Anyone listening? No evidence for eavesdropping on male singing interactions in the great tit, *Parus major*

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Observing interactions between others can provide important information to individuals. Male songbirds often engage in singing contests where they vary the type and timing of signals and provide eavesdropping individuals with information about their competitiveness. How this information is used and its effect on subsequent spatial behaviour and reproductive decisions of eavesdroppers is not well understood. Here we tested whether great tits use information gathered by eavesdropping on male singing interactions to assess rivals and (potential) mates. We used interactive playback experiments to engage territorial males in song contests with either a more (song overlapping and more persistent singing) or less challenging (song alternating and less persistent singing) intruder. We followed male and female movements by automated radiotracking, determined paternity using microsatellite analysis and maternal investment by quantifying egg weights and provisioning behaviour. We expected that mates of males exposed to the challenging treatment would subsequently foray more often off territory to assess other males and potential extrapair mates and invest less in their broods. Moreover, we expected that neighbours would adjust their foraging behaviour according to information gained by eavesdropping. Females, however, did not alter their foraying behaviour or brood investment and neither female nor male neighbours changed their visiting behaviour to playback territories. Our results provide no evidence that females used information gathered by eavesdropping on asymmetric song interactions in reproductive decisions or that song interactions affected movements across territories in the neighbourhood. Overlapping or singing for a longer time on an intruded upon territory may not always be perceived as a higher level of threat, and reproductive decisions and assessment of familiar individuals are likely to be based on multiple sources of information rather than on a single interaction.

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For many animals, social information plays a central role in individual decision making and can influence the choice of, for example, foraging places, breeding sites or mates. One way of gathering information is through observing the outcome of interactions between others (Danchin, Giraldeau, Valone, & Wagner, 2004). Aggressive interactions between males, for example, can provide information to uninvolved bystanders ('eavesdroppers') about motivation and fighting ability of both contestants and be used by these other individuals to adjust their own behaviour (Doutrelant & McGregor, 2000; Mennill, Ratcliffe, & Boag, 2002; Oliveira, McGregor, & Latruffe, 1998; Silk, 1999). In many territorial songbirds males engage in singing interactions and such vocal interactions are particularly well suited for eavesdropping, as acoustic signals travel some distance and thus allow others to eavesdrop and gain information without risking close-range interactions (McGregor & Peake, 2000; Todt & Naguib, 2000). Several studies have shown that both male (Akçay, Tom, Campbell, & Beecher, 2013; Naguib & Todt, 1997; Peake, Terry, McGregor, & Dabelsteen, 2001; Sprau, Roth, Amrhein, & Naguib, 2012) and female (Amy et al., 2008; Garcia-Fernandez, Amy, Lacroix, Malacarne, & Leboucher, 2010; Mennill et al., 2002; Otter et al., 1999) songbirds eavesdrop on such interactions.

Countersinging males can adjust their singing by either changing the type of signal or the timing of signals. How male songbirds use their signals in such singing interactions might communicate their fighting ability or willingness to escalate an interaction (Todt & Naguib, 2000). Matching the signal type of the other individual is often associated with escalated encounters and

has been interpreted as a signal of directed aggression or arousal in some species and contexts (Akçay et al., 2013; Krebs, Ashcroft, & Orsdol, 1981; Mennill & Ratcliffe, 2004a; Vehrencamp, 2001; but see for example Baker, Wilson, & Mennill, 2012; Searcy, Anderson, & Nowicki, 2006; Todt, 1981). Similarly, overlapping another's signal in time by starting a song before the opponent has finished singing has been shown to elicit strong vocal responses and has been interpreted as a signal indicating the willingness to escalate an interaction (Brindley, 1991; Mennill & Ratcliffe, 2004b; Naguib & Todt, 1997; but see for example Akçay, Porsuk, Avşar, Çabuk, & Bilgin, 2020; Wilson, Ratcliffe, & Mennill, 2016). Whether overlapping in song contests is always a signal and to what extent it signals a higher level of threat or arousal has been discussed critically as studies have varied in their findings and interpretations (Helfer & Osiejuk, 2015; Naguib & Mennill, 2010; Searcy & Beecher, 2009, 2011). While most playback experiments provide clear evidence that birds respond differently to overlapping versus alternating playback (reviewed in Naguib & Mennill, 2010), birds often do not increase overlapping rates when responding to playback during a simulated territorial intrusion and degree of overlap does not necessarily correlate with close approach (Helfer & Osiejuk, 2015; Searcy & Beecher, 2009). In the great tit, several studies have shown that male vocal responses to overlapping and alternating playbacks differ (Amy, Sprau, De Goede, & Naguib, 2010; Dabelsteen, McGregor, Shepherd, Whittaker, & Pedersen, 1996; Langemann, Tavares, Peake, McGregor, & Mc Gregor, 2000; Peake et al., 2001, 2002). Moreover, females have been found to approach males that overlap simulated intruders more often (Otter et al., 1999). However, some studies have reported no (Dabelsteen et al., 1996; Peake et al., 2001) or even a negative association between overlapping and approach or aggressive responses (Akçay et al., 2020), suggesting that overlapping may not always signal immediate aggression towards intruders in great tits.

Previous studies on songbirds have shown that singing on an intruded upon territory for longer and more persistently by moving within the territory elicits a stronger response by resident males to intruders (Poesel & Dabelsteen, 2005; Sprau, Roth, Amrhein, & Naguib, 2014). Eavesdropping on interactions between males and the singing behaviour of intruders could thus inform other males about the level of arousal or threat posed by rivals (Mennill & Ratcliffe, 2004a; Naguib, Amrhein, & Kunc, 2004; Peake et al., 2002).

