

Signal Interception and the Use of Soft Song in Aggressive Interactions

William A. Searcy* & Stephen Nowicki†

* Department of Biology, University of Miami, Coral Gables, FL, USA

† Evolution, Ecology and Organismal Biology Group, Department of Biology, Duke University, Durham

Correspondence

William A. Searcy, Department of Biology,
University of Miami, Coral Gables, FL 33124,
USA. E-mail: wsearcy@miami.edu

Received: September 15, 2005

Initial acceptance: November 2, 2005

Final acceptance: January 24, 2006

(S. Forbes)

doi: 10.1111/j.1439-0310.2006.01238.x

Abstract

Song sparrows, like many species of songbirds, produce songs of especially low amplitude during aggressive contests. Such 'soft songs' have been shown to be reliable signals of intention to attack in song sparrows. Low intensity is a paradoxical feature in a highly aggressive signal, in that it seems likely to make the signal less intimidating to an opponent. A hypothesis that resolves this paradox is that use of soft songs benefits a signaler by limiting the interception of his signals by third party receivers. Here, we test this hypothesis with respect to song sparrows and two classes of third party receivers, predators and conspecific males. We tested whether selection to avoid predation is responsible for use of soft song by examining whether male song sparrows increase production of soft song in an aggressive context when they also receive signals (alarm calls) that indicate a predator is present. We found that the proportion of soft song produced by male song sparrows was actually significantly lower in the predator context than in a control context, directly contradicting the prediction. We tested whether avoiding eavesdropping by conspecific males is a benefit of soft song by removing territory owners and simulating interactions on their territories using playback from two loudspeakers. We found that intrusions by third party males were more likely in trials in which the simulated owner countered an intruder's songs using soft songs than in trials in which the simulated owner countered with loud song, again directly contradicting the hypothesis. We conclude that limiting interception by predators and conspecific males does not provide an explanation for use of soft song by song sparrows.

Introduction

Many species of songbirds produce songs of unusually low amplitude during aggressive encounters (Dabelsteen et al. 1998); such low amplitude songs have been variously termed 'soft songs' (Nice 1943), 'strangled songs' (Snow 1958), and 'quiet songs' (Dabelsteen et al. 1998). In some species, soft songs are produced in courtship as well as in aggression, but in our study species, the song sparrow (*Melospiza*

melodia), soft songs have been noted only in aggressive contexts (Nice 1943; Beecher et al. 2000). Some birds are known to increase song amplitude when interacting with another male (Brumm & Todt 2004), which seems the logical strategy if the function of the signal is to intimidate a rival. By contrast, decreasing amplitude in an aggressive contest seems somewhat paradoxical. One way to escape the paradox is to suppose that soft song actually has a submissive message rather than an aggressive one;

however, we have found in song sparrows that soft song is aggressive, serving as a reliable signal of impending attack (Searcy et al. in press). More specifically, we have found that male song sparrows that attack a taxidermic mount produce significantly more soft songs than males that do not attack. In discriminant function analyses, soft song is a better predictor of impending attack than any other behavior we have measured, including total song production, song type matching, and song type switching.

An alternative hypothesis to explain the use of soft song is that a signaler benefits from using soft song during aggression because the signal's low amplitude limits the ability of third party receivers to intercept the signals (McGregor & Dabelsteen 1996); this benefit might outweigh any cost in decreased effectiveness in intimidating the immediate opponent. Here, we report on two tests of this signal interception hypothesis in song sparrows.

Signal interception refers to the general case in which an 'unintended' or 'third party' receiver uses information contained in a signal that is passed between a signaler and an intended receiver or receivers (Myrberg 1981; Searcy & Nowicki 2005). Eavesdropping is a more narrowly defined term, meant to be restricted to cases in which 'a third party (the eavesdropper) gains information from an interaction that could not be gained from a signal alone' (McGregor & Dabelsteen 1996). Thus, if a predator or parasite uses one of its prey's signals to locate that prey, this constitutes interception but not eavesdropping – the signal betrays the signaler's location irrespective of any signaling response by the intended recipient. If two males exchange signals in an aggressive interaction and a third male is able to tell from the relative signal characteristics which is the superior male, this constitutes eavesdropping – the third party has to hear both sides of the interaction in order to discern who is superior.

