



Dawn song predicts behaviour during territory conflicts in personality-typed great tits



Lysanne Snijders^{a, b, *}, Erica P. van Rooij^a, Marlijn F. A. Henskens^a, Kees van Oers^b, Marc Naguib^a

^a Behavioural Ecology Group, Wageningen University, Wageningen, The Netherlands

^b Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

ARTICLE INFO

Article history:

Received 8 May 2015

Initial acceptance 8 June 2015

Final acceptance 16 July 2015

Available online

MS. number: 15-00385R

Keywords:

dawn chorus
exploration
great tit
playback
proximity
signalling
territory defence

Territorial animals settle territory disputes and discourage conspecific intrusion via close-range confrontations as well as nonconfrontational long-range signalling. Since individuals often differ consistently in general aggression and risk taking, the relative use of either close- or long-range territorial defence behaviour is likely to vary with the personality of the territory owner. Here we quantified the relationship between dawn song, a well-studied long-range signal, and responses to a close-range confrontation as well as how individuals in a territorial population vary in this relationship. For this we recorded dawn song and experimentally simulated territory intrusions via playbacks in wild personality-typed male great tits, *Parus major*. We show that males that sang at a higher rate at dawn also showed stronger vocal responses towards a simulated intruder, but spent less time in proximity to the intruder. Moreover, males with a higher exploration score, an established proxy for personality traits, showed the strongest vocal and spatial responses during the confrontation, yet exploration behaviour did not predict the dawn song rate. These findings highlight the importance of both confrontational and nonconfrontational territorial behaviours as well as personality for the social and territorial dynamics of animal populations.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Individuals within a population often directly or indirectly affect each other's behaviour. In many group-living species (Couzin & Krause, 2003) and also in territorial species (Stamps, 1988) attraction to certain sites on a large spatial scale is positively influenced by the presence of conspecifics. Conversely, on a smaller spatial scale the presence of conspecifics will regularly repel territorial individuals from certain locations (Stamps & Krishnan, 2001). Territorial behaviour, including both close-range confrontations (Stamps & Krishnan, 1997) and long-range signalling (McGregor, 2005), often deters conspecifics from coming too close. These defence behaviours are crucial for territorial animal societies as they modulate the social dynamics and territory stability of a population (Bee & Gerhardt, 2002; Beletsky, 1992; Briefer, Rybak, & Aubin, 2008). However, since close- and long-range territorial defence behaviours are often studied in isolation, it is still not evident whether and how they are related.

Territorial long-range signals keep rivals at a distance and hence can prevent close-range confrontations (Bee & Gerhardt, 2002; Burmeister, Ophir, Ryan, & Wilczynski, 2002; Krebs, 1977), inherently linking signalling and confrontational behaviour together. For example, in Pacific tree frogs, *Hyla regilla*, calling led to wider spacing of individuals than expected from random spatial settlement (Whitney & Krebs, 1975). Additionally, familiarity with the specific long-range signal characteristics of neighbours has been shown to reduce excessive aggression among territorial neighbours, in systems ranging from fish (Myrberg & Riggio, 1985) to frogs (Bee & Gerhardt, 2002) to birds (Akçay et al., 2009; Briefer et al., 2008). This link between long-range signalling and potentially aggressive close-range interactions becomes especially relevant when individuals within a territorial population vary in their propensity to avoid close-range confrontations with rivals, as such variation could also be reflected in individual differences in signalling behaviour. Indeed, the overall likelihood of territorial males being in proximity to a male conspecific differed between individual male great tits, *Parus major*, with respect to their personality (Snijders et al., 2014). Moreover, the intensity of response to a close-range

* Correspondence: L. Snijders, Wageningen University, Department of Animal Sciences, Behavioural Ecology Group, P.O. Box 338, 6700 AH Wageningen, The Netherlands.

E-mail address: lysanne.snijders@wur.nl (L. Snijders).

confrontation with a simulated territorial intruder was similarly found to vary among territorial male great tits in relation to personality traits (Amy, Sprau, de Goede, & Naguib, 2010; Jacobs et al., 2014). Since male territorial songbirds connect by spatial proximity as well as by their song, a long-range signal (Amrhein, Kunc, & Naguib, 2004; Peake, Terry, McGregor, & Dabelsteen, 2002; Snijders et al., 2014), they are ideal models for studying how these close- and long-range territorial behaviours are related.

An important long-range signal of many territorial songbird species is the dawn song (McGregor, 2005; Staicer, 1996), a peak in singing activity just before sunrise. A predominant function of dawn song in territorial songbirds is territory advertisement to keep rivals at a distance (Kacelnik & Krebs, 1983; Kunc, Amrhein, & Naguib, 2005). Consequently, if individual songbirds vary in their motivation to avoid territorial confrontations, this should be reflected in their dawn singing behaviour. Certain dawn song traits have indeed been shown to predict various close-range behaviours, such as nest defence in willow tits, *Parus montanus* (Welling, Rytönen, Koivula, & Orell, 1997) and territory defence in blue tits, *Cyanistes caeruleus* (Poesel, Dabelsteen, & Pedersen, 2004). Moreover, differences in dawn song rate in territorial great tits vary between males depending on whether or not they share a territory boundary (Snijders et al., 2015).

Although both personality (Amy et al., 2010) and long-range song (Poesel et al., 2004) can predict short-range territorial behaviour, it remains unclear whether personality could drive both short- and long-range territorial behaviour. This relationship is important because if personality drives territorial behaviour at both scales, eavesdroppers would be able to predict the personality of a potential competitor and hence their likely response to future close-range confrontations. Evidence that this might be the case comes from the finding that great tit neighbours that eavesdrop on a simulated territory intrusion adjust their spatial behaviour in relation to the personality of their intruded-upon neighbour (Amy et al., 2010). Consistency in behaviour mediated by personality differences makes individuals predictable and thus allows greater social responsiveness by conspecifics (Wolf, Van Doorn, & Weissing, 2011).