As with other aspects of male singing (reviewed in Catchpole & Slater, 2008; Searcy & Yasukawa, 1996), countersinging by interacting males may play an important role in female choice of both social and copulation partners. Females may also eavesdrop on interactions to assess the quality of their mate and adjust their level of maternal investment accordingly ('differential allocation'; reviewed in Sheldon, 2000). Only a few studies have tested whether female birds use eavesdropping on male singing interactions in reproductive decision making. Otter et al. (1999) engaged territorial male great tits in interactive playback experiments and subsequently visually observed female movements to territories of other males. While they found that female great tits paired with a male whose songs were overlapped more often were more likely to foray into territories of other males (Otter et al., 1999), these forays did not lead to a higher likelihood of having extrapair offspring (Otter et al., 2001). In contrast, the mate choice decisions of female black-capped chickadees, *Poecile atricapillus*, were associated with information gained through eavesdropping: High-ranking males that 'lost' a song contest against a simulated intruder, because their song was overlapped and matched more often, had a higher proportion of extrapair offspring in their brood than high-ranking males that did not

'lose' the interaction. 'Losing' or 'winning' an interaction did not, however, influence paternity in the broods of low-ranking males (Mennill, Boag, & Ratcliffe, 2003; Mennill et al., 2002). Female domestic canaries, *Serinus canaria*, showed a preference for males that more frequently overlapped their opponent's song and performed more copulation solicitation displays when exposed to song they previously heard to be the overlapping song in an interaction (Amy et al., 2008; Leboucher & Pallot, 2004). Females stimulated with song of an overlapping male also laid eggs with a higher yolk content than females that were exposed to song that had previously been overlapped by another male. Other measures of resource investment such as egg mass and testosterone concentration in the yolk were not affected (Garcia-Fernandez et al., 2010). The fact that in some species eavesdropping is associated with mating decisions while in others it is not suggests that the role male song contests play in female assessment of potential mates is complex and not fully understood. Apart from the study on the domestic canary under laboratory conditions, we also know little about how information gained through eavesdropping affects female allocation of resources to their brood. Moreover, most studies have focused on the eavesdropping responses of resident males and/or their mates, and little is known about how singing interactions, which can be heard across a larger neighbourhood, affect the movement and behavioural decisions of eavesdropping neighbours (Bircher & Naguib, 2020; Fitzsimmons, Foote, Ratcliffe, & Mennill, 2008a; Naguib et al., 2004; Snijders, van Oers, & Naguib, 2017). Our understanding of the role of singing interactions in social and communication systems therefore remains incomplete.

In this study, we tested whether female and male great tits eavesdrop on male song interactions and alter their behaviour based on the information provided by the asymmetry in the interaction. We used interactive playback experiments to simulate territory intrusions just before and during egg laying, when females are assumed to be fertile (Birkhead, 1992) and might engage in extrapair copulations or change investment in eggs. We deployed an automated radiotracking system to track movements of both females and males into other territories ('forays'), Bircher, van Oers, Hinde, & Naguib, 2020, determined paternity in broods of playback subjects and measured egg weights and provisioning as a measure of female investment in their broods. We simulated intruders that overlapped a male's song and sang on the territory for a longer time versus intruders that alternated singing and sang for a shorter time. In line with previous playback studies in great tits (Otter et al., 1999; Peake et al., 2001, 2002), we refer to the overlapping intruder as 'more challenging' and the subject that is confronted with such an intruder as 'losing' the interaction. Assuming that intruders that overlap and sing for longer are perceived by the resident as more persistent and a higher threat, we expected that females paired with males exposed to the overlapping treatment would assess their mate as being less competitive. We expected these females to be more likely to foray off territory to assess other males, lay lighter eggs and reduce their nest visit effort in response to the playback treatment (Garcia-Fernandez et al., 2010; Mennill et al., 2002; Otter et al., 1999). Assuming that more challenged ('losing') males are perceived as less attractive, we also predicted that neighbouring females would be less attracted to territories of these males. In contrast we predicted that neighbouring males would be more likely to intrude upon the territories of these males if they are perceived as 'losing'. We subsequently also tested whether male and female neighbours change their overall foraying activity in response to playbacks. We expected that male neighbours would foray less after playbacks simulating a more challenging intruder, as they would be more prone to stay on their own territory to

guard it. On the other hand, we expected female neighbours to increase overall foraying activity as they may be incited to assess intruders in the surrounding area.

METHODS

Study Population and General Field Methods

We conducted this study in a long-term study population of great tits in Westerheide, near Arnhem, The Netherlands. Westerheide is a forest of mixed wood with approximately 200 nest-boxes distributed over a 1000 × 1200 m area. From mid-March to mid-June, we routinely checked nestboxes to determine the start of nest building, egg laying, hatching and fledging. At the end of March, prior to the start of nest building, we equipped 84 birds with an Encounternet tag and we carried out playbacks just before and during egg laying (see below). We caught parents when the chicks were 10 days old (day 0 being the hatching date) using spring traps and equipped them with an RFID tag embedded in a leg ring (Eccel Technology LTD, Glenfield, U.K.). We removed all remaining radiotags (Encounternet) from birds at that point. We measured tarsus length and wing length (as length of the third primary) to the nearest mm and recorded body weight. We ringed chicks with an individual aluminium ring when they were 14 days old and measured their tarsus length and body weight. For paternity analysis, we collected two blood samples of approximately 10 μL from the brachial vein of each parent and one sample of each chick. We suspended collected blood samples in Eppendorf tubes containing 1 mL of Queen's lysis or Cell lysis buffer.

Playback Stimuli

To construct the songs used as playback stimuli we used songs of male great tits recorded at least 8 years before the experiment at our study site. It was thus unlikely that individuals exposed to the playbacks had heard the exact same songs before. All stimuli songs were recorded using a Sennheiser ME66/K6 or ME67/K6 microphone (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) connected to a Marantz PMD660 recorder (D&M Holdings Inc., Kanagawa, Japan) with a sample frequency of 44.1 kHz and resolution of 16 bit. We constructed 44 stimuli songs using songs from 44 different males in Avisoft SASLAB PRO (Raimund Specht, Berlin, Germany) following the procedure in Amy et al. (2010): songs were filtered with a 2000 Hz high-pass filter and adjusted to the same peak amplitude. We then constructed songs that each consisted of six identical syllables with two or three elements at a syllable rate natural for the respective song type. Stimulus songs used in playbacks and included in analyses ($N = 33$) had a duration of 2.5 ± 0.09 s (mean ± SE).

