Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback

Ken Otter*, Peter K. McGregor, Andrew M. R. Terry, Fiona R. L. Burford, Tom M. Peake and Torben Dabelsteen

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

Male singing behaviour correlates with extra-pair success in several passerine birds. Singing interactions during territorial contests provide relative information on the males involved. Such information may be important in female extra-pair behaviour and eavesdropping on singing interactions among males may allow females to make such relative assessments. We used interactive playback to instigate singing contests with male great tits during the peak fertile period of their mate in an attempt to alter females' assessment of mates' quality relative to neighbours (potential extra-pair partners). We escalated a contest to one male (by overlapping his songs) and then subsequently de-escalated a contest (by alternating) to a neighbour. Intrusions onto neighbouring territories by females mated to either treatment male were then monitored. Females mated to escalation treatment males were more likely to intrude following playbacks than females mated to de-escalation treatment males. Although the absolute song output of males did not differ between treatments, males produced more song relative to playback in de-escalation treatments and relative song output was positively correlated with female intrusions. Therefore, female great tits eavesdrop on singing interactions and change their visitation rates to neighbouring territories according to their mate's singing performance relative to neighbours.

Keywords: song; eavesdropping; female intrusions; great tit; *Parus major*

1. INTRODUCTION

Aspects of male singing behaviour in several passerine species correlate with extra-pair success (Houtman 1992; Hasselquist *et al.* 1996; Kempenaers *et al.* 1997; Møller *et al.* 1998) and such behavioural traits are better predictors of reproductive success than morphological traits in many species (e.g. Kempenaers *et al.* 1997; Møller & Ninni 1998). However, females' use of song as a cue in extra-pair choice has only been inferred through correlation; there is still a critical lack of understanding of which aspects of song females use to assess extra-pair partners (Otter *et al.* 1999).

One mechanism of female assessment could be eavesdropping on singing males during territorial contests (McGregor & Dabelsteen 1996). The use of interactive song playback (Dabelsteen & Pedersen 1990) has revealed that male songbirds in some species indicate their willingness to escalate contests by song matching (McGregor *et al.* 1992; Otter *et al.* 1994; Beecher *et al.* 1996) or overlapping a competitor's songs (Dabelsteen *et al.* 1996, 1997); females could use such information to judge the relative fighting ability of the female's mates and neighbouring males. Great tits provide one of the best species with which to test these theories of female eavesdropping. The species is socially monogamous,

although females in other populations are known to engage in extra-pair copulations (Blakey 1994; Krokene *et al.* 1998; Strohbach *et al.* 1998). Furthermore, males indicate willingness to escalate disputes during territorial contests by overlapping (i.e. singing over) the songs of rivals (Dabelsteen *et al.* 1996), as well as song-type matching (McGregor *et al.* 1992). Using interactive playback, a researcher can respond song by song to subjects and control the outcome of simulated contests by either escalating or de-escalating playback. As great tits identify males from individual song characteristics (Weary & Krebs 1992; Lind *et al.* 1996), a sequential intrusion by a common 'stranger' can be simulated with playback and the playback stranger can respond differently to each male. Male great tits are known to eavesdrop on such playbacks, responding differently depending on whether the stranger has just won or lost against a neighbouring male (McGregor *et al.* 1997). Using interactive playbacks, we attempted to modify female perceptions of the relative fighting ability of her mate compared to that of neighbouring males. Two neighbouring males were selected and each assigned to one of two playback types: one male in the dyad was randomly chosen to receive a de-escalated treatment (alternate singing) and the other an escalated treatment (overlap singing). Alternating, particularly with lower song length, appears to be a less aggressive signal to great tits, while overlapping elicits the highest level of aggression from resident males and appears to

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

represent an escalated challenge in this species (Dabelsteen *et al.* 1996). The purpose of the two treatments was to give eavesdropping females the impression of one male having a difficult time evicting the playback stranger (escalation treatment), while the other male had a relatively easier time evicting the same stranger (de-escalation treatment). Our aim was to determine whether females eavesdrop on the interactions between neighbours and whether this subsequently affects female behaviour during the fertile period.