Here, we examined how dawn singing, a long-range signal, is related to close-range territorial behaviour in a wild population of territorial great tits by simulating intrusions of rival males through song playbacks. The individuals in this population were also tested for exploration behaviour, an established proxy for personality traits in this species. We predicted that slower explorers would show weaker close-range territory defence behaviour, because slower explorers tend to take less risk and are generally less aggressive than fast explorers (van Oers & Naguib, 2013). This is also in line with the findings of Amy et al. (2010) in the same population. Moreover, we expected birds that showed a weak confrontational response to the playback (slower birds) to sing more actively during dawn to discourage possible intruders (Kacelnik & Krebs, 1983) and thus decrease the chance of risky confrontations. This prediction does differ somewhat from the outcome of an earlier aviary study in which faster explorers actually sang more (Naguib, Kazez, Schaper, Van Oers, & Visser, 2010), but since the breeding pairs were housed in separate aviaries they did so while there was no risk of confrontations present. Additionally, we hypothesized that neighbourhoods (males living in close proximity to the playback subject) would react vocally more strongly to simulated intrusions in territories of those subject males that were generally more active singers at dawn, as we expected those males to increase singing activity the most and so trigger eavesdropping neighbours to also vocally defend their territories more intensely.

METHODS

Study Population

The study was conducted on our long-term nestbox population of great tits at Westerheide near Arnhem, The Netherlands. Throughout the year, birds caught for the first time (outside the breeding season) are tested for exploration behaviour using a standard validated protocol. Birds are caught either from their nestbox during a roost check at night or via mist netting during the day. After catching, the birds are immediately transported to the bird-housing facilities at the Netherlands Institute of Ecology (NIOO-KNAW) where they are weighed and subsequently individually housed in cages (0.9 × 0.4 m and 0.5 m high). The following morning, exploration behaviour is measured using the novel environment test following the procedure described in Dingemanse, Both, Drent, van Oers, and van Noordwijk (2002). Birds are individually tested in a room (4.0 × 2.4 m and 2.3 m high) with five artificial trees. After birds enter the experimental room by themselves, we record the total number of flights (movements between trees) and hops (movements within trees) within the first 2 min. These are subsequently used to calculate an overall exploration score ranging from low (slow explorers) to high (fast explorers) (Dingemanse et al., 2002), which is known to be repeatable and to correlate positively with aggression, boldness, risk taking and approach of conspecifics in great tits (Groothuis & Carere, 2005).

General Set-up

To simulate territory intrusions we conducted playback experiments in the mornings between 0800 and 1115 hours at the nestboxes of 37 male great tits in the Westerheide study site. Playbacks, broadcasting songs of an unfamiliar male great tit, were performed from 26 March until 7 April 2012, and were conducted near nestboxes with nest-building activity but without eggs (with the exception of one bird). On a given day, playbacks were conducted several territories apart following a procedure similar to that described by Amy et al. (2010). To quantify the relation between dawn song and responses to territory intrusion, song recordings were made during dawn on the day before the playback experiment using automatic song recorders. Additionally, song recordings were made during dawn after the intrusion to assess repeatability of the dawn singing behaviour. Neighbourhood dawn singing activity was scored daily throughout the breeding season (see below).

Dawn Song Recording

We recorded dawn song using time-programmable song recorders (Wildlife Acoustics Inc., Maynard, MA, U.S.A.; SM2 song meter and TASCAM DR-08) placed above nestboxes with nest-building activity. We were able to collect good-quality dawn song recordings for 23 playback subject males the dawn before the playback (for 22 playback subjects the dawn song was successfully recorded on both the dawn before and after the playback). Recordings were then analysed with Avisoft SASlab Pro (R. Specht, Berlin, Germany). As a standardized measure, the first 5 min from the time the bird started singing before sunrise was quantified. We measured song rate in number of songs ('strophes') per second and start time of dawn song in minutes before sunrise. Repeatability of start time of dawn song and song rate was tested, in accordance with Lessells and Boag (1987), using song recordings of two consecutive mornings for 27 male great tits (22 playback subjects and five additional males). Both the start time of dawn song

($r = 0.53$, $SE = 0.14$, $F_{26,27} = 3.30$, $P = 0.001$) and the song rate ($r = 0.49$, $SE = 0.15$, $F_{26,27} = 2.93$, $P = 0.004$) were highly and significantly repeatable. This repeatability of dawn song traits before egg laying is in accordance with the previously revealed repeatability of the same traits later in the season, during the egg-laying phase (Snijders et al., 2015).

Simulated Territory Intrusions

To attract attention, we used a 1 min lure with common goldcrest, *Regulus regulus*, and long-tailed tit, *Aegithalos caudatus*, calls, followed by a pause of 20 s, then 2 min of great tit song comprising a systematic repetition of one song type of a great tit recorded at least 2 years before. It is very unlikely that the subjects were familiar with the playback song given the short average life expectancy of wild great tits (1–2 years). To prevent pseudoreplication, each subject received a song recording from a different male (with two exceptions). The playback files were constructed using Adobe Audition by repeating one song of a unique bird with intervals of 4 s to 2 min and normalizing the peak amplitude to the same level for all songs. Songs were broadcast at 84 dB (measured at a neutral site at 1 m from the loudspeaker with a Voltcraft Digital sound-level meter 322) using a Yamaha NX-U10 loudspeaker (frequency range 90 Hz–20 kHz), connected with a 25 m cable to a media player (Archos 405, 30 GB). Subject responses were recorded using two Sennheiser ME66/K6 microphones (frequency range 40 Hz–20 kHz \pm 2.5 dB) and a Marantz PMD660 solid-state recorder (sampling frequency 44.1 kHz, frequency range 16 kHz \pm 0.5 dB) until 2 min after the playback had ended. From these recordings and from simultaneously recorded spoken notes we quantified two spatial response measures, (1) latency to approach within 5 m (s) and (2) total time spent within 5 m of the loudspeaker (s), as well as four vocal response measures: (3) number of song overlaps, (4) total song rate (songs/s during total observation time), (5) song rate during the actual playback (songs/s) and (6) total singing duration (s). All playback experiments were performed by the same observer (M.H.) and all subjects received only one playback.

An additional seven playback experiments were performed, but were left out of the analysis because of technical problems during the execution of the experiment ($N = 3$) or a total absence of noticeable vocal and spatial presence ($N = 4$). By excluding birds that did not show any visual and vocal presence during the experiment we minimized the possibility of wrongfully assigning a weak playback response to individuals that were out of hearing range at the time of the experiment. For 16 of the playback subjects the exploration score was available, but unknown to the observer at the time of the playback.