Playback Protocol and Male Vocal Response Measures

We carried out 44 playbacks in total but excluded 11 playbacks from all analyses as they were conducted when the female was already incubating ($N = 5$), the nests were abandoned during egg laying ($N = 2$), or the recordings were not of sufficient quality to measure the vocal response variables and verify that the treatment was successful ($N = 4$). Of the remaining 33 playbacks, most ($N = 28$) were carried out with the social mate of radiotagged females. For the analysis of neighbour responses to playback we also included playbacks conducted at boxes of females without a radiotag ($N = 5$). All playbacks were conducted between 0700 and 1400 hours, except one that took place at 1600 hours. We carried out playbacks close to the nestbox of the female just before or during egg laying (on average on day 4 of egg laying). We

determined the nestbox of radiotagged females during regular tracking rounds in the evening to detect females when roosting. We used two Megaboom loudspeakers (Ultimate Ears, Newark, CA, U.S.A.) placed within a maximum distance of 20 m from each other and the nestbox. Distances were measured with a Leica Rangemaster CRF 900 (Leica Geosystems AG, Heerbrugg, Switzerland). Playbacks consisted of a lure phase and an interactive phase. We played the lure song from one of the two loudspeakers and subsequently the interactive treatment from the other loudspeaker to standardize the distance between the subject and the interactive loudspeaker. We used a lure song to standardize the context of the playback interaction and incite the subject to sing, even though using a lure may level out differences in initial responses. All songs were played at a sound pressure level of 84–86 dB SPL at 1 m. This broadcast level was determined beforehand using the playback equipment and a Voltcraft Plus digital sound-level meter 200 with A weighting and fast response at a location outside the study site. We measured the SPL at 1 m for both a sine tone (2 kHz) and an example great tit song normalized to the same peak amplitude as the playback songs. Our broadcast level was thus similar to the estimated natural SPL at 1 m for great tit song (Blumenrath & Dabelsteen, 2004). The lure song was prepared in the same way as all other playback stimuli and we used the same lure song for all subjects. For the interactive part of the playback, we randomly assigned a different stimulus song to each bird. Because stimuli songs were assigned randomly and because we did not determine the full song repertoire size of all subjects, we did not consider whether the song we broadcast could be type matched by the specific subject. We initiated each playback when the female was present in the vicinity of the nestbox (determined by radiotracking for tagged females) by playing the noninteractive lure song on a loop for a maximum of 2 min to alert the social mate and incite it to sing. When the male started to sing, we stopped the lure song and started the interactive part of the playback with one of the two treatments (overlapping or alternating). If the male did not respond with song after 2 min of lure, we aborted the playback and tried again the next day.

In the alternating treatment ($N = 15$), we waited to broadcast a song until the male had finished his song and we stopped the playback if the male ceased to sing completely. In the overlapping treatment ($N = 18$), we broadcast a song as soon as the male started a song and we continued broadcasting songs at regular intervals (up to a maximum of 36 songs) even if the male ceased to sing completely. We played a maximum of 22 songs (range 4–22) in the alternating and 36 songs (range 26–36) in the overlapping treatment. We overlapped $61.4 \pm 4\%$ (mean ± SE) of the songs sung by a subject in the overlapping and $6.6 \pm 1.8\%$ (mean ± SE) in the alternating treatment, which is similar to the rate used in a previous study (Amy et al., 2010).

We recorded the songs of the focal male during the interactive playback with a Sennheiser M66/K6 microphone on to one channel with a Marantz PMD660 recorder (sample frequency 44.1 kHz; resolution 16 bit). On the other channel, we recorded spoken notes with a second microphone. From the recordings made during and after the playback we measured for each male (1) the song rate during the interaction (number of songs per min), (2) the mean duration of songs during the interaction, (3) the mean proportion of songs overlapped by the simulated intruder and (4) the number of songs within 1 min after the treatment ended. All analyses were done in Avisoft SASLAB PRO. All measures are absolute for either the subject (song rate, duration of songs, number of songs in the minute after treatment) or simulated intruder (proportion of subject songs he overlapped), thus did not compare the response of the subject relative to that of the simulated intruder. We also noted the closest approach to the treatment loudspeaker for each male

(0 m, <10 or > 10 m) measuring the distance between loudspeaker and the closest song post with a Leica Rangemaster CRF 900 or with a measuring tape. We only tested males on the same day that were several territories apart.

Radiotracking and Spatial Response Measures

We used the automated radiotracking system 'Encounternet' to follow the movements of birds (Bircher et al., 2020; Mennill et al., 2012; Snijders, van Oers, et al., 2017; Snijders et al., 2014). Encounternet consists of tags that send out digital individual ID signals every 5 s and receivers that store all signals of tags within range together with a signal strength measure (RSSI) and a time stamp. We caught female and male great tits during a routine roost check on 22 March 2017 and fitted them with an Encounternet tag weighing approximately 1.2 g. Breeding birds were recaught during provisioning in the nestling period using spring traps when nestlings were 10 days of age and all remaining tags removed. From the end of March onwards we regularly checked nestboxes and mounted Encounternet receivers in trees above nestboxes when nest building activity started. We used the RSSI signal strength measure to estimate the distance between a bird and a receiver. We evaluated all movements as extraterritorial forays when birds approached a nestbox other than their own within 15 m and remained within that range for at least 10 s. This way we excluded cases where birds moved past another nestbox without really staying there. We ran the Encounternet system from 28 March to 18 May. We did not have tracking data available for two of the females involved in playbacks, due to a technical problem with their radiotags. For all radiotagged females involved in playbacks with tracking data available ($N = 27$) we recorded forays made during the day before and day after playback. When a female was successfully tracked, but no foray was recorded on the respective days, we added a zero to the data set. We did not analyse the spatial response to playbacks of the playback subjects themselves as only eight of them were radiotagged.

