THE ROYAL SOCIETY

doi 10.1098/rspb.2001.1648

Male great tits eavesdrop on simulated male-to-male vocal interactions

T. M. Peake*, **A. M. R. Terry**, **P. K. McGregor** and **T. Dabelsteen**

Department of Animal Behaviour, Zoological Institute, Tagensvej 16, University of Copenhagen, 2200 Copenhagen N, Denmark

Animal communication generally occurs in the environment of a network of several potential signallers and receivers. Within a network environment, it is possible to gain relative information about conspecifics by eavesdropping on signalling interactions. We presented male great tits with the opportunity to gain such information by simulating singing interactions using two loudspeakers. Interactions were presented so that relevant information was not available in the absolute singing behaviour of either individual, only in the relative timing of their songs in the interaction as a whole. We then assayed the information extracted by focal males by subsequently introducing one of the 'interactants' (i.e. loudspeakers) into the territory of the focal male. Focal males responded with a reduced song output to males that had just 'lost' an interaction. Focal males did not respond significantly differently to 'winners' as compared with intruders recently involved in an interaction that contained no consistent information. Focal males also responded by switching song types more often when encountering males that had recently been involved in a low-intensity interaction. These results provide the clearest evidence yet that male songbirds extract information from signal interactions between conspecifics in the field.

Keywords: communication networks; signal interactions; eavesdropping; relative information

1. INTRODUCTION

It has recently been argued that the evolution of animal communication should be considered in terms of the selective environment of networks of signalling and receiving individuals (McGregor 1993; McGregor & Dabelsteen 1996; McGregor *et al.* 2000; McGregor & Peake 2000) rather than in terms of a simple dyadic environment. In a network environment there is the potential for non-signalling individuals to gain relative information about individuals involved in signalling interactions by eavesdropping. Eavesdropping in this sense is defined as the extraction of information that can only be gained from interactions, as opposed to information that is available by paying attention to the absolute outputs of the individuals involved (McGregor & Dabelsteen 1996). Eavesdropping has the advantage that information about the relative qualities of the interactants can be gained without the need to engage in costly interactions. The presence of potential eavesdroppers may thus impose a strong selection pressure on signallers, e.g. balancing the signalling strategy required to interact successfully with that needed to reduce (or enhance) the passage of information to others.

There is growing experimental evidence that non-signalling individuals may obtain information by eavesdropping and that individuals involved in interactions modify their behaviour in the presence of eavesdroppers (the so-called audience effect, e.g. Evans & Marler 1994). Information gained through eavesdropping on visual-display interactions by male Siamese fighting fishes (*Betta splendens*) may be used to direct future aggressive interactions. Males that have witnessed an interaction respond more strongly to the loser of that interaction than to the winner or to individuals involved in an unseen interaction (Oliviera *et al.* 1998). Male fighting fishes have also been shown to modify their display behaviour in the presence of a conspecific audience (Doutrelant *et al.* 2001). Preliminary studies of great tits (*Parus major*) have shown that males respond less strongly to intruders that had recently been involved in escalated interactions with neighbouring males than to intruders that had recently been involved in relatively weak interactions (McGregor *et al.* 1997*a*). Male nightingales (*Luscinia megarhynchos*) presented with interactions simulated using two loudspeakers responded more strongly to the leader of the vocal interaction (Naguib *et al.* 1999), suggesting that they extract relative information from the interaction.

Females may also use information gained by eavesdropping to choose extra-pair mates. Otter *et al.* (1999) found that female great tits preferentially intruded upon neighbouring territories more often when their mate had been experimentally manipulated so as to appear to fare worse in vocal interactions than neighbouring individuals. However, the interpretation of these results as demonstrating eavesdropping may be confounded if the differences shown result from changes in the behaviour of the manipulated male rather than from the information gained from the interaction. This difficulty of interpretation can be avoided by presenting subjects (i.e. potential eavesdroppers) with simulated interactions.

Great tits are a good model species for this kind of study because of the wealth of playback evidence that demonstrates the nature of interactions and the roles adopted by the interactants. Evidence from interactive playback experiments (McGregor *et al.* 1992; Dabelsteen *et al.* 1996; Langemann *et al.* 2000) indicates that male great tits signal high willingness to escalate by singing directly over the songs of rivals (overlapping), by increasing song length and by matching the song type of the rival. Adopting the opposite stance, i.e. avoiding overlap by alternating songs with those of rivals, decreasing song length and avoiding song matching, seems to indicate a much reduced willingness to escalate.