Predators constitute one category of potential third party receivers for song sparrow vocal interactions. Interception of prey signals by predators is a well-established phenomenon in many taxa (Zuk & Koluru 1998). Frog-eating bats (Ryan et al. 1982), cricket-eating geckos (Sakaluk & Belwood 1984), and petrel-eating skuas (Mougeot & Bretagnolle 2000) all use intercepted vocalizations to find their prey. In song sparrows, it seems possible that a territory owner distracted by an interaction with an intruder would be more vulnerable to predation by predators cuing in on acoustic signals, and so would be selected to produce soft song in this situation to reduce the probability of drawing a predator's atten-

tion. We tested this hypothesis by using playback of song sparrow alarm calls to create a situation in which the risk of predation would appear to be high to the test subject. We then tested the prediction that territory owners combating an intruder would rely more on soft song when the apparent likelihood of predation was high than when it was not.

Conspecific males and females form another class of potential third party receivers. Experiments with other species have shown that both male and female birds are able to abstract information from vocal interactions in which they themselves are not involved (McGregor et al. 2000). Female songbirds are more likely to trespass onto neighboring territories for mating if they hear their own mate lose a singing interaction than if they hear him win (Otter et al. 1999; Mennill et al. 2002, 2003). Male territory owners attend to singing interactions on neighboring territories, modulating their own response to particular males according to whether they have heard those males win or lose (Peake et al. 2001, 2002). For song sparrows, we know of no evidence that singing interactions reveal which interactant is winning and which is losing. Nevertheless, territory owners might benefit from concealing interactions from eavesdroppers of both sexes: from females because females may be reluctant to mate with a male who is perceived to be having difficulties with intruders, and from males because both floaters and territorial neighbors might take the opportunity to intrude on the territory of a male who appears already to be occupied with an intruder. Here, we test the latter possibility – that use of soft song helps conceal an interaction from other males. We do this by simulating interactions between a territory owner and an intruder and determining whether intrusions by third party males are less likely if the territory owner uses soft song than if he uses normal broadcast song.

Methods

Study Sites and Subjects

Both experiments were carried out in the vicinity of Hartstown, Crawford County, PA, U.S.A. during the 2005 breeding season. We performed trials for the intruder simulation experiment between May 13 and June 24, and trials for the predator simulation experiment between June 25 and July 5. All subjects were male song sparrows holding territories along edges between wooded areas and old fields or lawns. Before the first experiment, we captured color

banded, and released all territorial males in several neighborhoods, and then recorded these males and carefully mapped their boundaries. All subjects in the intruder simulation experiment came from among these banded males; only a subset of the males in the predator simulation experiment were color banded.

Predator Simulation Experiment

In this experiment, we used playback of song sparrow song paired with a taxidermic mount of a song sparrow to provoke aggressive signaling from territory owners, and tested whether the subjects were more likely to use soft song when we also simulated the presence of a predator than when we did not. We simulated the presence of a predator by playing song sparrow alarm calls; as a control we played songs of yellow warblers (*Dendroica petechia*). The alarm calls were chips produced by song sparrows of both sexes when a human observer approached their nests. Pilot experiments indicated that adult song sparrows were more agitated by playback of such alarm calls than by playback of the calls of a predator, the eastern screech owl (*Otus asio*).

Playback stimuli were recorded on stereo tapes, with song sparrow song on one channel and either the alarm calls or yellow warbler songs on the other. The predator treatment tapes started with 1 min of the alarm calls alone, followed by 9 min of both alarm calls and song sparrow songs. Similarly, the control treatment tapes started with 1 min of yellow warbler song alone, followed by 9 min of both yellow warbler and song sparrow songs. We used 14 pairs of tapes. Both tapes in a pair contained the same two song sparrow song types, recorded from a single male. Songs of 14 different males were used to make the 14 pairs of tapes. Songs were repeated at the rate of one song per 10 s, with the switch from one song type to the other occurring at the halfway point. Each of the 14 control tapes used a different yellow warbler song, also repeated at one song per 10 s. We obtained recordings of alarm calls from three different pairs of song sparrows; from these recordings we edited out 14 unique 20-s segments. Each of the experimental tapes used one of these segments repeated in a continuous loop.

