

Do great tits assess rivals by combining direct experience with information gathered by eavesdropping?

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Animals frequently use signals that travel further than the spacing between individuals. For every intended recipient of a given signal there are likely to be many other individuals that receive information. Eavesdropping on signalling interactions between other individuals provides a relatively cost-free method of assessing future opponents or mates. Male great tits (*Parus major*) extract relative information from such interactions between individuals unknown to them. Here, we show that male great tits can take information gathering a stage further and obtain more information about a previously unencountered intruder, by the hitherto unknown capability of combining information gathered by eavesdropping with that derived from their own direct interaction with an individual. Prior experience with an intruder (A) was achieved by subjecting a focal male to different levels of intrusion simulated using interactive playback. This intruder (A) then took part in a simulated interaction with an unknown male (B) outside the territorial boundary of the focal males. In response to subsequent intrusion by the second male (B), focal males showed low song output in response to males that had lost to a male that the subject was able to beat. Males of known high quality, or those about which information was ambiguous, elicited a high level of song output by focal males. We discuss the implications of this finding for the evolution of communication and social behaviour.

Keywords: communication networks; eavesdropping; signalling interactions; information gathering

1. INTRODUCTION

The majority of research in animal communication focuses on the transfer of information between signaller and receiver. In reality, many signals travel far in relation to the distance between signaller and receiver, thus the environment contains individuals that are not directly involved in a given signalling interaction but that are able to extract information from it (McGregor 1993; McGregor & Dabelsteen 1996; McGregor *et al.* 2000; McGregor & Peake 2000). Consideration of such communication networks suggests that individuals gathering information in this way represent a far from negligible selective force in the evolution of signalling and receiving strategies.

Experimental evidence is growing that non-signalling individuals pay attention to, and extract information from, signalling interactions (i.e. eavesdrop; e.g. Naguib & Todt 1997; Naguib *et al.* 1999). This information may be used in future aggressive encounters (e.g. Oliveira *et al.* 1998; Peake *et al.* 2001; McGregor *et al.* 2001; Earley & Dugatkin 2002) or in assessing potential mating partners (Otter *et al.* 1999; Mennill *et al.* 2002). In some cases, eavesdropping individuals may show clear physiological effects, e.g. fish that witness fights between conspecifics show elevated hormone levels (Oliveira *et al.* 2001). Eavesdropping is likely to be a relatively low-cost means of gathering information, certainly compared with the costs that may be incurred by interacting directly. Eavesdropping may also provide better quality information than

simply paying attention to the absolute signalling output of individuals, because it allows simultaneous comparison of at least two individuals in a directly competitive context (McGregor & Dabelsteen 1996).

If eavesdroppers represent a significant component of the communication environment, then we would expect signallers to respond to their presence. Indeed, the presence or absence of an audience has been clearly shown to affect the dynamics of interactions in fish (Doutrelant *et al.* 2001). While empiricism is clearly ahead of theory in understanding communication networks, a recent game-theoretical model that included individuals that gather information by eavesdropping concluded that eavesdropping can have important effects. In this model, the presence of eavesdroppers in fact, somewhat counter-intuitively, increased the levels of aggression in a population (Johnstone 2001).

Recently, we demonstrated that territorial male great tits extract information from interactions simulated in the field by means of two loudspeakers, the output of which was controlled by two portable computers (Peake *et al.* 2001). By varying the timing of output between the two speakers, interactions were presented in such a way that no information was available in the signalling behaviour of either individual alone, only in the interaction as a whole. In response to intruders that had been on the receiving end of an aggressive interaction, males showed a twofold reduction in song output, in contrast to the response to intruders that had been highly aggressive themselves, or intruders whose relative level of aggression was difficult to judge. That experiment demonstrated that not only do male great tits pay attention to the nature of the interaction, but also they take notice of the roles

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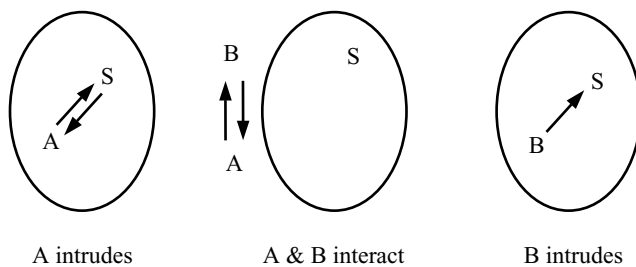


Figure 1. Schematic diagram showing the three-part experimental procedure. Ovals represent the territory boundary of the male subject (S). The positions relative to the territory boundary of loudspeakers playing back song from two other males are indicated by A and B. Two-way arrows indicate song interactions, the single arrow indicates looped song playback.