---

*Author for correspondence (tmpeake@zi.ku.dk).

Received 23 October 2000 *Accepted* 28 February 2001

Similar roles for the pattern of song use during interactions have been shown in European robins (*Erithacus rubecula*; Dabelsteen *et al*. 1997) and nightingales (Hultsch & Todt 1982; Naguib *et al*. 1999). Great tits of both sexes are able to recognize individual singers based on vocal characteristics (McGregor & Avery 1986; Weary & Krebs 1992; Lind *et al*. 1996); thus, we expect subjects to be able to associate the roles of the interactants with the identities of the singers.

We investigated the ability of male great tits to eavesdrop on male–male interactions by simulating interactions using two loudspeakers (see Naguib *et al*. 1999) that produced songs that consistently differed only in the relative timing of songs, such that different levels of escalation were produced. In this way, the difference in the relative performances of the two 'interactants' was varied while removing any absolute cues from the singing behaviour of the individuals. We took Naguib *et al*.'s (1999) experiment a stage further by subsequently introducing one of the 'interactants' into the focal male's territory (simulating a territorial intrusion) by means of playback in order to assay whether information had been extracted by the focal male, i.e. whether eavesdropping had occurred.

2. METHODS

Experiments were carried out at the Strødam Biological Field Station, Hillerød, Denmark between 07.30 and 13.00 on 8–22 April 2000, inclusive. The study area contains a largely nest-box breeding, colour-ringed population of great tits. We subjected each of 40 males to one of four playback trials (see § 2(b)), each comprising two parts: an interaction playback in which an 'interaction' was simulated between two loudspeakers placed outside the subject's territory boundary, and an assay playback in which an intrusion by one of the previously interacting 'males' was simulated by a third loudspeaker placed within the territory of the focal male. All focal males were mated and all experiments were carried out before the commencement of egg-laying.

(a) *Equipment*

Sounds were reproduced using two portable computers (Toshiba 2180CDT and Toshiba 210CDS; Toshiba Corporation, Tokyo, Japan) according to a balanced design, in order to avoid any effect of reproduction differences. Stimulus sounds (8 bit, 22 kHz, mono) were created from recordings made in the previous two seasons of males known not to be present within 1 km of the subject males in 2000. Sounds were digitized and filtered at 2 kHz high-pass and 8 kHz low-pass using Avisoft SASLab Pro (Raimund Specht, Berlin), and organized and broadcast using Screech, a program designed specifically for interactive playback (Peake *et al*. 2000). Sound from both computers was amplified (30 W) after passing through an analogue 8 kHz low-pass filter, and broadcast from Vifa 1 inch neodymium tweeter speakers (VifaSpeak A/S, Videbaek, Denmark) after passing through a 1.2 kHz high-pass filter (Larsen & Dabelsteen 1997). Sound was broadcast at a level corresponding to the natural level of song (65–67 dB(A) measured at 10 m; S. Blumenrath & T. Dabelsteen, unpublished data).

Vocal behaviour during experimental periods was recorded using a fixed array (approximately 35 m × 35 m) of four microphones (Sennheiser MKE 2; Sennheiser electronic Gmbh & Co., Wedermark, Germany) that could provide positional data for any males singing in the immediate area, as well as a record of the songs themselves (McGregor *et al*. 1997*b*). Each microphone was attached to a pole at a height of 2 m. Signals were passed from each microphone to pre-amplifiers (Shure FP11; Shure Inc., Evanston, IL, USA) via radio transmitters (Sennheiser SK 3063-U, EK 3041 receivers); signals from all four microphones were recorded simultaneously onto four-track DAT tape using a TEAC RD 130T PCM data recorder (TEAC Corporation, Tokyo, Japan).

(b) *Playback trials*

The first part of each trial (the interaction playback) was a simulated interaction between two loudspeakers situated facing each other 20 m apart at a height of 2 m, 5–10 m outside the territory of the focal male (figure 1*a*). In order to avoid responses from neighbouring males, all interactions were presented from areas containing no territory-holding males. Each loudspeaker produced sounds (recorded from a different male) organized into songs of five identical phrases. We used 41 song types from 21 males as stimuli; each song type was used once in each interactant role in order to remove stimulus effects. All the song types used were commonly found in our study population. In each interaction playback, one loudspeaker (the 'looped' male) produced songs separated by pseudo-random intervals that varied approximately normally between 1 s and 6 s (corresponding to the natural rhythm of males recorded performing solo singing in the previous season; K. A. Otter, A. M. R. Terry and T. M. Peake, unpublished data), referred to hereafter as a 'naturalized loop'. The output of the second loudspeaker (the 'interacting' male) was controlled by the experimenter and varied with respect to the looped male only in terms of the timing of song production. There were four treatments (types of interaction) based on three different types of relative timing (figure 2). Each interaction playback lasted for 2 min.