Neighbourhood Singing Activity

We conducted observation rounds of 30 min, in which we assessed singing activity in the whole study site, following methods given in Amrhein, Johannessen, Kristiansen, and Slagsvold (2008). These rounds were made every morning during the 2-week playback period. They began half an hour before sunrise and consisted of two fixed routes, which were alternated each day. The observer cycled along the fixed route (alternating start and end points within routes) and recorded on a map where a great tit was singing. For each playback subject the proportion of total singing points within 100 m of the playback location for the morning after the playback and during a control round were calculated, to determine overall neighbourhood singing activity. A control round was conducted within 4 to 2 days before the playback ($N = 6$) or 2 days after the playback ($N = 5$), restricted to days when no other playback trials

were performed nearby. Owing to the alternating routes in combination with the fact that playback locations on the same morning were as far apart as possible, we could only calculate a neighbourhood singing activity measure for 11 (of 23) subjects.

Subject Identification

During the breeding season we checked nestboxes twice a week using a standardized procedure (van Oers, Drent, Dingemanse, & Kempenaers, 2008). Playback subjects were identified by catching them inside their nestbox using spring traps on approximately the 7th day after chicks hatched. Playback subjects that we trapped during chick feeding, to establish their identity, were not inside their nestbox for longer than 15 min. We fitted unringed individuals with uniquely numbered aluminium leg rings and measured body mass and tarsus length within approximately 5 min.

Statistical Analysis

Latency to approach within 5 m was set to 320 s for the five birds that did not approach within 5 m of the loudspeaker, but that did respond vocally. We conducted a principal component analysis on the six behavioural measures comprising the total response of the subject during the playback experiment. Two principal components (varimax rotation with Kaiser normalization; rotation converged in three iterations; Appendix Table A1) had an eigenvalue larger than 1. Since our main focus in this study was on the close-range territory defence behaviour we also independently analysed the two spatial response behaviours: (1) latency to approach within 5 m (s) and (2) total time spent within 5 m of the loudspeaker (s).

Since availability of exploration scores significantly reduced our sample size, correlations were tested first excluding exploration behaviour as a variable ($N = 23$ for playback response and dawn song) and subsequently including it ($N = 16$ for playback response and exploration; $N = 17$ for dawn song and exploration). Because a complete data set (good-quality dawn song recording, playback response and exploration score) was not available for several subjects, sample size differs between models ($N = 14$ for all variables combined). Age of the subject (as a categorical factor: independent-samples t test of second calendar year or older: $1.6 > \text{all } t > -0.6$, all $P > 0.1$) and number of days to the first egg of the mate (as a continuous variable: Spearman correlation: $0.3 > \text{all } r > -0.2$, all $P > 0.3$) did not significantly influence the dawn song measures or either of the main response components during the playback experiment, and were a priori left out of the model. Additionally, minor variations in number of stimulus songs (mean = 18.5, $SD = 2.1$, $N = 37$; $0.06 > \text{all } r \text{ or } r_s > -0.25$, all $P > 0.1$) and total playback duration (mean = 319.35 s, $SD = 4.86$ s, $N = 37$; $0.35 > \text{all } r \text{ or } r_s > -0.35$, all $P > 0.05$) did not significantly bias the two main response components or the six response measures individually.

Whether territory intrusions resulted in persisting effects on the use of dawn song was tested with two paired-samples t tests comparing start time of dawn song and song rate during dawn before and after the playback ($N = 22$). To examine whether typical dawn singing behaviour (before playback) was associated with neighbourhood vocal response, we quantified the change in relative neighbourhood singing activity by calculating the proportion of neighbours singing during the control round and subtracting this from the proportion of neighbours singing the morning after the playback. Calculated proportions for neighbourhood singing activity were arcsine transformed and zero values were replaced by $(1/4N)$ (Zar, 1999). General linear models were used to analyse whether or not dawn signalling traits from the dawn before the

playback (still undisturbed by potential playback effects) predicted longer term changes in (relative) neighbourhood singing activity after a simulated territorial confrontation for 11 males. Possible effects on relative neighbourhood singing activity caused by the territorial defence behaviour of the territory owner were tested in a separate linear model to prevent collinearity problems with the dawn song traits.

A backward model selection procedure was conducted for all models, removing the least significant terms, until only factors with $P < 0.1$ remained (final model). Residuals of the models were normally distributed according to the Kolmogorov–Smirnov test. All statistical analyses were performed using IBM SPSS Statistics 21 (SPSS, Inc., Chicago, IL, U.S.A., www.spss.com).

Ethical Note

Birds caught for personality testing were transported from the field to the research institute by car within 1.5 h after the first bird was caught (the car ride lasted a maximum of 20 min). During transport we housed the birds individually in a compartment ($10 \times 10 \times 10$ cm) of a standard darkened wooden carrier. We measured tarsus and weight (handling time of 5 min) before individuals were housed in the individual cages. The birds were provided with water and food ad libitum, including sunflower seeds, mealworms, fat balls and apple. We conducted the novel environment test between 0800 and 1200 hours. The indoor cages connected to the room via a 20–20 cm sliding door so a bird could enter the experimental room without being handled, following darkening of the individual cage. The test was terminated after at most 10 min, after which the experimental room was darkened and we caught the bird by hand to release it back to its cage within 1 min. Individuals do not usually lose weight outside their natural range (Dingemanse et al., 2002) during this routine procedure. Within 24 h we released birds back in the field close to their nestbox. This procedure was approved by the Institutional Animal Care and Use Committee: the Koninklijke Nederlandse Akademie van Wetenschappen–Dier Experimenten Commissie (KNAW-DEC license NIOO 10.05 to M.N. and K.V.O.).

RESULTS

Response to a Territory Intrusion

The main vocal component (PC1: higher value reflects stronger response) including all four song measures explained 52% of the total variation. The main spatial component (PC2: lower value reflects stronger response) including the two approach measures explained 29% of the total variation (Appendix Table A1). The total approach response (PC2) was negatively predicted by the dawn song rate (Pearson correlation: $r_{21} = 0.50$, $P = 0.015$; Fig. 1a), with birds singing at the highest dawn song rate showing the weakest approach response. Considering the spatial territorial response behaviours separately, males with a higher dawn song rate spent significantly less time within 5 m of the simulated intruder (Pearson correlation: $r_{21} = -0.55$, $P = 0.007$), but there was no correlation with the latency to approach (Spearman correlation; $r_s = 0.28$, $N = 23$, $P = 0.20$).