adopted by each of the interactants. In that experiment, the simulated interaction occurred between two males that the subject had not previously encountered; therefore, the response to later intrusion was based purely on the nature of the interaction. The information extracted by males on the fighting ability of intruders is therefore somewhat indirect. Experiments on green swordtail fish (*Xiphophorus helleri*; Earley & Dugatkin 2002) suggested that the greater accuracy of information obtained by direct interaction may negate the more indirect information obtained by eavesdropping in situations where both sorts of information are available. In the natural setting, male great tits may well have interacted with a number of males previously and hence have some prior information on their relative qualities. Previous studies suggest that both males (McGregor *et al.* 1997) and females (Otter *et al.* 1999) may use neighbours and (in the case of females) mates as a 'yardstick' by which to judge unknown intruders. However, the lack of control over the 'quality' of, and individuals' prior knowledge about, these yardsticks make results difficult to attribute directly to this phenomenon. Using interactive playback and simulating interactions between loudspeakers, we were able to have complete control over the information available to subject males. Here, we present the results of an experiment controlled in this way, and designed to assess whether males are able to combine information gained from a previous interaction with a male with information gained by eavesdropping on that male's subsequent interactions with others.

2. MATERIAL AND METHODS

Experiments were carried out between 07.30 and 13.00 on 11–24 April 2001 inclusive at the Strødam Biological Field Station near Hillerød, Denmark. Forty-one male great tits were each subjected to one of four playback treatments (see later) that each consisted of three parts (figure 1): (i) a territorial intrusion simulated by a single loudspeaker placed inside the subject's territory; (ii) a simulated interaction between two loudspeakers placed outside the territory boundary of the subject; and (iii) a further intrusion simulated by a speaker inside the subject's territory. All broadcast songs consisted of five identical repeated phrases played according to the natural rhythm for that song type; only song types commonly heard in the study area were used as stimuli. Vocal responses of subject males were recorded using Sennheiser MKH-816T microphones (Sennheiser

electronic GmbH & Co., Wedermark, Germany), AKB-11 pre-amplifiers (Audio Engineering Ltd, London, UK) and Marantz CP430 cassette recorders (Marantz Japan Inc., Sagamahira City, Japan). In total we used, as stimuli, 31 songs recorded from a total of 23 males; each song type was used no more than three times and the use of song types was balanced across different male roles.

Territorial intrusions and interactions were simulated by song broadcast via loudspeakers from portable computers using methods and equipment identical to those used by Peake *et al.* (2001). As figure 1 shows, song from one male (A) was first broadcast from within the subject's territory, simulating a territorial intrusion by an individual unknown to the subject. In order to obtain an approach and vocal response from the subject, we began by broadcasting song every 5 s for up to 1 min. If the subject did not produce a vocal response, we waited for 15 min before trying again. Subjects that did not respond to the second intrusion were not used further. Once a subject had begun to sing in response to our initial probe, we then continued with playback contingent on the response of the male on a song-by-song basis, so-called interactive playback (Dabelsteen 1992; Dabelsteen & McGregor 1996). In this way, we were able to simulate intruders representing different levels of aggression or willingness to escalate the contest further. In order to play an aggressive role, we began each stimulus song immediately the subject male began to sing (overlapping; Dabelsteen *et al.* 1996; Langemann *et al.* 2000). In order to adopt a less aggressive approach (Dabelsteen *et al.* 1996), we allowed subjects to overlap stimulus songs by producing stimulus songs 1 s following the cessation of singing by the subject male. For convenience, we shall say that in the former case male A wins the interaction, in the latter male A loses. We do not suggest that our treatments replicate the internal changes associated with 'winning' or 'losing' singing interactions; the term 'winner' is used simply to refer to individuals that have been presented with a simulated intruder playing a low aggression role and the term 'loser' refers to individuals that have been presented with an aggressive simulated intruder. In both cases, the interactive portion of the playback lasted for 2 min from the first song of the subject; only males that produced at least 10 songs during this interactive period were considered to have received the treatment.

Fifteen minutes after the end of the initial intrusion we simulated, by playback from two loudspeakers, an interaction outside the subject's territory boundary between male A and a male unknown to the subject (B). Male A was simulated using the same song type recorded from the same male as used in the initial intrusion. In this simulated interaction, male A either won (i.e. played an aggressive role, by overlapping male B) or lost (by being overlapped by male B) during a 2 min interaction. Protocols for carrying out these interactions were identical to those reported earlier (Peake *et al.* 2001). Speakers were situated facing each other 20 m apart at a height of 2 m, 5–10 m outside the subjects' territory boundaries, and in areas not occupied by neighbouring males. Songs were broadcast at a natural level (65–67 dB (A) at 10 m; S. Blumenrath and T. Dabelsteen, unpublished data).