In the first treatment, the interacting male began singing immediately after the looped male, such that interacting songs were broadcast over the top of looped songs after a small delay (overlapping). In the second treatment, each interacting song was broadcast only after the end of each looped song (alternating) such that the interacting song never overlapped the looped song (the looped song occasionally overlapped the interacting song). In the third treatment, the interacting song was a naturalized loop such that there was no concordance in timing between the looped and the interacting males. After each of these three treatments, the looped male played the role of the intruder in the assay playback. The fourth treatment was identical to the first except that, following the interaction playback, the interacting male intruded during the assay playback instead of the looped male.

After the end of the interaction playback, the singing behaviour of the focal male was recorded for 2 min or until song ceased, whichever occurred later. After a further 15 min we carried out the assay playback (figure 1*b*), in which the songs of one of the interactants were broadcast for 5 min as a naturalized loop from a third loudspeaker placed 20–30 m inside the territory boundary, and from the same direction as the interaction playback had been performed. Males' responses during and after playback were recorded, as before.

During playbacks, we recorded the following information: closest approach (m); latency to closest approach (s); number of songs; number of phrases per song; number of song types;

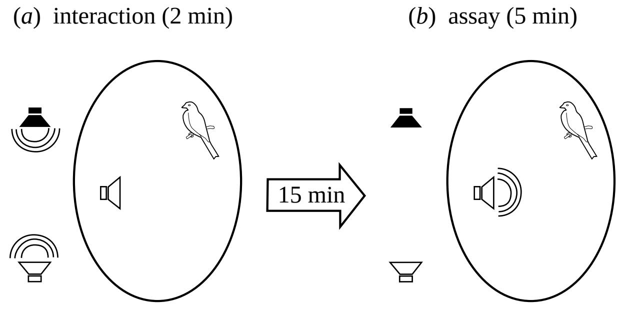

Figure 1. Schematic representation of the playback protocol. The territory boundary is represented by the ellipse, loudspeakers broadcasting sound are indicated by the concentric semicircles. In the example shown, songs broadcast from the open loudspeaker during the interaction playback (*a*) were broadcast from the 'intruding' loudspeaker during the assay playback (*b*); see § 2(b) for details.

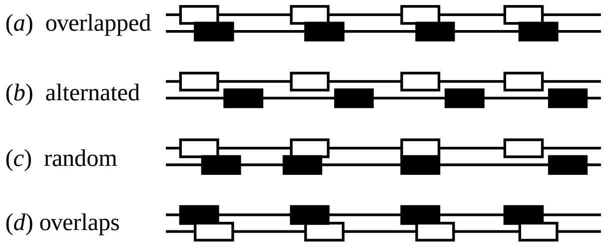

Figure 2. Schematic representation of the four treatments used during the simulated interactions. Each box represents a song (consisting of five phrases). In each case the upper sequence represents the bird that was played as a naturalized loop (i.e. the intervals between the songs were pseudo-random within natural limits), the lower sequence represents the bird whose songs were played 'interactively' (see § 2(b) for details). Open boxes represent the songs of the individual that subsequently 'intruded' into the territory of the focal male.

latency to first song (s); number of songs after playback; and the time taken to stop singing after the end of playback (s).

Analyses were carried out using SPSS (SPSS, Inc., Chicago, IL, USA). Two measures (number of songs after playback and the time taken to stop singing after the end of playback) were highly correlated following both the interaction ($r = 0.902$, $n = 40$, $p < 0.001$) and the assay playbacks ($r = 0.913$, $n = 40$, $p < 0.001$); thus, we did not consider the time spent singing after playback in further analyses. Two measures (the latency to closest approach and the latency to first song) were log transformed before analysis so that the data would conform to a normal distribution.