When exploration behaviour was included in the model ($N = 14$), it significantly positively predicted the total spatial response, with faster explorers showing a stronger response (Table 1, Fig. 1b). When we again considered the spatial territorial response behaviours separately, fast explorers spent more time within 5 m of the loudspeaker, but there was no effect on latency to approach (Table 1). When we included exploration behaviour there was no longer a significant effect of the dawn song rate on the total

spatial response (PC2) but the significant correlation between the time spent within 5 m and the dawn song rate of a territory owner remained (Table 1).

The total vocal response (PC1) during the simulated intrusion was predicted by both the dawn song rate and the exploration behaviour of territory owners, with strong vocal responders also having the highest dawn song rate (Pearson correlation: $r_{21} = 0.51$, $P = 0.014$) and fastest exploration score (Table 1). Start time of dawn song was not predictive for any of the close-range territorial defence behaviours, both when excluding (all $P > 0.1$) and when including exploration behaviour (Table 1).

Dawn Singing Behaviour

The start time of dawn song (paired-samples t test: $t = -0.22$, $N = 22$, $P = 0.83$) and the song rate ($t = -1.50$, $N = 22$, $P = 0.15$) did not differ significantly between the dawn following a playback and the dawn before the playback.

The exploration behaviour of the territory owner did not correlate with the start time of dawn song (Pearson correlation: $r_{15} = -0.17$, $P = 0.53$) or dawn song rate ($r_{17} = -0.21$, $P = 0.41$; Fig. 1c) on the day before the playback or with the change in start time of dawn song ($r_{10} = 0.26$, $P = 0.39$) and song rate ($r_{10} = -0.12$, $P = 0.71$) the morning after a playback.

Neighbourhood Response

The relative neighbourhood singing activity the morning after the playback significantly decreased compared to the control round when the territory owner's undisturbed dawn song rate (the morning before the playback) was higher (general linear model: $F_{1,9} = 5.22$, $P = 0.048$) but was unrelated to the start time of dawn song ($F_{1,8} = 2.48$, $P = 0.15$). This negative correlation between dawn song rate and change in relative neighbourhood singing activity was unlikely to have been mediated by the playback response of the territory owner as the total vocal response (PC1) and total spatial response (PC2) during the territorial confrontation were both unrelated to the change in relative neighbourhood singing activity (PC1: $F_{1,14} = 0.004$, $P = 0.95$; PC2: $F_{1,14} = 0.62$, $P = 0.45$). Finally, the change in relative neighbourhood singing activity was unrelated to the exploration behaviour of the eight males for whom we had data on both measures (Pearson correlation: $r_8 = 0.53$, $P = 0.18$).

DISCUSSION

Here we have shown that (1) a long-range territorial signal correlates negatively with the close-range territorial defence to a simulated intruder, (2) exploration behaviour can predict the strength of both the close-range vocal and spatial response to an intruder, but not the typical long-range signalling behaviour and (3) a long-range territorial signal can predict the vocal neighbourhood response after a territory intrusion.

The Role of Personality in Territory Defence Behaviour

Dawn song, a long-range signal, predicted the spatial response during a simulated intrusion, a behaviour that is likely to be risky in a territorial population. Indeed, our finding that faster explorers, which are generally seen as being more risk taking, spent significantly more time in proximity to a simulated intruder, confirms similar findings by Amy et al. (2010) in this study population. One likely explanation is that individuals that take lower risks in spatial confrontations signal more actively in a nonconfrontational setting, to keep rivals at a distance. Long-range vocalizations as stay-away signals are widespread among many diverse territorial species,

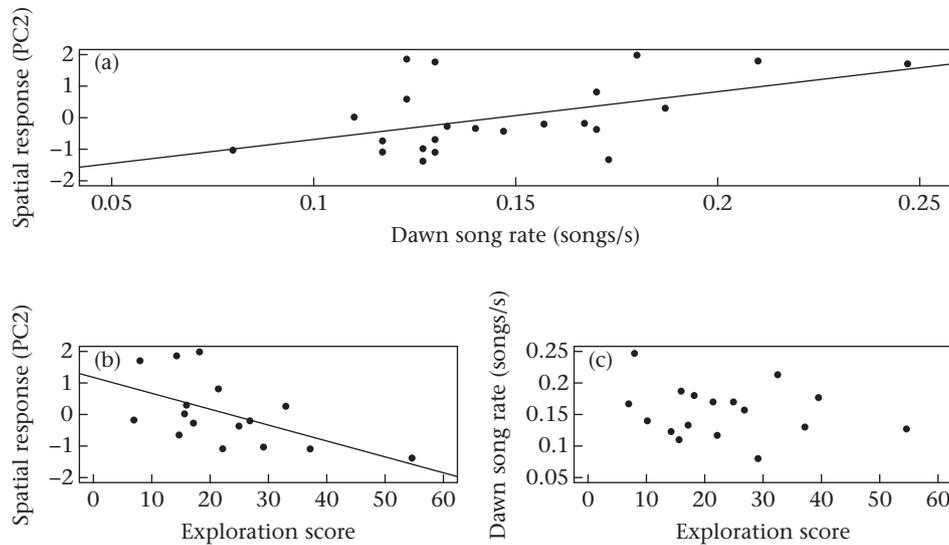


Figure 1. Relationships between dawn song rate, spatial response to the playback and exploration score. Spatial response (lower value reflects stronger response) as a function of (a) dawn song rate and (b) exploration score. (c) Dawn song rate as a function of exploration score. Lines represent significant correlations.

such as Lusitanian toadfish, *Halobatrachus didactylus*, Pacific tree frogs (Whitney & Krebs, 1975), mantled howling monkeys, *Alouatta palliata palliata* (Whitehead, 1987) and great tits (Krebs, 1977). Furthermore, a radiotracking study on nightingales, *Luscinia megarhynchos*, showed that males with higher daily song output received fewer intrusions by neighbouring males (Naguib, Altenkamp, & Griessmann, 2001; Naguib, Kunc, Sprau, Roth, & Amrhein, 2011).