Based upon the combinations of possible outcomes from both playback periods (see table 1), we arrived at four treatment groups: (i) male A beats subject then male A beats male B; (ii) A loses to subject then beats B; (iii) A beats subject then loses to B; and (iv) A loses to subject then loses to B. In treatments (i) and (iv), the qualities of B relative to the subject remain ambiguous, either both have lost to A (i) or both have

Table 1. The status of a simulated intruder (B) relative to the subject (S) if the outcomes of two singing interactions are combined. Each interaction had a single winner and loser. 'A' and 'B' represent intruders simulated by means of playback. 'Implication' is the logical combination of information on the status of B relative to S provided in the two interactions.

		A versus subject			
		A wins		A loses	
A versus B	A wins	(i)	A>S A>B implication: B?S	(ii)	A<S A>B implication: S>B
	A loses	(iii)	A>S A<B implication: B>S	(iv)	A<S A<B implication: B?S

beaten A (iv). In treatments (ii) and (iii) the relative quality of B is clearer. In (ii), B has lost to A who lost to the subject, thus B should be of low quality relative to the subject. In the case of treatment (iii) the opposite is true, B beats A who had previously beaten the subject, B thus should be of high quality relative to the subject. The four treatments were presented according to a balanced design in order to avoid differences in response due to time of day or location. We then assayed the information extracted by the subject from the two interactions, the one in which he took part and the one he heard, and hence the ability of males to combine information from two sources, by intruding upon the territory using a loudspeaker broadcasting the songs of male B as a 5 min naturalized loop (see Peake *et al.* 2001). The response of subjects to the assay was measured as the total number of songs produced and the number of song types used, the two variables that had revealed differences in responses to interactions between unknown males (Peake *et al.* 2001). For the sake of completeness, we took four further measures; the mean number of strophes per song, the closest approach to the intrusion speaker (in metres), the latency to the first song (in seconds) and the number of songs sung in 2 min following cessation of playback.

3. RESULTS

During the initial intrusion, there was no significant difference in the number of songs produced by males that were overlapped by playback as compared with those that were allowed to overlap playback ($t_{39} = 1.68$, $p = 0.11$). In the overlapping intrusion playback, we successfully overlapped on average 86.7% of subject songs with 3.4% of subject song overlapping playback songs. During intrusions in which subjects were allowed to overlap playback, subjects overlapped 54.0% of playback songs and playback overlapped 3.5% of subject songs. Thus, we were satisfied that the two treatments differed sufficiently and consistently with respect to our aims of adopting more and less aggressive roles, respectively.

During the assay playback, there was a significant effect of treatment on the song output of subjects (figure 2; $F_{3,37} = 3.35$, $p = 0.029$). Post-hoc analyses attribute this effect to a significant threefold reduction in song, in response to intruders, by males that had been involved in treatment (ii) (least significant differences, (ii) versus (i): $p = 0.008$; (ii) versus (iii): $p = 0.027$; (ii) versus (iv): $p = 0.014$), the treatment in which the available information implies that B is of low status relative to the subject

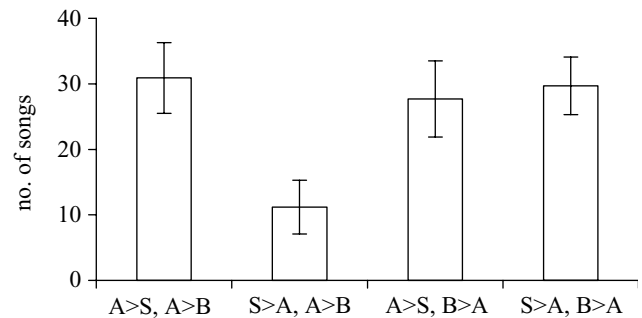


Figure 2. The number of songs sung by male great tits during 5 min of playback simulating an intrusion by male B. Four playback treatments varied in information content on the status of male B relative to the subject (see table 1). The effect of treatment on song output is significant ($F_{3,37} = 3.35$, $p = 0.029$, $n = 11, 10, 10, 10$, respectively).

(table 1). There was no significant difference between the other three treatments in song production ($p > 0.65$ for all comparisons). There was no significant effect of treatment on the number of song types used by males in response to the assay loop ($F_{3,37} > 0.552$, $p = 0.651$). As in the previous experiment, there was no effect of treatment on four other measures of response (see § 2; $F_{3,37} > 1.501$, $p > 0.230$ in all cases).