We used a paired design, in which we played to a subject both tapes in a pair, at least 2 d apart and counterbalancing whether the yellow warbler or alarm call treatment occurred first. We placed two Nagra DSM speakers on the subject's territory, centrally located within the boundaries and spaced 5 m

apart. After the first trial on a particular territory, speaker positions were marked with flagging, so that the same positions could be used in the second trial with the same male. A taxidermic mount of a song sparrow, protected by a small wire cage, was placed on top of the speaker that was to play song sparrow songs. The mount was used to increase the level of aggressiveness shown by the subjects. Song sparrow songs were played at a mean amplitude of 83 dB SPL (range 80–86, measured with a GenRad 1565D sound level meter on C setting), yellow warbler songs at a mean of 84 dB SPL (range 80–88), and song sparrow alarms at a mean of 75 dB SPL (range 71–78). The amplitude for the alarm calls was chosen to match by ear the level of these alarms as given by song sparrows in the field.

We decided in advance that the main response variable would be the proportion of soft songs out of total songs given by the subjects during the 9 min of song sparrow playback. Classification of songs as loud or soft was done by one observer in the field during the trial. We have found the distribution of songs produced in aggressive contexts is bimodal; songs tend to be either very loud (80–85 dB SPL) or very soft (55–60 dB SPL), with a few intermediates. We have also found that a human observer tested blind in the field with playback is quite accurate in classifying songs as loud or soft. Specifically, we tested the same observer used in this experiment (WAS) at the same observation distance with playback of a variety of song sparrow songs of known calibrated amplitudes, ranging in 3 dB intervals from 89 to 57 dB SPL (measured at 1 m). Taking 77 dB as the cutoff between loud and soft songs, accuracy in classifying songs as loud was 78% (7/9) for songs played at 78–80 dB and 100% (42/42) for songs played at ≥ 81 dB. Accuracy in classifying songs as soft was 74% (14/19) for songs played at 75–77 dB and 100% (79/79) for songs played at ≤ 74 dB.

Intruder Eavesdropping Experiment

The design of this experiment called for us to capture and hold a male while we staged a virtual vocal interaction on his territory. Interactions were simulated using two speakers placed 5 m apart on the removal territory, along a boundary with one of the neighbors. During each interaction, we played from one speaker songs from an 'intruder', a male recorded at least 1 km distant and therefore presumed to be unfamiliar to the subject and his neighbors. We always played intruder songs at normal broadcast amplitudes. From the second speaker, we played

songs of the removed owner; in the 'loud owner' treatment these songs were played at normal broadcast amplitudes and in the 'soft owner' treatment they were played at soft song amplitudes. Staged interactions lasted 1 h, and throughout this time two observers watched the removal territory for intrusions by male song sparrows. We again used a paired design, in which each removed male was used in two trials, one with the loud owner treatment and the other with the soft owner treatment. Successive tests with one focal male were staged at least 2 d apart. Order of the two treatments was counterbalanced such that the loud owner and soft owner treatments occurred first equally often.

Before each trial, we recorded the focal male, using a Realistic Omnidirectional microphone, a Sony PBR-330 parabola (Sony, Tokyo, Japan), and a Sony TCM 5000 cassette recorder (Sony). We recorded songs to be used as intruder songs, using the same equipment. Field tapes were reviewed to ensure that we had good quality recordings of at least two song types per male. Songs to be used in playback were digitized using SIGNAL v. 3.1 software (Engineering Design, Berkeley, CA, USA) to construct playback tapes from the stored songs. Playback tapes were recorded on a Sony TC D5M stereo cassette recorder, with the territory owner's songs on one channel and the intruder's songs on the other. Playback tapes alternated 6 min of song with 6 min of silence for a total of 60 min. Within each 6-min song segment, owner songs alternated with intruder songs, with each recorded at one song per 12 s. The first song played was that of the simulated intruder, followed by a response from the simulated owner 6 s later (i.e. the owner and intruder songs were interleaved at evenly spaced intervals). Both intruder and owner treatments switched to a second song type after 3 min in every 6-min cycle. The soft owner treatment used the same song types as the loud owner treatment, played at lower amplitude. We have found that the majority of soft songs produced by male song sparrows in our population are normal song types from their broadcast song repertoires, sung at lower amplitudes (R. Anderson, unpublished data).