3. RESULTS

All 40 males responded by approaching the loudspeakers during either the interaction playback or the assay playback, and 37 out of 40 males responded with song during one or both playbacks. Unsurprisingly, given the difference in loudspeaker position between the interaction playback and the assay playback (i.e. outside versus inside the territory boundary), males approached significantly closer ($t = 3.118$, d.f. $= 39$, $p = 0.003$) and with significantly shorter latencies ($t = -3.378$, d.f. $= 39$, $p = 0.002$) during the assay playback. Males that sang after playback also sang significantly more songs ($t = 2.813$, d.f. $= 36$, $p = 0.008$) after the assay playback than after the interaction playback. There was no significant difference in the song rate (number of songs per minute) elicited by the interaction and the assay playbacks ($t = -0.688$, d.f. $= 36$, $p = 0.50$).

During the interaction playbacks, there was no significant effect of treatment on any aspect of singing or approach behaviour ($p > 0.28$ for all seven measures).

However, during the assay playback there was a significant effect of treatment on both song output (in terms of the number of songs produced; $F_{3,33} = 4.00$, $p = 0.015$; figure 3*a*) and the number of song types used ($F_{3,33} = 5.86$, $p = 0.003$; figure 3*b*) by focal males. Post-hoc analyses showed that males sang significantly fewer songs in response to an intruder that had been overlapped during the interaction treatment (Least Significant Difference test (LSD), $p < 0.02$ for all three comparisons), with no significant differences between the other three treatments (LSD, $p > 0.42$ for all comparisons). Males sang a significantly greater number of song types in response to individuals with which playback had alternated during the interaction playback (LSD, $p < 0.015$ for all three comparisons), with no significant differences between the other three treatments (LSD, $p > 0.145$ for all comparisons). There was no significant effect of treatment on the remaining five measures ($p > 0.05$ in all cases). Despite the fact that we analysed seven response measures, we are confident in the importance of the significant results for two reasons. First, a significant effect of treatment was found for two out of seven measures compared with one out of 20 expected by chance alone at the 5% level (the results were actually significant at probabilities of 0.015 and 0.003, respectively). Given a sample size of ten individuals in each of four treatments and an α of 0.05, the *a priori* power of the statistical tests to detect a medium (power $= 0.235$) or large effect (power $= 0.590$) is low (Cohen 1988). Second, if communication networks are an important part of the social environment then we would expect (as we find) differences in singing behaviour to be more pronounced than measures such as the latency to, and the extent of, the closest approach. This is because behaviours that involve purely movement are much less likely to be detected by neighbouring individuals than changes in the patterns of song production, given that all such movements take place within the territories of the focal males.

4. DISCUSSION

The results show a clear effect of treatment on the singing behaviour of males in response to a subsequent simulated intrusion. Males that had previously been on the receiving end of a highly aggressive response (overlapped or 'losers') elicited a much lower level of song production than males that had previously been highly aggressive themselves (overlappers or 'winners'), males that had been involved in a low-intensity interaction (alternated) and males about which no consistent information had been available from the interaction. Inferring the level of aggression from a reduction in song output is problematic. Whereas a reduction may reflect a lower perceived threat to territorial integrity (eliciting a less

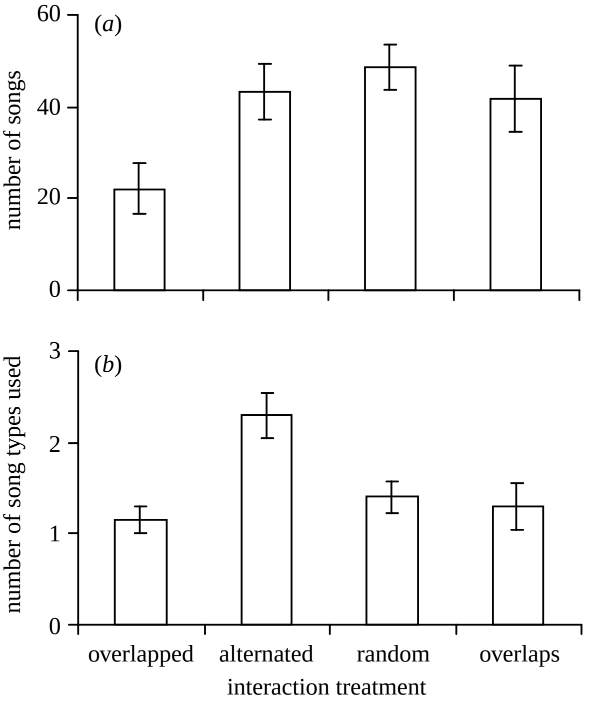

Figure 3. Effect of treatment on (*a*) the song output and (*b*) the number of song types produced by the focal male during the assay playback. Values shown are means ± s.e.m., $n = 10$, 8, 9 and 10 for the four treatments, respectively.

aggressive response), it may also result from an increased performance of more directly aggressive behaviours (e.g. visual displays or searching for the opponent) that we were unable to measure.