2. METHODS

(a) *Study area and monitoring territorial pairs*

The study was conducted in a 50 ha section of woodland at the Strødam Biological Station near Hillerød, Denmark. Adult birds were ringed with a numbered aluminium band and an individual combination of coloured leg bands during February–March 1998. Each bird was sexed by breast stripe width (Gosler 1993) and sexing confirmed by behavioural observations in the spring. We began daily censuses of the study site on 1 April, identifying breeding pairs and locating territorial boundaries by observing territorial disputes and areas of exclusive foraging by pairs. During this period, the songs of each territorial male were recorded opportunistically throughout the day starting during the dawn chorus. Each territory was revisited to obtain sufficient recordings of males to determine their repertoires (mean: three to four song types, and range: two to nine song types, similar to previous studies, e.g. McGregor & Krebs (1982)).

Nest-boxes were checked every two days during April to determine the stage of nesting. Playback subjects were two neighbouring males (the dyad) chosen for their similarity in stage of nesting. First playbacks to a dyad occurred during the female's fertile period (on average, one day prior to egg laying; range: days -7 to $+3$ of egg laying; the average clutch size in the population was eight to nine eggs). The playback stimulus was a song type common to both males of the dyad and a different song type was used for each of the nine dyads ($n=18$ males) in the study.

(b) *Playback treatments*

Playbacks were conducted between 08.00 and 12.00 with the playback speaker placed near the centre of a male's territory. Each playback began with a 2 s song played every 10 s for a maximum of 2 min to initiate a song response from the resident male. Once the male responded with the first song, one of the two treatments (de-escalation or escalation) was initiated. In de-escalation, we did not overlap any of the male's songs during the 3 min playback, responding only after the male had stopped (alternate singing). We responded only with songs of three to four phrases or a song with one phrase less than the male, whichever was less. Once we had decreased the phrase number of the response, we did not increase it again for subsequent songs. After 2 min, we responded only to every second song of the male. If the male stopped singing during the trial, we remained silent until either singing resumed or the trial ended. In escalation, we overlapped each song sung by the male during playback. We initiated playback when the male began singing and continued for at least two phrases after the male had stopped. If the male stopped singing during the 3 min trial, we repeated the last playback song once every 10 s until the male either resumed singing (in which case we resumed overlapping) or the trial ended. The playbacks to the two males within a

dyad were separated by approximately 10 min. The following measurements were extracted from recordings of the playback trials: (i) number of phrases per song of a male, (ii) number of phrases per song in the playback response, (iii) delay (in seconds) of a male's song from the start of the last playback song, (iv) delay in playback response to a male, (v) total songs of the subject during the 3 min trial, and (vi) the total playback songs in response. These were used to calculate both the absolute song output of the male during playbacks and his song output relative to the playback stranger. Relative measures of song were derived by directly dividing the measures of each song with the same measure from the immediate response song of the playback (as indicated in figure 1).

(c) *Monitoring female behaviour*

Two 15 min focal observations were performed on each pair within each dyad. The first was conducted the afternoon (13.00–16.00) of either day 1 or 2 of playback (chosen randomly for each dyad) and the second the following morning (06.00–08.00). Females mated to the two males within a playback dyad were sampled during the same observation periods on a given day. Each minute, we recorded (i) the location of the male and female, (ii) the distance between the male and female (<1 m, <5 m, <10 m, <15 m, <20 m and >20 m), and (iii) whether the male had sung in the previous minute. We noted forays off territory (movements >20 m beyond areas defended by the pair) and intrusions into neighbouring territories (movements >20 m into an area defended by another pair and into an area in which the intruding bird had not been seen during previous surveys). Movements were monitored with respect to the study area's surveyed $50\text{ m} \times 50\text{ m}$ quadrates. Using survey marker posts, 160 nest-boxes distributed throughout the area and natural landmarks, positions could be estimated to within 10 m on survey maps.