Exploration behaviour has been linked to several forms of risk taking in the field, such as nest defence in great tits (Hollander, Van Overveld, Tokka, & Matthysen, 2008), song post height in male collared flycatchers, *Ficedula albicollis* (Garamszegi, Eens, & Török, 2008) and aggressive territory defence by helpers in a cooperative breeding cichlid, *Neolamprologus pulcher* (Bergmüller & Taborsky, 2007). However, exploration behaviour as a correlate of risk-taking behaviour can only partially support our findings. While we found a positive correlation between exploration behaviour and the time spent close to the simulated intruder, we did not find a relationship between exploration behaviour and the dawn singing behaviour. Although we initially predicted slow birds to be more active singers at dawn, in a study concerning singing activity in captive great tits fast-exploring birds sang more (Naguib et al., 2010). However, the captive fast birds in this study sang more throughout the whole day, not just dawn, which could also be a

reflection of fast birds generally being more active in captivity (Carere, Welink, Drent, Koolhaas, & Groothuis, 2001). Comparison between behaviour indoors and territorial behaviour in the wild remains challenging, since the constraints on the time and energy budgets are very different. In the wild, birds have a much larger area to defend and have to spend significantly more time and energy on finding food while avoiding predation, resulting in a very different trade-off in time and energy expenditure. Studies including additional personality traits that relate more directly to the tendency to avoid or seek out confrontations, such as boldness, aggression or risk taking, might give more insight into whether long-range signalling, such as dawn singing behaviour, and proximity during confrontational territory conflicts are correlated via variation in risk-prone personalities.

In contrast to this study and the study of Amy et al. (2010), a recent study by Jacobs et al. (2014) revealed that slower explorers in their population show a stronger spatial response to a simulated intruder. This confirms previous studies that showed that behavioural variation between personality types is often context or population dependent (Dingemanse & de Goede, 2004; van Oers, Klunder, & Drent, 2005). This study and the study by Amy et al. (2010) were conducted before egg laying, while Jacobs et al. (2014) study also included the egg-laying phase. The female is fertile during the egg-laying phase and as a consequence males are

Table 1

GLM results for subject main playback response components and the two spatial playback response behaviours individually as a function of dawn song traits and exploration score

Response variable	Independent	Test statistic	P	N
PC2 (spatial response)	Dawn song rate	$F_{1,10}=1.36$	0.27	14
	Dawn song start time	$F_{1,11}=3.07$	0.11	14
	Exploration	$F_{1,14}=6.53$	0.02	16
Total time spent within 5 m (s)	Dawn song rate	$F_{1,11}=5.55$	0.04	14
	Dawn song start time	$F_{1,10}=0.56$	0.47	14
	Exploration	$F_{1,11}=5.04$	0.046	14
Latency to approach within 5 m (s)	Dawn song rate	$F_{1,10}=0.50$	0.50	14
	Dawn song start time	$F_{1,10}=1.65$	0.23	14
	Exploration	$F_{1,10}=1.49$	0.25	14
PC1 (vocal response)	Dawn song rate	$F_{1,11}=19.39$	0.001	14
	Dawn song start time	$F_{1,10}=2.02$	0.19	14
	Exploration	$F_{1,11}=10.25$	0.008	14

Significant values are in bold.

highly engaged in mate guarding and thus have to make different trade-offs when responding to territorial intrusions. Moreover, the frequency distribution of exploration scores in [Jacobs et al. \(2014\)](#) great tit population included many slow explorers, while the distribution in our study was more uniform. Differences in the frequency distribution of personality types in a population can be the result of natural selection since fitness consequences of certain personality types are known to vary in contrasting ways possible due to specific environmental conditions ([Dingemanse, Both, Drent, & Tinbergen, 2004](#)). When there are many slow explorers in a population, slow individuals might benefit from taking more social risks as the chance of encountering fast explorers (which are generally more aggressive, [Groothuis & Carere, 2005](#)) is lower. In contrast, fast explorers, living in a population with many slow explorers, might have experienced that a less spatial and a more vocal defence (song type switching) is enough to settle disputes. Indeed, exploration behaviour itself has been shown to be adaptively plastic when environmental circumstances are changed ([Nicolaus et al., 2012](#)). [Jacobs et al. \(2014\)](#) raised the variation in the signal strength of the playbacks as another potential explanation for varying results between playback subjects. This could indeed explain some of the differences between the three playback studies. For example, the study by [Amy et al. \(2010\)](#) consisted of a 1 min playback of noninteractive songs, followed by a 2 min interactive playback from another loudspeaker, while we conducted a noninteractive playback for 2 min and the [Jacobs et al. \(2014\)](#) study broadcast noninteractive songs for only two times 45 s. Thus variation in perceived intruder determinedness (signal strength) could be influencing the defence strategy of the playback subjects, with fast explorers responding more aggressively to a more persistent intruder in [Amy et al. \(2010\)](#) study and slow explorers taking more risks with a less persistent intruder in [Jacobs et al. \(2014\)](#) study. Certainly, great tits are known to alter the intensity of their response when an intruder is likely to be perceived as less threatening ([Peake, Terry, McGregor, & Dabelsteen, 2001](#)).

The Predictive Value of a Long-range Signal

Our findings that dawn song predicted behaviour during a territory intrusion underlines the signal value of dawn song, as it is not only consistent ([Snijders et al., 2015](#)) but also predictive for other contexts. As we anticipated, more active long-range signallers (i.e. males with a higher dawn song rate) showed a weaker spatial response, but a stronger vocal response during the intrusion. The finding that dawn song behaviour can predict behaviour in other contexts conforms to studies of long-range song in other bird species ([Naguib et al., 2001](#); [Poesel et al., 2004](#); [Welling et al., 1997](#)). Also, territorial song in general can provide important predictive information. Male song sparrows, *Melospiza melodia*, responded adaptively by varying their response to the playback of songs of conspecific males that were known to differ in their aggressiveness ([Hyman & Hughes, 2006](#)). Moreover, long-range territorial signalling behaviour can predict fitness in both territorial bats ([Behr et al., 2006](#)) and birds ([Hasselquist, Bensch, & von Schantz, 1996](#); [Mennill, Ratcliffe, & Boag, 2002](#)). Predictive information transfer of individual quality and motivation via long-range territorial signalling therefore seems to be a common phenomenon in territorial systems.