For the analysis of the neighbour spatial response, we included all individuals that were likely to hear the playback interaction at the respective nestbox. The range over which a signal can be detected and recognized by conspecifics depends on the signal characteristics, level of background noise, transmission characteristics of the environment and the sensitivity of the receiver (Brumm & Naguib, 2009). Great tit song has been estimated to range as far as ca.180 m (Blumenrath & Dabelsteen, 2004). We thus included all neighbours within 150 m of the boxes exposed to playback in the neighbour response analysis. We excluded playbacks at 11 nestboxes from the analysis as they did not have any radiotagged neighbours within 150 m or those neighbours never visited the area of the playback during the tracking season. All remaining boxes ($N = 22$, of which 10 were exposed to an overlapping and more persistent treatment and 12 to an alternating and less persistent treatment) had at least one (and maximum five) radiotagged neighbours within 150 m. In total 31 individuals ($N_{females} = 20$, $N_{males} = 11$) were included as neighbours. We recorded the number of visits by female and male neighbours to playback territories and the number of female and male neighbours visiting during the day before and day after playback for each box. When no visits were recorded during the respective days by females and/or males, but the target nestbox in the respective territory did have female and/or male neighbours that visited at other times, we added a zero to the data set accordingly. Subsequently, we also analysed the overall foraying behaviour of close neighbours before and after playbacks, including their forays to all monitored territories ($N = 74$) within the study site, not only the territories within which playbacks took place. Some individuals ($N = 11$) were

neighbours to more than one playback territory and the treatment days of these playbacks overlapped; thus, we excluded these individuals from this analysis. We had data on overall foraying behaviour for a total of 30 neighbours ($N_{females} = 20$, $N_{males} = 10$) of 28 playback subjects ($N_{overlapping} = 14$, $N_{alternating} = 14$). We recorded the number of forays these individuals made, on the day before and day after playbacks took place, into neighbouring territories where playbacks occurred. If individuals were successfully tracked during the entire time, but no forays were recorded on these days, we added a zero to the data set accordingly.

Egg Weights and Female Provisioning Behaviour

We used egg weight and provisioning rate of offspring as a measure of female investment in broods as previous studies on differential allocation have indicated that females vary egg size and provisioning rate according to the quality of their mate. For example, in mallards, *Anas platyrhynchos*, females lay larger eggs when paired with more attractive males (Cunningham & Russell, 2000). In blue tits, *Parus caeruleus*, females provision their offspring at a lower rate when paired with less attractive males with reduced UV coloration which leads to reduced skeletal growth in offspring (Limbourg, Mateman, Andersson, & Lessells, 2004). For 23 of 33 nestboxes in the playback territories, we weighed eggs laid before and after playback to the nearest 0.01 g using a digital scale. Between day 12 and 14 after hatching we recorded female nest-visiting behaviour continuously during an entire day using RFID readers (Dorset ID, Aalten, The Netherlands) with antennas mounted around the nestbox opening. The RFID data did not allow us to determine whether females fed chicks during all visits to nestboxes. We therefore used these nest visits as an estimation of provisioning. We obtained data on provisioning behaviour for 29 of the 33 females that had potentially eavesdropped on a playback interaction. Since females may adjust provisioning frequency and/or duration, we quantified both the time (h) between the first and the last presumed visit ('provisioning time') and the provisioning rate (number of nest visits/provisioning time per h) for each female. Females sleep in the nestboxes overnight; thus, we excluded the very first log of the day, as this was likely to be the time the female emerged from the box and treated the second log as the first provisioning visit. We treated transponder reads within 17 s of each other as one visit, as they were likely to be caused by the female staying in the nestbox or near the nestbox opening when feeding as a comparison of RFID data and video recordings has shown (L. Zandberg, personal communication, 1 February 2018).

Paternity Analysis

We used five microsatellite markers to determine parentage: *PmaTAGAn71*, *PmaGAn27*, *PmaTGAn33*, *PmaC25* and *PmaD105* (Saladin, Bonfils, Binz, & Richner, 2003). We extracted DNA from blood samples with the FavorPrep 96-well Genomic DNA Kit (Favorgen Biotech Corporation, Ping-Tung, Taiwan) and amplified the isolated DNA with the QIAGEN multiplex PCR kit (QIAGEN GmbH, Hilden, Germany) following the manufacturer's protocol. We prepared PCR products on ABI plates with a molecular size standard (GeneScan LIZ, Applied Biosystems, Foster City, CA, U.S.A.). The sequence analysis of PCR products was carried out by BaseClear BV (BaseClear BV, Leiden, The Netherlands). We determined the size of the sequenced PCR products and derived the genotype for each individual using GeneMapper v. 5.0 (Applied Biosystems). We determined whether a chick was within-pair or extrapair with CERVUS v. 3.0.7 (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998) testing all chicks against their putative fathers using the following

parameters: 98% of loci typed, error rate 0.01%, 10 000 cycles and two candidate parents. We treated chicks as extrapair if there were two or more mismatches with the putative father and the putative father was not the most likely parent according to the analysis in CERVUS. The combined exclusion probability for all microsatellites was > 99.9%. One of our loci deviated significantly from the Hardy–Weinberg equilibrium when the genotypes of all sampled individuals in the 2017 study population were included in the analysis ($PmaTAGAn71$: $\chi_{10}^2 = 37.54$, $P \leq 0.001$), most likely due to the family structure of the data. We determined paternity in 27 of the 33 playback boxes that were included in the analysis, of which 10 contained extrapair offspring (EPO), a typical proportion in our population (van Oers, Drent, Dingemanse, & Kempenaers, 2008). We were unable to determine paternity in the remaining six boxes, because we did not catch the father to obtain a blood sample or we did not have blood samples available for chicks as they died before the age of 2 weeks.