3. RESULTS

Females mated to escalation treatment males intruded into neighbouring territories significantly more often during observations (seven out of nine dyads) than females mated to de-escalation treatment males (one out of nine dyads) (Fisher's exact test, $p=0.02$) (figure 2). One additional pair forayed off territory (dyad 8) and entered an area where all three neighbours had been seen foraging, but which no pair had been seen actively defending. Of the eight intruding females, six intruded during a morning observation period (three of these females intruded in both morning and afternoon observation periods).

Of the seven females mated to escalation treatment males who intruded into neighbouring territories, six chose a male who had received a de-escalation treatment (five chose the dyadic counterpart to their mate and one chose a neighbouring male who had been the de-escalation treatment male of a dyad initiated several days earlier). As females had an average of four contiguous neighbouring territories, intruding females preferentially chose territories occupied by males who easily evicted our playback strangers (binomial test, $p=0.001$).

Males followed their mates in 9 out of 12 intrusions and three females intruded without their mate present. No male entered a neighbouring territory without their mate. During intrusions, males neither foraged nor sang, they merely orientated towards their mates. Five out of

Figure 1. Exemplars of (a) de-escalation (alternating) and (b) escalation (overlapping) playback. Numbers above spectrograms identify the individual phrases of two playbacks and one male song. Measures of delay in response to the opponent by the focal male and the playback are also indicated.

Figure 2. Female movements following playbacks. Playback territories are shaded. Arrows indicate the direction and extent of off-territory movement. Dyads are similarly numbered; the order of numbering matches the order in which playbacks were conducted. Females that intruded into the same territory twice (morning and afternoon observations) are indicated by an asterisk beside the head of the arrow.

the nine males sang when within their own territory (binomial test, $p=0.03$) and all nine males foraged within their own territory. None of the intruding pairs later defended these areas. Following their female may therefore represent mate guarding, but it may be relatively ineffective; in both cases where the intruding pair

was discovered, the intruding male but not female was chased from the territory.

There was no significant difference in the number of songs or song length produced by males in either playback treatment (there was a significant difference in delay as a consequence of overlapping) and there was no significant relationship between absolute singing behaviour and female intrusions (table 1). However, relative to the playback stranger, de-escalation treatment males sang more, had more phrases per song and had a shorter delay in response than did males in the escalation treatment (table 1). Females were more likely to intrude when their mates had a lower number of phrases per song and longer delay times in relation to the playback (table 1), supporting the idea that females eavesdrop. In addition, all six females mated to escalation males which intruded into the territory of another playback male chose a male who had a higher song output in relation to playback than the female's mate. All these chosen males sang a greater number of songs relative to the playback (Wilcoxon signed-ranks test, $t=0$ and $p=0.03$) (figure 3a), sang a greater number of phrases per song relative to the playback ($t=0$ and $p=0.03$) (figure 3b) and had a faster response in relation to the playback than did the females' mates ($t=0$ and $p=0.03$) (figure 3c).

4. DISCUSSION

McGregor & Dabelsteen (1996) defined eavesdropping as extracting information from interactions between others (e.g. the relative singing behaviour of males). The subsequent behaviour of the eavesdropper may then be based on this information. Females in our study were more likely to intrude if their mate's song output was low relative to the playback. Furthermore, females tended to intrude into territories of males who had a higher relative

Table 1. *Differences in absolute versus relative song output during playback and their effect on female intrusions*

(Median values are given, with ranges of the data in parentheses. Tests are two-tailed Mann–Whitney *U*-tests. The female in dyad 8 was excluded from analysis of intrusion behaviour due to the ambiguous foray of this pair during observations. Inclusion of this female as ‘intruding’ does not alter the results presented.)