In contrast to song rate, the start time of dawn song, although repeatable, did not predict behavioural responses to intrusions. Several studies have shown that the start time of dawn song correlates with components of individual quality, for instance earlier-singing kingbirds, *Tyrannus tyrannus*, and blue tits experience certain fitness benefits ([Murphy, Sexton, Dolan, & Redmond, 2008](#); [Poesel, Kunc, Foerster, Johnsen, & Kempenaers, 2006](#)).

Nevertheless, individual variation in the start time of dawn song might be restricted by the environment as start time is also known to be driven by environmental factors such as lunar phase ([York, Young, & Radford, 2014](#)), artificial light ([Kempenaers, Borgström, Loès, Schlicht, & Valcu, 2010](#)), night temperature ([Godfrey & Bryant, 2000](#)) or noise levels ([Gil, Honarmand, Pascual, Pérez-Mena, & Macías Garcia, 2014](#)). Moreover, start time might be affected by the social environment through social facilitation ([Clayton, 1978](#)), as it was recently shown that similarity in start time was higher for males breeding in closer proximity ([Snijders et al., 2015](#)).

In several different fish and bird species conspecifics are known to react to information indicating relative quality and motivation of signallers gathered from eavesdropping on signal interactions ([Fitzsimmons, Foote, Ratcliffe, & Mennill, 2008](#); [Mennill et al., 2002](#); [Naguib & Todt, 1997](#); [Oliveira, McGregor, & Latruffe, 1998](#); [Peake et al., 2001](#); [Webster & Laland, 2013](#)). Next to signal interactions, long-term changes in individual signalling behaviour could signal relevant information. Similar playback studies on winter wrens, *Troglodytes troglodytes* ([Amrhein & Erne, 2006](#)) and black-capped chickadees, *Poecile atricapillus* ([Foote, Fitzsimmons, Mennill, & Ratcliffe, 2011](#)) found long-term changes in dawn song traits of the territory owner after a simulated intrusion. These changes can be detected by all conspecifics in hearing range and could change their behaviour. However, we did not find evidence for such a significant long-term change in the subject's song traits after the intrusion in this study. Possibly the changes in signalling behaviour are only short term in great tits or the long-term changes in signalling are too subtle to detect as there are many different individual and environmental factors influencing dawn song behaviour ([Foote et al., 2011](#)).

Surprisingly, relative neighbourhood singing activity was lower the morning after the simulated territory intrusion for subjects with a higher dawn song rate. We expected neighbours of birds with a higher dawn song rate to respond by increasing rather than decreasing their singing activity, especially since these birds also showed a stronger vocal response during the intrusion. Possibly birds with a lower song rate, which also showed a stronger spatial response during the intrusion, became more spatially active by defending their territory boundaries and so arousing their neighbours to vocally defend their own territories more intensively during the next dawn chorus. Replicate studies tracking playback subjects and their neighbours following a territory intrusion would be necessary to confirm this hypothesis. Insights into long-range territorial signalling behaviour, including consistent signal characteristics, signal interactions and changes in signalling behaviour, are very relevant in social behaviour studies as long-range signals reveal information about the signaller not only to the intended receiver but also to all other conspecifics in range ([McGregor, 2005](#)). Territorial long-range signals thus have the potential to affect the social dynamics of many individuals within a population simultaneously.

Conclusion

Our findings provide new insights into the links between individual long-range and close-range territorial behaviour. We have shown that individuals varying in personality use a different mix of negatively correlated territorial behaviours. Therefore studies examining the social dynamics of territorial populations, for example social network studies, would benefit from integrating both close- and long-range social connectivity. The rapid technological developments in recording specific signal interactions in small animals ([Anisimov et al., 2014](#)) will make this goal more achievable in the near future.

Acknowledgments

We are grateful to Piet de Goede for his very much appreciated work in the field. We also thank Stichting Geldersch Landschap en Kasteelen for permission to do fieldwork in the Westerheide forest and Marylou Aaldering and Franca Kropman for animal caretaking during the time the birds were in the laboratory. This work was supported by The Netherlands Organisation for Scientific Research (NWO) with an ALW open competition grant (821.01.01) to M.N. A number of the automatic song recorders were funded with a grant from the Dobberke Stichting (UPS/BP/5215) awarded to M.N.