The lack of a significant difference between the response to 'winners' and that to individuals about which no information was available may make sense, as the potential threat posed by such individuals is unknown, i.e. focal males could be 'playing safe' by assuming such a threat to be high, or by attempting to elicit a higher level of response from the intruder in order to gain a better estimate of the intruder's resource-holding potential.

The direction of responses during the assay playback agrees with those found by Naguib *et al.* (1999) as, in both cases, perceived winners elicited a stronger response (in terms of a greater level of singing behaviour) than perceived losers. The direction of response towards winners and losers is opposite to that found in male fighting fishes (Oliviera *et al.* 1998), in which males responded less quickly to perceived winners than to losers. However, the difficulty in interpreting response measures in terms of whether a response is more or less aggressive may make it difficult to compare the studies. Regardless of the direction of response, males responded differently to treatments differing only in the relative timing of songs produced by the two loudspeakers; information was available only in the interaction between singers, thus, male great tits must eavesdrop in order to extract that information.

The fact that the two overlapping treatments were identical until the assay stage is evidence that increased motivation elicited by hearing an escalated interaction cannot be responsible for the observed effect of treatment. In fact, our results demonstrate that males pay close attention to the individual roles of the interactants as well as the nature of the interaction.

The results cannot be explained in terms of simple features such as the first or last song heard during the interaction. The 'overlapped' treatment was one of three in which the intruder was the first male heard, and one of two in which the non-intruding individual was the last male heard (not including the random treatment in which neither interactant consistently stopped first).

Focal males responded to individuals that had recently been involved in relatively weak interactions (alternated) with a higher level of song-type switching when compared with other treatments. A number of studies have associated song-type switching with male–male aggression, with switching generally evoked during territorial intrusions (D'Agincourt & Falls 1983; Simpson 1985) or with increasingly aggressive interactions (Kramer *et al.* 1985). In the context of our experiment, focal males may have responded more strongly to males that had recently been involved in a low-intensity interaction as a tactic to elicit an aggressive response and thus gain better information about the individual than that gained from hearing the relatively weak interaction.

In contrast to Naguib *et al.* (1999), we found no effect of treatment on behaviour performed during the interaction itself. This is probably due to the fact that interactions were simulated outside the territory of the focal male (i.e. a centre–edge effect, see Stoddard *et al.* 1991); indeed, levels of approach and post-playback song were lower during the interaction playback than during the assay playback.

In our experiment, we manipulated only the relative timing of the songs of the interactants in order to ensure that the information content of the song outputs of the individual interactants did not provide absolute cues. However, experiments show that many other features of interactions contain information that may allow eavesdroppers to judge the relative qualities of the interactants (Todt & Naguib 2000). Of particular importance in signalling willingness to escalate in great tits and other species seem to be relative song length and song-type matching (Langemann *et al.* 2000); thus, there is much potential for further studies of this kind. It seems from our results, however, that relative timing provides a sufficient cue to the roles of the interactants.

We consider that we have presented the most convincing field evidence yet for the existence of eavesdropping as a means of gathering information. Male great tits are not only capable of extracting relative information from interactions, but we have also shown that they use that information in subsequent encounters. Evidence of this kind is crucial to our understanding of how communication systems have evolved within the social environment of communication networks.

T.M.P. was supported by the European Union (Marie Curie Fellowship 9900164). A.M.R.T. was supported by the Leverhulme Trust. Further support came from Statens Naturvidenskabelige Forskningsråd grant 9801928 to P.K.M. and the Danish National Research Foundation to T.D. We thank Ann Sofie Aarøe for field assistance, two anonymous referees for comments that improved the manuscript, the Strødam Committee for allowing us to use the Strødam Biological Field Station, and the Bird Ringing Centre, Zoological Museum, Copenhagen University for allowing us to colour-ring individuals.

REFERENCES

Cohen, J. 1988 *Statistical power analysis for the behavioral sciences*. New York: Academic Press.