Focal males were captured on the morning of a trial using mist nets or walk-in traps baited with grain. We did not use song playback in capturing these males, so that we would not have simulated an intrusion on the focal territory before the trial. Males were captured for removal between 06:00 and 09:30 hours. The removed male was held away from the territory, in a covered cage supplied with food

and water, and then released at the end of the trial. No male was held for >2 h. All of the removed males regained their territories after being released.

Once a focal male had been captured, we set out two Nagra DSM speakers on his territory, 5 m apart, and approx. 2–3 m from a boundary with an adjacent male that we had color banded. Focal males were chosen so that the same adjacent male (i.e. the male deemed most likely to intrude because it shared the territorial boundary where we set up the playback speakers) was never used with more than one focal male. Territories were carefully mapped before trials, so that we had good knowledge of the boundaries. An intrusion was defined as occurring when another male song sparrow moved over a boundary decided on in advance of the trial, into space that we had observed the focal male to occupy previously. During the trial, two observers stood 20–25 m from the speakers, separated so that they had good views of different parts of the focal territory. Their observations were recorded onto flow sheets divided into 10-s intervals.

A coin flip was used to decide which of the two speakers would be used to play the owner songs and which the intruder songs. During all trials, the output level on the speaker playing the intruder song was set to produce approx. 85 dB SPL at 1 m (range 83–87; measured with GenRad 1565D sound level meter on C setting). For the loud owner treatment, the speaker playing the owner song was also set to produce output of approx. 85 dB SPL, whereas in the soft owner treatment this speaker was set to produce an output of 62 dB SPL (range 61–63).

The two treatments thus simulated a series of 6-min interactions in which a territory owner replied to a consistently loud intruder with either consistently loud or consistently soft song of his own. We have evidence that both types of responses are used by territorial males in our study population. For example, in the control trials in the predator simulation experiment of this study, we simulated 9 min of intrusion by a loud intruder; three of 14 territory owners sang 100% soft song through the 9 min, whereas two of 14 sang 100% loud song.

Results

Predator Simulation Experiment

This experiment tested the hypothesis that song sparrows use soft song in aggressive encounters to avoid attracting the attention of a predator. The specific prediction we tested is that males would depend

on soft song more when they were alerted to the presence of a predator in the vicinity than when they were not alarmed. We found the opposite result. Male song sparrows produced a significantly lower proportion of soft songs when a simulated intrusion was paired with song sparrow alarms than when an intrusion was paired with a control stimulus, yellow warbler song (Fig. 1). Thus, our results directly contradict the hypothesis of interest.

We observed a significant correlation between the proportion of soft songs used by different individuals in the alarm call trials and the proportion the same individuals used in the control trials ($r = 0.834$, $N = 14$, $p < 0.0001$). Individual subjects thus showed strong consistency in their use of soft song across the two trials, despite the effects of the treatments on soft song use. Individuals also showed some consistency in their distance to the speaker averaged over the 9 min of song sparrow playback, though the correlation ($r = 0.565$, $p = 0.017$) was not as high as for the proportion of soft song. Mean distance to the intruder speaker was no different in trials with alarm calls (3.6 ± 0.7 m) than in control trials (3.3 ± 0.6 m; Wilcoxon Matched Pairs test, $z = -0.251$, $p = 0.80$).

Intruder Eavesdropping Experiment

Intrusions were quite common under the conditions of this experiment (Table 1). In only two trials of 20 did we fail to observe any intrusion; these two trials were a matched pair done on the territory of a single subject. The majority of the intrusions were of the type that the experiment was intended to provoke,

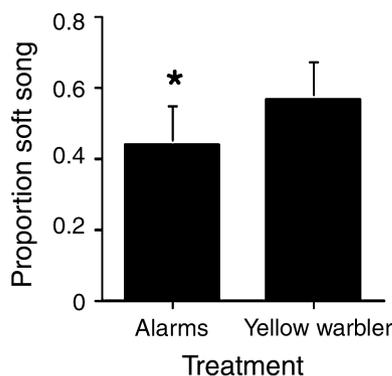


Fig. 1: The proportion of soft songs produced by males song sparrows during simulated intrusions that were coupled with playback of song sparrow alarms vs. yellow warbler songs. Male song sparrows used a higher proportion of soft songs in the alarm context than in the control (yellow warbler) context (Wilcoxon Matched Pairs Test $z = -2.103$, $N = 14$ pairs, $p = 0.036$)