Statistical Analysis

Sample sizes vary between analyses because we were not able to collect all data for all nestboxes or individuals. We conducted all statistical analysis in R (R Core Team, 2020) and fitted all generalized linear (mixed) models and linear mixed models using the packages lme4 (Bates, Mächler, Bolker, & Walker, 2015) and MASS (Venables & Ripley, 2002). To test whether treatments affected measures of male vocal response and female provisioning behaviour (provisoning time and provisioning rate), we used unpaired t tests for normally distributed and Mann–Whitney rank sum tests for non-normally distributed data. We tested whether egg weight was affected by treatments using a linear mixed model with time of laying (before or after playback) and treatment and their interaction (laying time*treatment) as fixed effects and nestbox ID as a random factor, and determined significance using likelihood ratio tests (LRT). To compare female foraying behaviour and neighbour visiting behaviour between the day before and the day after the treatments we were not able to use Mann–Whitney rank sum tests, as there were many cases in which both counts were zero and the test could not compute an exact P value. We thus used Poisson generalized linear models to model counts of forays and number of boxes visited on these days. For overdispersed counts we used quasi-Poisson generalized linear models. To test whether the number of forays females made and the number of boxes females visited (response variables) differed between the day before and after a playback we fitted a Poisson or quasi-Poisson generalized linear model with the day relative to the day of playback (-1 and 1) as fixed effect. We fitted a separate model for females exposed to an overlapping/persistent and alternating/less persistent treatment. We tested whether females with EPO differed from females without EPO in their response to treatments by fitting a Poisson or quasi-Poisson generalized linear model with presence of EPO (yes/no) and treatment and their interaction (EPO*treatment) as fixed effects and the number of forays made and number of boxes visited the day after the playback day as response variables. To test whether the number of visits by neighbours and the number of neighbours visiting a playback nestbox (response variables) differed between the day before and after a playback we fitted a Poisson or quasi-Poisson generalized linear model with the day relative to the day of playback (-1 and 1) as fixed effect. We tested male and female neighbours separately for each treatment. Additionally, we tested whether the number of total forays by female neighbours (including forays to nestbox areas other than playback boxes) differed between the day before and day after playbacks. We fitted a quasi-Poisson generalized linear (mixed) model for each

treatment separately with the day relative to the day of playback (-1 and 1) as fixed effect, adding individual ID as a random factor when some individuals in the respective data subset were neighbours to several boxes.

Ethical Note

Birds involved in playback experiments were tagged as part of a larger study on foraying behaviour from 2016 to 2017 and the permission for this work was granted by the Dutch legal entity Dier Experimenten Comissie (DEC) no. NIOO-10.05 to MN and KvO and no. NIOO 12.02 to KvO. The Encounternet tags we used were designed to be as small and lightweight as possible, while still providing automated simultaneous tracking of multiple individuals. The weight of all tags deployed in 2016 and 2017 (1.26 ± 0.05 g) was within the natural range of daily body weight changes of great tits (van Balen, 1967). We tagged birds early in the breeding season before the start of egg laying. Birds were removed from roosting boxes during a routine roost check and brought to a car to fit tags using nylon leg-looped backpack harnesses. The entire procedure takes only a few minutes and afterwards birds were immediately brought back to the box they were caught in. We removed any remaining tags during standard capture sessions at the end of the season (when chicks were 10 days of age), up to 2 months after tagging. An analysis of possible tagging effects using the same type of tags (among others) in the same study population showed that tag effects depend on the timing of tagging (season start versus during chick feeding) and the general environmental conditions of the breeding season: Under normal conditions at our study site and if fitted on birds early in the season as we did in 2016 and 2017, these tags were not found to have a negative impact on the likelihood of a bird breeding, provisioning behaviour of parents and condition of chicks raised by tagged parents (Snijders, Nieuwe Weme, et al., 2017).

RESULTS

Male Vocal Response

In the overlapping treatment, playbacks lasted significantly longer (unpaired t test: $t_{31} = -3.1$, $P = 0.005$) and songs of subjects were overlapped more often (Mann–Whitney rank sum test: $W = 0$, $P < 0.001$; Fig. 1). Playbacks lasted for 4.2 ± 0.25 min (mean $\pm$ SE) in the overlapping treatment and 2.9 ± 0.36 min (mean $\pm$ SE) in the alternating treatment. Males exposed to the overlapping treatment ($N = 18$) did not differ from males exposed to the alternating treatment ($N = 15$) in their song rate (unpaired t test: $t_{31} = 1.16$, $P = 0.26$), mean song duration (Mann–Whitney rank sum test: $W = 161.5$, $P = 0.35$), number of songs during the minute after playback (Mann–Whitney rank sum test: $W = 139$, $P = 0.89$) and closest approach to the loudspeaker (Fisher's exact test: $P = 0.26$).

Female Spatial Behaviour

Foraying behaviour of radiotagged females with social partners exposed to a playback was not affected by either the overlapping or alternating treatment: Females did not differ in the number of forays made or in the number of other territories visited between the day before and after the playback (Fig. 2; female forays overlapping treatment: GLM: $t_{29} = -0.11$, $P = 0.91$, $N = 15$; female forays alternating treatment: GLM: $t_{23} = 0.0$, $P = 1$, $N = 12$; territories visited by females overlapping treatment: GLM: $t_{29} = 0.60$, $P = 0.56$, $N = 15$; territories visited by females alternating treatment: GLM: $Z_{23} = 1.26$, $P = 0.21$, $N = 12$). Females with EPO
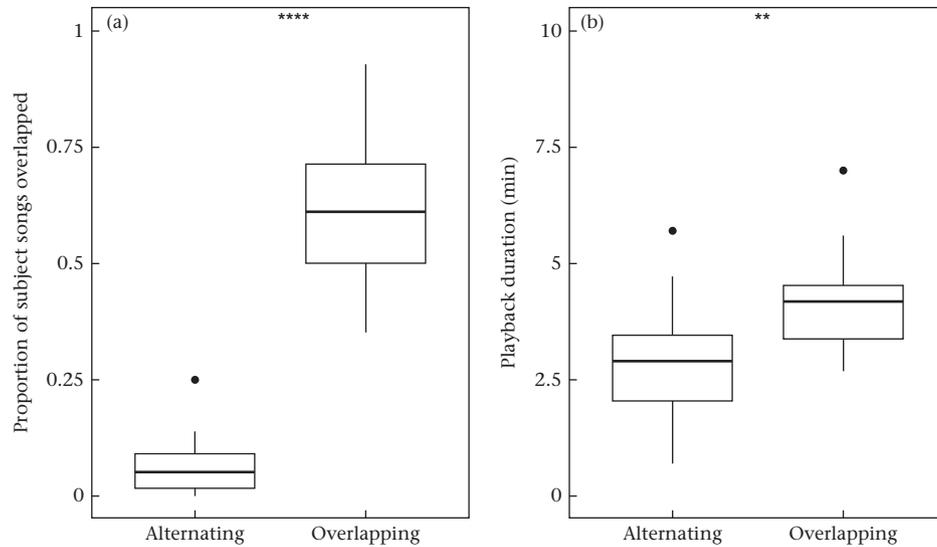
Figure 1. Comparison of playback treatments. (a) Proportion of songs of subjects that were overlapped and (b) duration of playbacks in the overlapping treatment ($N = 18$), which simulated a more challenging and persistent intruder, and in the alternating, less challenging treatment ($N = 15$). Each box represents the interquartile range and median, whiskers represent the range of data within 1.5 times the interquartile range, and dots represent data points exceeding that range. ****$P < 0.0001$; **$P < 0.01$.
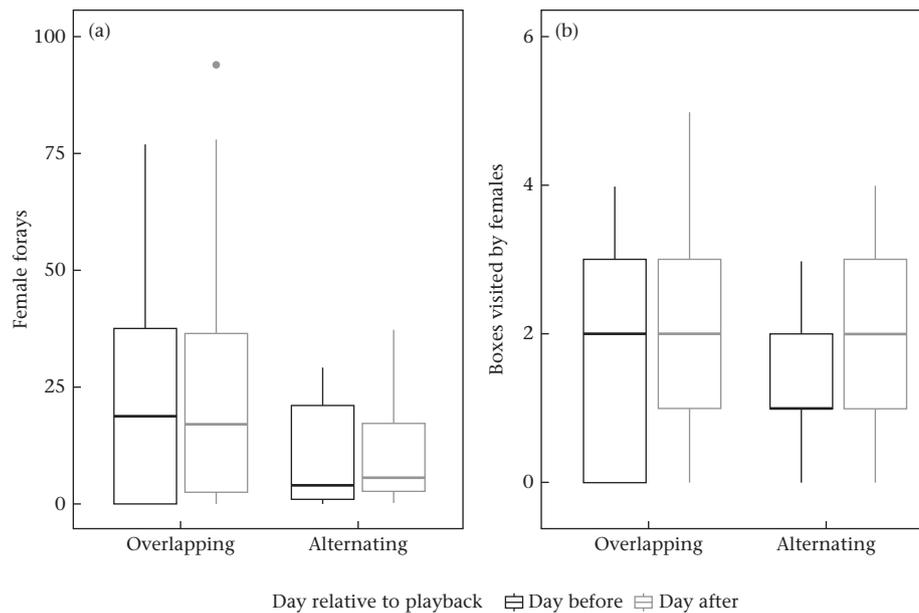