Dabelsteen, T., McGregor, P. K., Shepherd, M., Whittaker, X. & Pedersen, S. B. 1996 Is the signal value of overlapping singing different from that of alternating singing during matching in Great Tits? *J. Avian Biol.* **27**, 189–194.

Dabelsteen, T., McGregor, P. K., Holland, J., Tobias, J. & Pedersen, S. B. 1997 The signal value of overlapping singing in male robins (*Erithacus rubecula*). *Anim. Behav.* **53**, 249–256.

D'Agincourt, L. G. & Falls, J. B. 1983 Variation of repertoire use in the eastern meadowlark, *Sturnella magna*. *Can. J. Zool.* **61**, 1086–1093.

Doutrelant, C., McGregor, P. K., Oliviera, R. F. 2001 The effect of an audience on intra-sexual communication in male Siamese fighting fish, *Betta splendens*. *Behav. Ecol.* (In the press.)

Evans, C. S. & Marler, P. 1994 Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Anim. Behav.* **47**, 1159–1170.

Hultsch, H. & Todt, D. 1982 Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos* B.). *Behav. Ecol. Sociobiol.* **11**, 253–260.

Kramer, H. G., Lemon, R. E. & Morris, M. J. 1985 Song switching and agonistic stimulation in the song sparrow (*Melospiza melodia*): five tests. *Anim. Behav.* **33**, 135–149.

Langemann, U., Tavares, J. P., Peake, T. M. & McGregor, P. K. 2000 Response of great tits to escalating patterns of playback. *Behaviour* **137**, 451–471.

Larsen, O. N. & Dabelsteen, T. 1997 The Vifa 1 Neodymium Tweeter. *Bioacoustics* **8**, 323–326.

Lind, H., Dabelsteen, T. & McGregor, P. K. 1996 Female great tits can identify mates by song. *Anim. Behav.* **52**, 667–671.

McGregor, P. K. 1993 Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Phil. Trans. R. Soc. Lond.* B **340**, 237–244.

McGregor, P. K. & Avery, M. I. 1986 The unsung songs of great tits (*Parus major*): learning neighbours' songs for discrimination. *Behav. Ecol. Sociobiol.* **18**, 311–316.

McGregor, P. K. & Dabelsteen, T. 1996 Communication networks. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 409–425. New York: Cornell University Press.

McGregor, P. K. & Peake, T. M. 2000 Communication networks: social environments for receiving and signalling behaviour. *Acta Ethologica* **2**, 71–81.

McGregor, P. K., Dabelsteen, T., Shepherd, M. & Pedersen, S. B. 1992 The signal value of matched singing in great tits: evidence from interactive playback experiments. *Anim. Behav.* **43**, 987–998.

McGregor P. K., Dabelsteen, T., Holland, J. 1997*a* Eavesdropping in a territorial songbird communication network: preliminary results. *Bioacoustics* **8**, 253–254.

McGregor, P. K., Dabelsteen, T., Clark, C. W., Bower, J. L., Tavares, J.-P. & Holland, J. 1997*b* Accuracy of a passive acoustic location system: empirical studies in terrestrial habitats. *Ethol. Ecol. Evol.* **9**, 269–286.

McGregor, P. K., Otter, K. A. & Peake, T. M. 2000 Communication networks: receiver and signaller perspectives. In *Animal signals* (ed. Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 405–416. Trondheim, Norway: Tapir Publishers.

Naguib, M., Fichtel, C. & Todt, D. 1999 Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc. R. Soc. Lond.* B **266**, 537–542.

Oliviera, R. F., McGregor, P. K. & Latruffe, C. 1998 Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc. R. Soc. Lond.* B **265**, 1045–1049.

Otter, K. A., McGregor, P. K., Terry, A. M. R., Burford, F. R. L., Peake, T. M. & Dabelsteen, T. 1999 Do female great tits *Parus major* assess extra-pair males by eavesdropping? A field study using interactive song playback. *Proc. R. Soc. Lond.* B **266**, 1305–1310.

Peake, T. M., Otter, K. A., Terry, A. M. R. & McGregor, P. K. 2000 Screech: an interactive playback program for PCs. *Bioacoustics* **11**, 69–75.

Simpson, B. S. 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, 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.

Todt, D. & Naguib, M. 2000 Vocal interactions in birds: the use of song as a model in communication. *Adv. Study Behav.* **29**, 247–297.

Weary, D. M. & Krebs, J. R. 1992 Great tits classify songs by individual voice characteristics. *Anim. Behav.* **43**, 283–287.