a mean repertoire of eight songs. Nevertheless our sample size was large enough to show significant matching (at $P < 0.05$) if our subjects had matched at the 50–60% level shown by song sparrows (Stoddard et al. 1992; Anderson et al. 2005). In addition, we found that attackers were not more likely than nonattackers to match the playback with their first reply, nor did they produce more matching songs overall. The likelihood of matching has been suggested to be a graded signal of the likelihood of attack (Krebs et al. 1981), but our results do not support that interpretation for swamp sparrows.

Multiple Aggressive Signals and Reliability

An important difference in our song sparrow and swamp sparrow results is that, in song sparrows, soft song was the only display that contained information about attack likelihood (Searcy et al. 2006), whereas in swamp sparrows, both wing waves and rasps contributed additional information. The occurrence of soft song and wing waving was strongly positively correlated in swamp sparrows: individuals that produced many soft songs also tended to produce many wing waves. At least for the 1-min period before attack, attack likelihood could be predicted better using both wing waves and soft song than using either alone. These two signals, then, seem to fit well with the redundant signals hypothesis (Møller & Pomiankowski 1993; Johnstone 1995). The two signals convey essentially the same information, and are consequently strongly positively correlated with each other and with the same signaller attribute (aggressiveness). Both signals contain some error, so more information can be garnered by attending to both rather than to either alone. The fact that one of these signals is auditory and the other visual may be significant; it may often be beneficial for an animal to use different signalling modalities for redundant signals, so that if one signal channel is occluded, the other signal may still get through.

Many of the displays that we measured, both in song sparrows (Searcy et al. 2006) and in swamp sparrows,

appear to convey no information on attack likelihood. This result could be explained by either the multiple message hypothesis or the unreliable signal hypothesis. The rate of broadcast songs, for example, might contain information on the singer's condition rather than on its aggressive intentions, information that would still be of interest to aggressive opponents. Alternatively, the rate of broadcast songs might once have been a signal of aggressive intentions but has since lost this information because of the spread of bluffing (Andersson 1980). It seems possible, however, that some of the signals that we measured, such as song type matching and song type switching, are not and never have been used as aggressive signals in swamp sparrows.

A signal is considered to be reliable if 'some characteristic of the signal ... is consistently correlated with some attribute of the signaller or its environment' and 'receivers benefit from having information about this attribute' (Searcy & Nowicki 2005, page 3). Receivers ought to benefit from knowing in advance whether or not an opponent will attack, so aggressive signals can be said to be reliable if they are consistently correlated with subsequent attack. Early theoretical analyses of aggressive communication sometimes doubted whether signals would ever be reliable in this sense (Maynard Smith 1974, 1979), and some empirical analyses have concluded that signals are either poor predictors of aggression (Caryl 1979) or are downright deceptive (Adams & Caldwell 1990; Backwell et al. 2000). Nevertheless, reliability of aggressive signals has been supported in some cases, for example, in little blue penguins, *Eudyptula minor* (Waas 1991b), cricket frogs, *Acris crepitans* (Wagner 1992) and green anoles, *Anolis carolinensis* (Hurd 2004). A general problem with applying the above definition of reliability lies in deciding how strong a correlation between the signal and the attribute being signalled must be before concluding that the signal is reliable. Even if an animal is striving for perfect honesty, errors in the production of the signal or in our measurement of it will prevent the correlation from being perfect (Searcy & Nowicki 2005). In the present study, we acknowledge that some error must have occurred in our measurement of the signals being given; for example, we may have sometimes missed recording a particular vocalization or made a mistake in attributing a vocalization to our subject. Given these constraints, the level of reliability that we have actually measured in the aggressive signalling of swamp sparrows is quite impressive.

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