References

- Akçay, Ç., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E., & Beecher, M. D. (2009). Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. *Animal Behaviour*, 78, 97–102. <http://dx.doi.org/10.1016/j.anbehav.2009.03.023>.
- Amrhein, V., & Erne, N. (2006). Dawn singing reflects past territorial challenges in the winter wren. *Animal Behaviour*, 71, 1075–1080. <http://dx.doi.org/10.1016/j.anbehav.2005.07.023>.
- Amrhein, V., Johannessen, L. E., Kristiansen, L., & Slagsvold, T. (2008). Reproductive strategy and singing activity: blue tit and great tit compared. *Behavioral Ecology and Sociobiology*, 62, 1633–1641. <http://dx.doi.org/10.1007/s00265-008-0592-6>.
- Amrhein, V., Kunc, H. P., & Naguib, M. (2004). Non-territorial nightingales prospect territories during the dawn chorus. *Proceedings of the Royal Society B: Biological Sciences*, 271, S167–S169. <http://dx.doi.org/10.1098/rsbl.2003.0133>.
- Amy, M., Sprau, P., de Goede, P., & Naguib, M. (2010). Effects of personality on territory defence in communication networks: a playback experiment with radio-tagged great tits. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3685–3692. <http://dx.doi.org/10.1098/rspb.2010.0598>.
- Anisimov, V., Herbst, J., Abramchuk, A., Latanov, A., Hahnloser, R., & Vyssotski, A. (2014). Reconstruction of vocal interactions in a group of small songbirds. *Nature Methods*, 11, 1135–1137. <http://dx.doi.org/10.1038/nmeth.3114>.
- Bee, M. A., & Gerhardt, H. C. (2002). Individual voice recognition in a territorial frog (*Rana catesbeiana*). *Proceedings of the Royal Society B: Biological Sciences*, 269, 1443–1448. <http://dx.doi.org/10.1098/rspb.2002.2041>.
- Behr, O., von Helversen, O., Heckel, G., Nagy, M., Voigt, C. C., & Mayer, F. (2006). Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behavioral Ecology*, 17, 810–817. <http://dx.doi.org/10.1093/beheco/arl013>.
- Beletsky, L. D. (1992). Social stability and territory acquisition in birds. *Behaviour*, 123, 290–313. <http://dx.doi.org/10.2307/4535074>.
- Bergmüller, R., & Taborsky, M. (2007). Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecology*, 7, 12. <http://dx.doi.org/10.1186/1472-6785-7-12>.
- Briefer, E., Rybak, F., & Aubin, T. (2008). When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, *Alauda arvensis*. *Animal Behaviour*, 76, 1319–1325. <http://dx.doi.org/10.1016/j.anbehav.2008.06.017>.
- Burmeister, S. S., Ophir, A. G., Ryan, M. J., & Wilczynski, W. (2002). Information transfer during cricket frog contests. *Animal Behaviour*, 64, 715–725. <http://dx.doi.org/10.1006/anbe.2002.4012>.
- Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M., & Groothuis, T. G. G. (2001). Effect of social defeat on a territorial bird (*Parus major*) selected for different coping styles. *Physiology & Behavior*, 73, 427–433. [http://dx.doi.org/10.1016/S0031-9384\(01\)00492-9](http://dx.doi.org/10.1016/S0031-9384(01)00492-9).
- Clayton, D. A. (1978). Socially facilitated behavior. *Quarterly Review of Biology*, 53, 373–392.
- Couzin, I. D., & Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*, 32, 1–75.
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64, 929–938. <http://dx.doi.org/10.1006/anbe.2002.2006>.
- Dingemans, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B: Biological Sciences*, 271, 847–852. <http://dx.doi.org/10.1098/rspb.2004.2680>.
- Dingemans, N. J., & de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, 15, 1023–1030. <http://dx.doi.org/10.1093/beheco/arh115>.
- Fitzsimmons, L. P., Foote, J. R., Ratcliffe, L. M., & Mennill, D. J. (2008). Eavesdropping and communication networks revealed through playback and an acoustic location system. *Behavioral Ecology*, 19, 824–829. <http://dx.doi.org/10.1093/beheco/arn036>.
- Foote, J. R., Fitzsimmons, L. P., Mennill, D. J., & Ratcliffe, L. M. (2011). Male black-capped chickadees begin dawn chorusing earlier in response to simulated territorial insertions. *Animal Behaviour*, 81, 871–877. <http://dx.doi.org/10.1016/j.anbehav.2011.01.028>.
- Garamszegi, L. Z., Eens, M., & Török, J. (2008). Birds reveal their personality when singing. *PLoS One*, 3, e2647. <http://dx.doi.org/10.1371/journal.pone.0002647>.
- Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., & Macías García, C. (2014). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral Ecology*, 25, 435–443. <http://dx.doi.org/10.1093/beheco/aru207>.
- Godfrey, J., & Bryant, D. (2000). State-dependent behaviour and energy expenditure: an experimental study of European robins on winter territories. *Journal of Animal Ecology*, 69, 301–313. <http://dx.doi.org/10.1046/j.1365-2656.2000.00393.x>.
- Groothuis, T. G. G., & Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews*, 29, 137–150. <http://dx.doi.org/10.1016/j.neubiorev.2004.06.010>.
- Hasselquist, D., Bensch, S., & von Schantz, T. (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, 381, 229–232. <http://dx.doi.org/10.1038/381229a0>.
- Hollander, F. A., Van Overveld, T., Tokka, I., & Matthysen, E. (2008). Personality and nest defence in the great tit (*Parus major*). *Ethology*, 114, 405–412. <http://dx.doi.org/10.1111/j.1439-0310.2008.01488.x>.
- Hyman, J., & Hughes, M. (2006). Territory owners discriminate between aggressive and nonaggressive neighbours. *Animal Behaviour*, 72, 209–215. <http://dx.doi.org/10.1016/j.anbehav.2006.01.007>.
- Jacobs, C. G., van Overveld, T., Careau, V., Matthysen, E., Adriaensen, F., & Slabbekoorn, H. (2014). Personality-dependent response to field playback in great tits: slow explorers can be strong responders. *Animal Behaviour*, 90, 65–71. <http://dx.doi.org/10.1016/j.anbehav.2014.01.016>.
- Kacelnik, A., & Krebs, J. R. (1983). The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour*, 83, 287–308. <http://dx.doi.org/10.1163/156853983x00200>.
- Kempnaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, 20, 1735–1739. <http://dx.doi.org/10.1016/j.cub.2010.08.028>.
- Krebs, J. R. (1977). Song and territory in the great tit *Parus major*. In B. Stonehouse, & C. M. Perrins (Eds.), *Evolutionary ecology* (pp. 47–62). London, U.K.: Macmillan.
- Kunc, H. P., Amrhein, V., & Naguib, M. (2005). Seasonal variation in dawn song characteristics in the common nightingale. *Animal Behaviour*, 70, 1265–1271. <http://dx.doi.org/10.1016/j.anbehav.2005.02.010>.
- Lessells, C., & Boag, P. T. (1987). Unrepeatable repeatabilities: a common mistake. *Auk*, 104, 116–121. <http://dx.doi.org/10.2307/4087240>.
- McGregor, P. K. (2005). *Animal communication networks*. Cambridge, U.K.: Cambridge University Press.
- Mennill, D. J., Ratcliffe, L. M., & Boag, P. T. (2002). Female eavesdropping on male song contests in songbirds. *Science*, 296, 873. <http://dx.doi.org/10.1126/science.296.5569.873>.
- Murphy, M. T., Sexton, K., Dolan, A. C., & Redmond, L. J. (2008). Dawn song of the eastern kingbird: an honest signal of male quality? *Animal Behaviour*, 75, 1075–1084. <http://dx.doi.org/10.1016/j.anbehav.2007.08.020>.
- Myrberg, A. A., & Riggio, R. J. (1985). Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). *Animal Behaviour*, 33, 411–416. [http://dx.doi.org/10.1016/S0003-3472\(85\)80065-8](http://dx.doi.org/10.1016/S0003-3472(85)80065-8).
- Naguib, M., Altenkamp, R., & Griessmann, B. (2001). Nightingales in space: song and extra-territorial forays of radio tagged song birds. *Journal of Ornithology*, 142, 306–312. <http://dx.doi.org/10.1046/j.1439-0361.2001.01005.x>.
- Naguib, M., Kazek, A., Schaper, S. V., Van Oers, K., & Visser, M. E. (2010). Singing activity reveals personality traits in great tits. *Ethology*, 116, 763–769. <http://dx.doi.org/10.1111/j.1439-0310.2010.01791.x>.
- Naguib, M., Kunc, H. P., Sprau, P., Roth, T., & Amrhein, V. (2011). Communication networks and spatial ecology in nightingales. *Advances in the Study of Behavior*, 43, 239–271. <http://dx.doi.org/10.1016/B978-0-12-380896-7.00005-8>.
- Naguib, M., & Todt, D. (1997). Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Animal Behaviour*, 54, 1535–1543. <http://dx.doi.org/10.1006/anbe.1997.9997>.
- Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P. M., Ubels, R., Both, C., et al. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4885–4892. <http://dx.doi.org/10.1098/rspb.2012.1936>.
- van Oers, K., Drent, P. J., Dingemans, N. J., & Kempnaers, B. (2008). Personality is associated with extrapair paternity in great tits, *Parus major*. *Animal Behaviour*, 76, 555–563. <http://dx.doi.org/10.1016/j.anbehav.2008.03.011>.
- van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, 16, 716–723. <http://dx.doi.org/10.1093/beheco/ari045>.
- van Oers, K., & Naguib, M. (2013). Avian personality. In C. Carere, & D. Maestripieri (Eds.), *Animal personalities: Behavior, physiology and evolution* (pp. 66–95). Chicago, IL: The University of Chicago Press.
- Oliveira, R. F., McGregor, P. K., & Latruffe, C. (1998). Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society B: Biological Sciences*, 265, 1045–1049. <http://dx.doi.org/10.1098/rspb.1998.0397>.
- Peake, T. M., Terry, A. M. R., McGregor, P. K., & Dabelsteen, T. (2001). Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proceedings of the Royal Society B: Biological Sciences*, 268, 1183–1187. <http://dx.doi.org/10.1098/rspb.2001.1648>.