Table 1: Results of the intruder simulation experiment

Subject	Owner		Intrusion		Intruder identities
	playback	Date	time (s)		
1	Soft	5/13	0		No intrusion
	Loud	5/22	0		No intrusion
2	Soft	5/26	530		Adjacent neighbor ^a
	Loud	5/20	400		Non-adjacent neighbor ^a , adjacent neighbor
3	Soft	5/21	830		Non-adjacent neighbor ^a
	Loud	5/27	10		Non-adjacent neighbor
4	Soft	5/24	45		Adjacent neighbor ^a
	Loud	6/2	180		Adjacent neighbor
5	Soft	5/31	1460		Adjacent neighbor ^a
	Loud	5/25	20		Adjacent neighbor
6	Soft	5/26	2620		Non-adjacent neighbor ^a , adjacent neighbor
	Loud	5/29	50		Adjacent neighbor
7	Soft	6/3	1300		Non-adjacent neighbor ^a
	Loud	6/1	155		Adjacent neighbor
8	Soft	6/19	25		Adjacent neighbor ^a , non-adjacent neighbor
	Loud	6/17	995		Floater ^a , adjacent neighbor ^a
9	Soft	6/23	4850		Floater ^a , adjacent neighbor ^a , non-adjacent neighbor ^a , second floater ^a
	Loud	6/21	2330		Floater ^a , adjacent neighbor ^a , non-adjacent neighbor ^a
10	Soft	6/22	440		Adjacent neighbor ^a
	Loud	6/24	140		Adjacent neighbor

^aMale sang while intruding on removal territory.

in which the adjacent neighbor came across the boundary to the vicinity of the playback speakers during the simulated interaction. We also observed an appreciable number of intrusions that involved other neighbors, whose territories were not adjacent to the loudspeakers, or males that we never observed holding their own territories and whom we therefore assumed to be non-territorial floaters (Table 1). Intrusions by non-adjacent neighbors and floaters tended to be more serious, in the sense that the intruders ranged over a larger proportion of the subject's territory than did adjacent neighbors during their intrusions.

We designed this experiment to test the hypothesis that owners benefit from using soft song because doing so conceals from other males the fact that the resident is pre-occupied with fending off an intruder. The hypothesis predicts that there will be less intrusion by third-party males when the owner uses soft song to counter an intruder than when he uses loud song. We again found the opposite result from that predicted. In the soft owner trials, we observed a mean of 1210 s (± 480 SE) of intrusion per trial,

compared with a mean of 428 s (± 232) of intrusion during the loud owner trials (Wilcoxon matched pairs test $z = -1.836$, $N = 10$ pairs, $p = 0.066$). Our results thus contradict the hypothesis.

Discussion

The results of neither experiment supported the general hypothesis that male song sparrows benefit from using soft songs in aggressive interactions because the lower amplitude of these songs limits their interception by third party receivers. Our test of the importance of interception by predators was indirect, in that we did not directly measure whether use of soft song lowers the likelihood of predation on the signaler. Given the rarity of predation – we have never actually observed a single instance of predation on adult song sparrows – such a test would be logistically impossible. Instead, we tested a prediction derived from the predation hypothesis: if predators exert selection in favor of using soft song to combat intruders, then song sparrows should be more likely to use soft song when risk of predation is high than when it is not. The negation of this prediction does not necessarily disprove the hypothesis. Possibly, song sparrows have evolved the tactic of using soft song because of an increased risk of predation during aggressive encounters, in general, without evolving the additional flexibility to adjust their use of soft song in response to variation in predation risk across aggressive encounters. However, alteration of aggressive or sexual signaling in response to perceived predation risk has been demonstrated in fish and other birds (Candolin 1999; Lange & Leimar 2001) and so seems a reasonable expectation in song sparrows. Moreover, the fact that our subjects did change their use of soft song in response to the predation risk stimulus, although in the opposite direction to the prediction, argues that this tactic is indeed flexible. Thus, the result that the response went significantly in the opposite direction to that predicted by the predation hypothesis provides strong evidence against an anti-interception benefit for soft song.