Day relative to playback   ⊟ Day before   ⊟ Day after

Figure 2. Spatial response of females. (a) The number of forays females made and (b) the number of nestbox areas they visited compared between the day before and the day after the playback for the overlapping ($N_{females} = 15$) and the alternating treatment ($N_{females} = 12$). Box plots as in Fig. 1.

($N = 10$) did not differ in their response to the playback treatments from females without EPO ($N = 17$; number of forays on day after playback: EPO*treatment: GLM: $t_{26} = 1.2$, $P = 0.24$; number of other boxes visited on day after playback: EPO*treatment: GLM: $Z_{26} = 0.75$, $P = 0.45$).

Egg Weights and Female Provisioning Behaviour

Eggs weighed on average 1.61 ± 0.02 g (mean $\pm$ SE), similar to what has previously been reported in this species (Lessells, Dingemanse, & Both, 2002). Eggs laid before and after an alternating treatment or before and after an overlapping treatment did not differ in their weight (LMM: $\chi^2_3 = 1.35$, $P = 0.72$, $N = 184$ eggs of 23 females). The duration between the first and the last provisioning visit on the day of observation lasted on average 12.7 ± 0.26 h

(mean $\pm$ SE). Parents made between 3.7 and 40.3 provisioning visits/h, a range that is similar to what has been reported elsewhere for great tits (Wilkin, King, & Sheldon, 2009). The average female provisioning rate was 23.37 ± 1.26 (mean $\pm$ SE) visits/h. Females with social mates exposed to overlapping treatments did not differ from females with social mates exposed to alternating treatments in the duration between the first and the last nestbox visit (Mann—Whitney rank sum test: $W = 77$, $P = 0.25$, $N = 29$) and provisioning rate (unpaired *t* test: $t_{27} = 0.81$, $P = 0.46$, $N = 29$).

Neighbour Spatial Behaviour

Visiting behaviour to playback nestbox areas of both female and male neighbours did not differ between the day before and day after for either treatment (Fig. 3; female visits overlapping
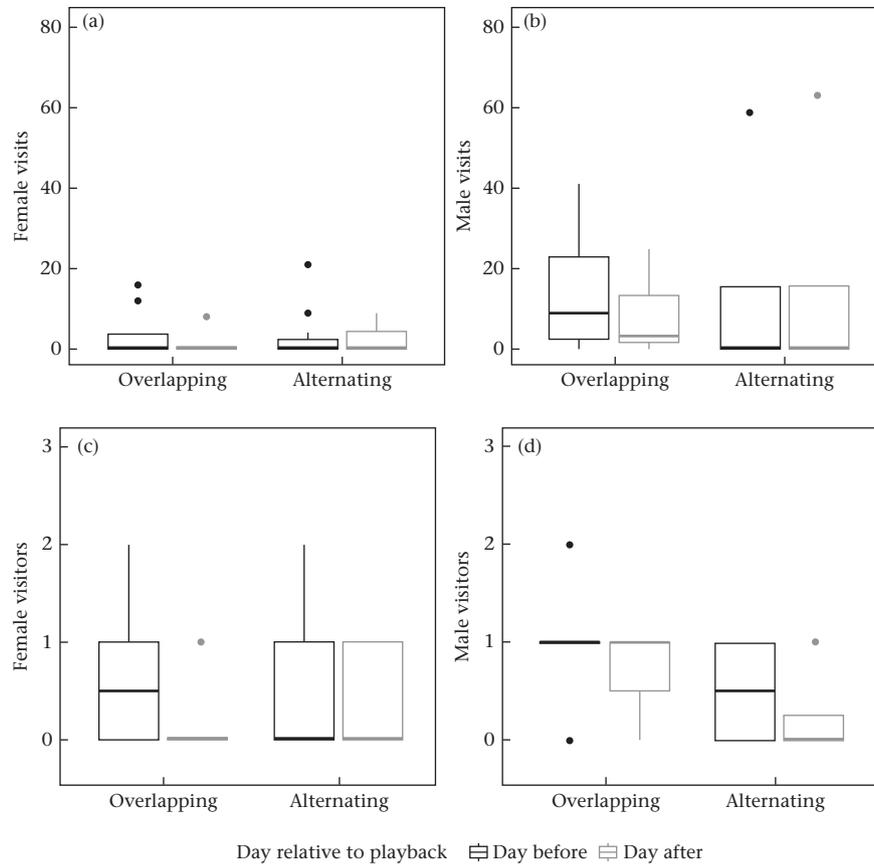
Figure 3. Visiting behaviour of close neighbours to playback territories. Number of (a, b) visits and (c, d) visitors to territories where overlapping and alternating playbacks took place compared between the day before and the day after the playback. (a, c) Female neighbours and (b, d) male neighbours ($N_{\text{overlapping boxes with female neighbours}} = 8$, $N_{\text{overlapping boxes with male neighbours}} = 7$, $N_{\text{alternating boxes with female neighbours}} = 11$, $N_{\text{alternating boxes with male neighbours}} = 4$). Box plots as in Fig. 1.