measures of male singing	de-escalation treatment (<i>n</i> = 9)	escalation treatment (<i>n</i> = 9)	<i>U'</i>	<i>p</i>	female intrudes (<i>n</i> = 8)	female does not intrude (<i>n</i> = 9)	<i>U'</i>	<i>p</i>
absolute singing behaviour								
total number of songs	31 (21–99)	48 (13–73)	43	0.8300	58 (13–99)	36 (21–64)	44	0.44
average number of phrases per song	5.4 (3.25–8.2)	4.6 (2.4–6.7)	53.5	0.2500	4.4 (2.4–6.7)	5.4 (3.3–8.2)	47.5	0.27
average delay to opponent's song (s)	3.2 (1.1–8.1)	5.35 (3.75–7.8)	67	0.0200	4.8 (1.1–7.8)	3.4 (1.8–8.1)	47.5	0.27
relative singing behaviour compared to playback								
total number of songs (male relative to playback)	1.2 (1.0–1.5)	0.9 (0.4–1.0)	79	0.0007	0.9 (0.4–1.5)	1.1 (0.6–1.4)	52	0.12
average number of phrases per song (male relative to playback)	2.2 (1.5–3.0)	0.8 (0.5–1.0)	81	0.0003	0.8 (0.5–1.9)	1.7 (0.7–3.0)	59	0.03
average delay to opponent's song (male relative to playback)	1.0 (0.4–2.2)	7.4 (4.1–10.4)	81	0.0003	8.6 (0.5–10.4)	1.1 (0.4–7.0)	61	0.02

Figure 3. (a) Number of songs relative to the playback, (b) number of phrases per song relative to the playback, and (c) delay in response relative to the playback between chosen males (occupant of the territory upon which the female intruded) and female's mate's. Data are from the six females mated to escalation treatment males who intruded into territories of males involved in playback treatments. Comparisons are Wilcoxon signed-ranks (all $p = 0.03$).

song output towards the playback stranger than had the females' mates, suggesting that females were eavesdropping on the interactions we created. This is supported by our finding that absolute measures of singing by a female's mate had little influence on whether or not she would subsequently intrude. Thus, it is the interaction—the singing behaviour of the mate or neighbour relative to playback—that contains the relevant information for females, fulfilling the definition of eavesdropping. Our results not only indicate transitive inference of relative assessment, but also suggest that females are able to assess a network of signalling males (Dabelsteen & McGregor 1996; McGregor & Dabelsteen 1996).

Our study provides insight into possible mechanisms that females may use in assessing potential extra-pair partners. However, it remains to be seen whether intrusions lead to mixed paternity of clutches. No extra-pair copulations were witnessed during any of the intrusions in this study. However, in other species, the number of extra-pair copulations witnessed during

intrusions (Neudorf *et al.* 1997; Stutchbury 1998) did not necessarily coincide with the levels of extra-pair paternity found (Stutchbury *et al.* 1997). Furthermore, within-pair copulations were rarely observed in our population, despite extensive observations. The witnessed intrusions may also have been attempts by females to gather more information on the neighbouring males prior to any actual copulation. As our playbacks randomly assigned males into escalation and de-escalation treatments, the information females gathered by eavesdropping may have countered previous assessment of the relative quality of the two males. Thus, females may have intruded in attempts to verify information. Either interpretation of the data suggests females are highly attentive to the performance of males during territorial interactions.

Our study has shown that females discriminate between males on the basis of short-term behavioural differences. This is interesting because recent studies on great tits have found no indications that extra-pair males differ from the females' mates in morphological characteristics and, thus,

did not support predictions associated with the 'genetic benefits' hypothesis of why females pursue extra-pair copulations (Krokene *et al.* 1998; Strohbach *et al.* 1998). Previous studies that have found that females prefer a particular subset of males as extra-pair partners have found that the traits that distinguish males are often behavioural, such as song or dominance rank, rather than morphological (Smith 1988; Hasselquist *et al.* 1996; Kempenaers *et al.* 1997; Otter *et al.* 1998). This supports the importance of behavioural cues during extra-pair assessment (Møller & Ninni 1998; Otter *et al.* 1999), and emphasizes that such traits should be considered alongside their morphological counterparts prior to discounting the possibility that females discriminate between extra-pair partners based on disparity in perceived quality.

The significant difference in intrusion rates detected in our study is all the more notable because of the relatively short playbacks (6 min of treatment over two days) and brief observation period for detecting intrusions (15 min). This suggests that females have been selected to pay close attention to the outcome of territorial singing interactions. It is also possible that the effect of playback is long lasting and influences the relative fighting ability of males for several hours after playback. Thus, females could continue to discriminate between males long after the playback treatments had finished.

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