We can only speculate as to why male song sparrows lowered their use of soft song when they heard song sparrow alarms. Playback of alarm calls simulates the presence of one or more additional conspecifics on the territory, and possibly it is to this that the owners responded rather than to an increased predation threat. The presence of additional conspecifics, however, ought if anything to increase aggressiveness in the territory owner, and thus increase the incidence of soft song, which is the opposite of

what we observed. Another possibility is that the alarm stimulus took some of the attention of our subjects away from the intruder stimuli, and therefore decreased their level of aggressiveness. Because soft song is strongly associated with aggressiveness in song sparrows (Searcy et al. in press), lowering aggressiveness would lower use of soft song. Against this hypothesis, however, is the result that the subjects did not approach the intruder stimuli more closely during control trials than during the alarm trials. Approach to an aggressive stimulus is usually taken to measure aggressiveness, so this result indicates that the song sparrows were not more aggressive during control trials than during alarm trials. We are left with no good explanation for why use of soft songs was lower during alarm trials.

Our test of the male interception hypothesis was direct: we directly determined whether use of soft song lowers intrusion by third party males. The results were again opposite to the prediction, with more intrusion by other males when the simulated owner replied to an intruder with soft songs than when he replied with normal songs. In hindsight, we believe this result is interpretable. The original hypothesis is based on the assumption that hearing both the owner and the intruder singing on the owner's territory would help other males discern that an intrusion was taking place. Song sparrows, however, have a well-developed capacity to recognize individuals by song alone (Stoddard et al. 1991, 1992; O'Loughlen & Beecher 1997; Searcy & Nowicki 1999). Male song sparrows are very likely able to recognize by song all the territorial males in their neighborhood and associate them with the correct territory (Stoddard et al. 1991). Therefore, a male does not have to hear two males interacting on a territory to know that an intrusion is occurring; he will know this as soon as he hears the intruder sing. As soft song is probably inaudible to most males off of the focal territory, a soft owner/loud intruder interaction may appear to eavesdropping males to represent an intrusion by a strange male that is not being contested by the owner of the territory. This situation could encourage other males to intrude for two reasons. First, if no territory owner is apparent, both neighbors and other floaters might perceive an opportunity to acquire all or part of the territory for themselves or to perform an extra-pair copulation with the resident female. Alternatively, the absence of a response by an established territory owner to an apparent intrusion might lead a neighbor to intrude to eject from the neighborhood a floater who is also a potential threat to the neighbor's territory.

We have not tested the effects of use of soft song on female eavesdroppers, but we think the same reasoning ought to apply with female eavesdroppers as with male. Female song sparrows are able to recognize individual males by song (O'Loughlen & Beecher 1997; Searcy & Nowicki 1999), and therefore they too should be able to detect intrusions by hearing an intruder sing, whether or not they hear the owner reply. Thus, we would expect that females also will interpret a soft owner/loud intruder interaction as an uncontested intrusion and a loud owner/loud intruder interaction as a contested one. If females lower their estimation of a territory owner when they hear evidence of an intrusion on his territory, the effect ought to be at least as strong for an uncontested intrusion as for a contested one.

We conclude that signal interception does not provide a rationale for the use of soft song in aggressive encounters. Use of soft song seems unrelated to the possibility of interception by predators. Countering an intruder with soft song seems to be counterproductive in its effect on eavesdropping males, at least in cases where the intruder sings, and in our observations intruders do sing in the majority of cases (Table 1). We are left with no good explanation for why males use soft song in highly aggressive situations as their most intensely aggressive signal. Any explanation that is proposed needs to take into account the strong correlation we found in the predator simulation experiment between the proportionate use of soft song on successive trials with the same male, which suggests that males have consistent individual strategies with respect to use of this signal.

Acknowledgements

We thank Christopher Searcy for help with fieldwork, Martin Beebe, and Rindy Anderson for providing recordings of yellow warblers, and Jeremy Hyman for providing recordings of song sparrow alarm calls. We thank the Pennsylvania Game Commission and Pymatuning State Park for access to study sites. Financial support was provided by grants from the National Science Foundation to WAS (IBN-0315566) and to SN (IBN-0315377).