treatment: GLM: $t_{15} = -0.08$, $P = 0.3$, $N = 8$; female visitors overlapping treatment: GLM: $Z_{15} = -0.81$, $P = 0.14$, $N = 8$; male visits overlapping treatment: GLM: $t_{13} = -0.28$, $P = 0.39$, $N = 7$; male visitors overlapping treatment: GLM: $Z_{13} = -0.58$, $P = 0.56$, $N = 7$; female visits alternating treatment: GLM: $t_{21} = 0.38$, $P = 0.74$, $N = 11$; female visitors alternating treatment: GLM: $Z_{21} = 0.0$, $P = 1.0$, $N = 11$; male visits alternating treatment: GLM: $t_7 = 0.04$, $P = 0.97$, $N = 4$; male visitors alternating treatment: GLM: $Z_7 = -0.57$, $P = 0.57$, $N = 4$). Moreover, male and female neighbours did not change their overall foraging activity before and after treatments (overlapping treatment $_{\text{females}}$: GLMM: $t_{21} = 0.34$, $P = 0.73$, $N_{\text{females}} = 14$; alternating treatment $_{\text{females}}$: GLMM: $t_{14} = -1.02$, $P = 0.33$, $N_{\text{females}} = 11$; overlapping treatment $_{\text{males}}$: GLMM: $t_{10} = -1.65$, $P = 0.13$, $N_{\text{males}} = 7$; alternating treatment $_{\text{males}}$: GLM: $t_{17} = -0.6$, $P = 0.56$, $N_{\text{males}} = 9$).

DISCUSSION

In this study we generated asymmetric singing interactions between a territorial male and a simulated intruder: we exposed territorial male great tits to an intruder that either sang on the territory for longer and overlapped the subject's songs more often or sang for a shorter time and alternated songs with the subject. Whether or not the simulated intruder overlapped the resident's songs and was persistent, did not influence the behaviour of females paired to resident males. Females changed neither their foraging behaviour into core neighbouring territories nor their egg investment (egg weight) or nest visits (as proxy for provisioning) after playbacks. Females with broods containing extrapair offspring did not foray more often to other territories in response to intrusions than females without extrapair offspring. Neither female nor male neighbours changed their foraging behaviour in response to the simulated intrusions. These findings do not support our predictions that females and males respond to asymmetries in the singing interactions between the playback subject and the simulated intruder and differ from results of previous studies that showed differential effects of overlapping and alternating playback on eavesdropping individuals (reviewed in Naguib & Mennill, 2010).

We observed no difference in the subject's singing or approach behaviour in response to the two treatments, suggesting that song overlap and singing persistence by the intruder was not perceived as a larger threat by the resident. Studies on a range of species have shown that vocal responses of resident males depend on whether the playback overlaps or alternates with their songs (reviewed in Naguib & Mennill, 2010), specifically so in long-distance vocal interactions (reviewed in Naguib, Kunc, Sprau, Roth, & Amrhein, 2011). However, this has not been reported in all studies, and there is evidence in some species (Baker et al., 2012; Osiejuk, Ratyńska, & Cygan, 2004; Wilson et al., 2016), including great tits (Akçay et al., 2020), that overlapping an individual's song is unlikely to signal aggression, measured as spatial response. The function of song overlap as an aggressive signal during interactions therefore remains controversial (reviewed in Helfer & Osiejuk, 2015; Searcy & Beecher, 2009, 2011). The controversy, in part, may stem from different authors using the term 'aggressive' in different ways: song overlapping might not be used as an aggressive signal predicting attack during close-range conflicts but instead could be more

relevant at an earlier level of escalation such as during long-distance interactions or when no other information is available (Naguib et al., 2011).

Regardless of whether song overlap and persistence indicate a more threatening intruder in all contexts, there is ample evidence that females eavesdrop on male vocal interactions and use information gained by eavesdropping to (re)assess the quality of males relative to others and alter their reproductive decisions accordingly (Amy et al., 2008; Garcia-Fernandez et al., 2010; Mennill et al., 2002; Otter et al., 1999). However, we found no evidence that female great tits changed their foraying behaviour into other territories or their investment in clutches and brood attendance. Moreover, in our study females with broods containing extrapair offspring did not differ in their foraying behaviour in response to either treatment. Since we ascertained that radiotagged females were present during the entire playback via radiotracking and via visual observations for the untagged females, it is unlikely that the lack of response is due to females not having had the opportunity to eavesdrop on the interaction. Instead, it is possible that, in our study, being overlapped by another male's signal, in combination with the lack of the subject's response, was not indicative of 'losing' an interaction. Thus the interaction may have provided little information for females to reassess male quality. Otter et al. (1999) in a study on great tits also found no difference in the absolute singing responses by males to playback treatments. However, they did find a strong response by females paired to males subjected to overlapping playbacks. One reason may be that in addition to overlapping the resident's song, Otter et al. (1999) manipulated the number of phrases per song strophe. Song strophe duration has been shown to correlate with dominance in great tits (Lambrechts & Dhondt, 1986) and may therefore have provided eavesdropping females with information about male quality. A similar argument can be made for results of a study on black-capped chickadees (Mennill et al., 2002). Based on Mennill et al.'s (2002) study, we expected females mated to males whose song was overlapped to foray more often to assess other males. However, playback stimuli used by Mennill et al. (2002) overlapped and also frequency matched the songs of subject males. Because both overlapping and frequency matching have been documented in aggressive contexts in black-capped chickadees (Fitzsimmons, Foote, Ratcliffe, & Mennill, 2008b; Mennill & Ratcliffe, 2004b, but see Baker et al., 2012; Wilson et al., 2016), the interaction could have provided eavesdropping females with more information about participating males than was available to females in our study.