- Peake, T. M., Terry, A. M. R., McGregor, P. K., & Dabelsteen, T. (2002). Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceedings of the Royal Society B: Biological Sciences*, 269, 1925–1929. <http://dx.doi.org/10.1098/rspb.2002.2112>.
- Poesel, A., Dabelsteen, T., & Pedersen, S. (2004). Dawn song of male blue tits as a predictor of competitiveness in midmorning singing interactions. *Acta Ethologica*, 6, 65–71. <http://dx.doi.org/10.1007/s10211-004-0086-0>.
- Poesel, A., Kunc, H. P., Foerster, K., Johnsen, A., & Kempenaers, B. (2006). Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Animal Behaviour*, 72, 531–538. <http://dx.doi.org/10.1016/j.anbehav.2005.10.022>.
- Snijders, L., van der Eijk, J., van Rooij, E. P., de Goede, P., van Oers, K., & Naguib, M. (2015). Song trait similarity in great tits varies with social structure. *PLoS One*, 10, e0116881. <http://dx.doi.org/10.1371/journal.pone.0116881>.
- Snijders, L., van Rooij, E. P., Burt, J. M., Hinde, C. A., van Oers, K., & Naguib, M. (2014). Social networking in territorial great tits: slow explorers have the least central social network positions. *Animal Behaviour*, 98, 95–102. <http://dx.doi.org/10.1016/j.anbehav.2014.09.029>.
- Staicer, C. A., Spector, D. A., & Horn, A. G. (1996). The dawn chorus and other diel patterns in acoustic signaling. In D. E. Kroodsma, & E. H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 426–453). London, U.K.: Cornell University Press.
- Stamps, J. A. (1988). Conspecific attraction and aggregation in territorial species. *American Naturalist*, 131, 329–347. <http://dx.doi.org/10.2307/2461973>.
- Stamps, J. A., & Krishnan, V. V. (1997). Functions of fights in territory establishment. *American Naturalist*, 150, 393–405. <http://dx.doi.org/10.1086/286071>.
- Stamps, J. A., & Krishnan, V. V. (2001). How territorial animals compete for divisible space: a learning-based model with unequal competitors. *American Naturalist*, 157, 154–169. <http://dx.doi.org/10.1086/318634>.
- Webster, M. M., & Laland, K. N. (2013). Local enhancement via eavesdropping on courtship displays in male guppies, *Poecilia reticulata*. *Animal Behaviour*, 86, 75–83. <http://dx.doi.org/10.1016/j.anbehav.2013.04.014>.
- Welling, P. P., Rytkönen, S. O., Koivula, K. T., & Orell, M. I. (1997). Song rate correlates with paternal care and survival in willow tits: advertisement of male quality? *Behaviour*, 134, 891–904. <http://dx.doi.org/10.2307/4535478>.
- Whitehead, J. M. (1987). Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata palliata*. *Animal Behaviour*, 35, 1615–1627. [http://dx.doi.org/10.1016/S0003-3472\(87\)80054-4](http://dx.doi.org/10.1016/S0003-3472(87)80054-4).
- Whitney, C. L., & Krebs, J. R. (1975). Spacing and calling in Pacific tree frogs, *Hyla regilla*. *Canadian Journal of Zoology*, 53, 1519–1527. <http://dx.doi.org/10.1139/z75-187>.
- Wolf, M., Van Doorn, G. S., & Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278, 440–448. <http://dx.doi.org/10.1098/rspb.2010.1051>.
- York, J. E., Young, A. J., & Radford, A. N. (2014). Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. *Biology Letters*, 10, 20130970. <http://dx.doi.org/10.1098/rsbl.2013.0970>.
- Zar, J. H. (1999). Data transformations—The arcsine transformation. In J. H. Zar (Ed.), *Biostatistical analysis* (pp. 278–280). Upper Saddle River, NJ: Prentice-Hall.

Appendix

Table A1

Rotated component matrix with component loadings of the measured playback response behaviours

Playback response measures	Component	
	1	2
Latency to approach within 5 m (s)	0.06	0.92
Total time within 5 m of speaker (s)	–0.04	–0.93
Number of overlaps	0.84	0.23
Total song rate (songs/s)	0.92	0.00
Song rate during playback (songs/s)	0.90	0.06
Total singing duration (s)	0.87	–0.04

The Kaiser–Meyer–Olkin measure of sampling adequacy = 0.68 and Bartlett's test of sphericity was significant ($P < 0.001$). The highest component loading for each playback response behaviour is in bold.