Literature Cited

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000: Song-type matching between neighbouring song sparrows. *Anim. Behav.* **59**, 21–27.

- Brumm, H. & Todt, D. 2004: Male-male vocal interactions and adjustment of song amplitude in a territorial bird. *Anim. Behav.* **67**, 281–286.
- Candolin, U. 1999: The relationship between signal quality and physical condition: is sexual signalling honest in the three-spined stickleback? *Anim. Behav.* **58**, 1261–1267.
- Dabelsteen, T., McGregor, P. K., Lampe, H. M., Langmore, N. E. & Holland, J. 1998: Quiet song in birds: an overlooked phenomenon. *Bioacoustics* **9**, 80–105.
- Lange, H. & Leimar, O. 2001: The influence of predation risk on threat display in great tits. *Behav. Ecol.* **12**, 375–380.
- McGregor, P. K. & Dabelsteen, T. 1996: Communication networks. In: *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, NY, pp. 409–425.
- McGregor, P. K., Otter, K. & Peake, T. M. 2000: Communication networks: receiver and signaller perspectives. In: *Animal Signals: Signalling and Signal Design in Animal Communication* (Espmark, Y., Amundsen, T. & Rosenqvist, G., eds). Tapir Academic Press, Trondheim, pp. 329–340.
- Mennill, D. J., Ratcliffe, L. M. & Boag, P. T. 2002: Female eavesdropping on male song contests in songbirds. *Science* **296**, 873.
- Mennill, D. J., Boag, P. T. & Ratcliffe, L. M. 2003: The reproductive choices of eavesdropping female black-capped chickadees, *Poecile atricapillus*. *Naturwissenschaften* **90**, 577–582.
- Mougeot, F. & Bretagnolle, V. 2000: Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Anim. Behav.* **60**, 647–656.
- Myrberg, A. A. 1981: Sound communication and interception in fishes. In: *Hearing and Sound Communication in Fishes* (Tavolga, W. N., Popper, A. N. & Fay, R. R., eds). Springer-Verlag, Heidelberg, pp. 395–425.
- Nice, M. M. 1943: Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerines. *Trans. Linn. Soc. N. Y.* **6**, 1–328.
- O'Loughlen, A. L. & Beecher, M. D. 1997: Sexual preferences for mate song types in female song sparrows. *Anim. Behav.* **53**, 835–841.
- Otter, K., McGregor, P. K., Terry, A. M. R., Burford, F. R. L., Peake, T. M. & 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, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2001: Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proc. R. Soc. Lond. B* **268**, 1183–1187.
- Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2002: Do great tits assess rivals by combining

- direct experience with information gathered by eavesdropping? *Proc. R. Soc. Lond. B* **269**, 1925–1929.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982: Bat predation and sexual advertisement in a neotropical anuran. *Am. Nat.* **119**, 136–139.
- Sakaluk, S. K. & Belwood, J. J. 1984: Gecko phonotaxis to cricket calling song: a case of satellite predation. *Anim. Behav.* **32**, 659–662.
- Searcy, W. A. & Nowicki, S. 1999: Functions of song variation in song sparrows. In: *The Design of Animal Communication* (Hauser, M. & Konishi, M. eds). MIT Press, Cambridge, MA, pp. 577–595.
- Searcy, W. A. & Nowicki, S. 2005: *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton Univ. Press, Princeton, NJ.
- Searcy, W. A., Anderson, R. C. & Nowicki, S. in press: Bird song as a signal of aggressive intent. *Behav. Ecol. Sociobiol.* in press.
- Snow, D. W. 1958: *A Study of Blackbirds*. G Allen and Unwin, London.
- Stoddard, P. K., Beecher, M. D., Horning, C. L. & Campbell, S. E. 1991: Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behav. Ecol. Sociobiol.* **29**, 211–215.
- Stoddard, P. K., Beecher, M. D., Loesche, P. & Campbell, S. E. 1992: Memory does not constrain individual recognition in a bird with song repertoires. *Behaviour* **122**, 274–287.
- Zuk, M. & Kolluru, G. R. 1998: Exploitation of sexual signals by predators and parasitoids. *Quart. Rev. Biol.* **73**, 415–438.