It is also possible that females did not use eavesdropping to (re)assess (potential) mates in our study because they used the response of their mate rather than the interaction between the intruder and their mate, to assess the intruder. Like their mate, females did not respond differently to the two playback treatments. Alternatively, the lack of response by females may simply indicate that short-term interactions between males are not relevant to (extrapair) mating decisions in great tits (Otter et al., 2001). Females have long-term experience of their mate and accumulate information based on many interactions. It may therefore not pay to reassess reproductive decisions based on a single short-term interaction. Reassessment based on a single interaction, as reported for black-capped chickadees (Mennill et al., 2002), may be the result of an exceptionally strong change in perceived quality of the mate: only females mated with dominant black-capped chickadees that 'lost' their interaction were more likely to adopt a mixed mating strategy. Females mated with subordinate males that 'lost' an interaction did not change their mating decisions, possibly because their mate 'loses' more interactions in general and thus does not suffer as big a change in perceived quality.

A final reason for the lack of changes in female foraying behaviour could be that males increased mate-guarding effort at the time of our playbacks (mostly during early egg laying) and thus prevented females from increased foraying. We were not able to test this, as most of the playback subjects were not radiotagged. In several other species, however, the first eggs of a clutch are more likely to be fertilized by extrapair mates than eggs laid later (Cordero, Wetton, & Parkin, 1999; Krist, Nádvorník, Uvírová, & Bureš, 2005; Schlicht, Girg, Loës, Valcu, & Kempenaers, 2012), indicating that extrapair mating is more likely to happen before the first egg is laid. Thus, the time window in which females are most likely to seek extrapair copulations might have been prior to our playback experiment.

We found no evidence that females allocated resources differentially based on information they could have gathered by eavesdropping. Previous studies have shown that female allocate androgens differentially to eggs based on male quality signalled by song (Gil, Graves, Hazon, & Wells, 1999; Gil, Leboucher, Lacroix, Cue, & Kreutzer, 2004; Tanvez, Béguin, Chastel, Lacroix, & Leboucher, 2004). However, the egg weight measures used here might not have been sensitive enough to capture any playback-related changes, as we were unable to conduct playbacks on the same day in the laying sequence of all clutches and there is substantial weight variation within a clutch through the laying sequence (Lessells et al., 2002; Ojanen, 1983). Garcia-Fernandez et al. (2010) showed that female canaries laid eggs with greater yolk to egg ratio when exposed to song they had previously heard as being the overlapping song in a song contest, while other measures of resource investment, including egg weight, were not affected by being exposed to overlapping song (Garcia-Fernandez et al., 2010). We did not determine yolk to egg ratio or testosterone concentrations in our study and it is possible that females did in fact alter their investment, but we did not detect it with our measurements of egg mass and provisioning behaviour.

Intrusion by a male into another male's territory may threaten the established neighbourhood and so neighbouring individuals would be expected to eavesdrop on these interactions and adjust their social behaviour accordingly (Fitzsimmons et al., 2008a; Naguib et al., 2011; Peake et al., 2002; Snijders, van Oers, et al., 2017). The nature of the intrusion and the perception of the interaction between intruder and resident could lead to territory prospecting by males into the territory and visits by females. Contrary to our expectations, male and female neighbours did not change their spatial behaviour in response to intrusions that may have been perceived as less or more challenging. In our study, neighbours could have assessed both the relative differences between the intruder and the resident male or the singing behaviour of the intruder alone. Previous studies have shown that both male and female neighbours change their spatial behaviour in response to interactions between two contestants (Otter et al., 1999; Snijders, van Oers, et al., 2017). In contrast, in our study visits by neighbours into an intruded male's territory and other territories did not differ before and after playbacks. As discussed above for females, the difference between the intruder and the resident male may not have been relevant to neighbours or they attended to the response of the resident. Indeed, a previous study in nightingales, *Luscinia megarhynchos*, showed that neighbour responses depend on the subject's response to playback and not on the relative timing between signals. This suggests that birds use the response of the territory owner as reference for their own response (Naguib et al., 2004) and may not respond to an intrusion in the neighbourhood if the resident male fails to respond. A recent study on great tits also showed an association between movements by male and female neighbours and the strength of the resident's singing response to

playback intrusions (Snijders, van Oers, et al., 2017). Neighbours in our study may thus have focused more on the absolute vocal response by the resident to the simulated intruder rather than on the interaction itself. Our sample size of tagged male neighbours was small and therefore our results regarding visits by males to playback territories and male foraging behaviour to other territories should be interpreted with caution. Moreover, it is possible that neighbours reacted in ways we could not assess here: neighbouring males may not respond spatially, but react vocally through a higher song output as was observed in black-capped chickadees (Fitzsimmons et al., 2008a) and nightingales (Naguib et al., 2004).

Conclusion

Our results provide no support for the notion that females used information from eavesdropping on male song contests for their reproductive decision making. Additionally, we found no evidence that neighbouring males and females change their prospecting behaviour to playback territories or their overall foraging activity in response to simulated intrusions. This suggests that male territorial interactions may not necessarily influence close-range associations between individuals through eavesdropping by neighbours. Our findings shed a different light on the role of eavesdropping in communication networks because information that may be available to individuals that eavesdrop on asymmetric singing interactions during territorial disputes is not always used. One reason for this may be that longer-term assessment of familiar individuals (mates and neighbours) outweigh short-term assessment based on brief single interactions. Alternatively, overlapping or singing for a longer time in an intruded territory may not be perceived as a higher level of threat, at least not in all contexts. Overall, while a growing body of studies shows the importance of eavesdropping on male song contests for information gathering, our study emphasizes that further investigation is needed to pinpoint which specific aspects of male singing in interactions are assessed and how this information is used by others.

Acknowledgments

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