4. DISCUSSION

Male great tits reduced song output when confronted with an intruder that had been on the receiving end of a highly aggressive response from (i.e. lost to) an individual that had allowed the subject to behave aggressively towards it (a known loser). This result is entirely consistent with our previous eavesdropping experiment (Peake *et al.* 2001) in two ways. First, subjects responded to intruders that were clear losers with significantly reduced song output. Second, no difference was observed in response to intruders that had either won the interaction or had been involved in interactions providing ambiguous information. More importantly, the results we report here show that males are capable of combining information from more than one such interaction, including those in which they are directly involved, and use that information in a consistent way. Males are clearly not basing decisions on just their own recent interactions as this would predict a difference in song response between males in treatments

in which they successfully won their previous interaction (iv) compared with those who lost ((i) and (iii)). Nor are males simply basing decisions on the most recently heard interaction, as the prediction here would be a difference in response to males that recently won ((iii) and (iv)) or lost (i) an interaction.

While males clearly combine the information available from the two interactions presented, it is possible that males do not take the identity of the initial intruder into account. It may be that the response is based upon a combination of winning an interaction and subsequently facing an individual heard to lose. The fact that male great tits have been shown to identify individuals by song features (Weary & Krebs 1992; McGregor & Avery 1986), and follow the roles of individual singers during interactions (Peake *et al.* 2001), may make this a less likely explanation. However, further experiments are required to investigate this possibility.

It is difficult to interpret a reduction in song output as being a more or less aggressive response to intrusion as the reduction may be due to an increase in more overtly aggressive behaviours, such as searching for the intruder or visual displays. However, a reduction in song may indicate that the male is less concerned with the presence of an intruder that offers little threat. When considered in terms of communication networks, a reduction in song means that less information is available to neighbouring individuals. Looked at from another angle, the high level of song maintained in response to high-quality intruders or intruders whose quality is difficult to judge, may be an aggressive response directed towards the intruder or may, indeed, be a signal to listeners that the male is capable of maintaining his territory in the face of such an intrusion.

It is likely that the most accurate information available to an individual on the fighting ability of an opponent is gained through direct interaction. In the absence of such information, gathering information on the relative fighting abilities of potential opponents by observing their interactions with others has been shown to occur in a number of species of birds (Naguib *et al.* 1999; Otter *et al.* 1999; Peake *et al.* 2001; Mennill *et al.* 2002) and fishes (Oliveira *et al.* 1998; Earley & Dugatkin 2002). Here, we have clearly demonstrated that male great tits are able to combine information from both of these sources and respond in a way that appears logical.

These results have important consequences for the evolution of long-range communication. That male songbirds can and do make use of information obtained by eavesdropping emphasizes that social environment is an important component of communication. In our experiment, subjects were given a relatively small amount of information upon which to base future decisions regarding rival males. Mennill *et al.* (2002) recently showed that female black-capped chickadees (*Poecile atricapilla*) can make long-term decisions regarding the paternity of their offspring based on hearing their mates involved in similarly short-lasting interactions. In reality, male great tits are likely to have an even greater knowledge of individuals that occupy neighbouring territories, as neighbours will have been encountered on several occasions. Male great tits can therefore use eavesdropping to provide information on the nature of potential intruders—a form of early warning system. Such a system has been suggested

previously as a possible function of territoriality in terms of the detection of intruders (Eason & Stamps 1993). Our results suggest that the information available by paying attention to the nature of interactions between intruders and neighbours goes beyond simply detecting intruders and can, in fact, allow males to assess the likely threat posed by these individuals. Individual-based models of territory establishment and defence focus on the importance of information gained by direct interaction with competitors (Stamps & Krishnan 1999; Switzer *et al.* 2001); it is likely that these models would benefit greatly by the inclusion of the possibility of individuals gathering information from interactions between others.

Studies of the cognitive abilities of birds with respect to communication have focused primarily on learning and production (Pepperberg 2000). Our results imply a level of information processing by non-signalling members of communication networks that warrants further study, using approaches such as cognitive ecology (Healy & Braithwaite 2000) that integrate psychology, neurobiology and behavioural ecology.

The results presented here also have important implications outside the fields of animal communication and cognition. Explanations for the evolution of altruism either by direct or indirect reciprocity require that animals are able to associate individuals with their actions (Nowak & Sigmund 1998). Knowledge of individual actions through observation of interactions is an important component of theory surrounding the evolution of indirect reciprocity through image scoring (Nowak & Sigmund 1998), which has been suggested as an important stage in the evolution of human society (Wedekind & Milinski 2000). Studies of eavesdropping behaviour may provide valuable insight into the information-gathering abilities of animals in a variety of social contexts.

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