

Effects of personality on territory defence in communication networks: a playback experiment with radio-tagged great tits

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Individuals often differ consistently in behaviour across time and contexts, and such consistent behavioural differences are commonly described as personality. Personality can play a central role in social behaviour both in dyadic interactions and in social networks. We investigated whether explorative behaviour, as proxy of personality of territorial male great tits (*Parus major*), predicts their own and their neighbours' territorial responses towards simulated intruders. Several weeks prior to playback, subjects were taken from the wild to test their exploratory behaviour in a standard context in the laboratory. Exploratory behaviour provides a proxy of personality along a slow–fast explorer continuum. Upon release, males were radio-tracked and subsequently exposed to interactive playback simulating a more or a less aggressive territorial intruder (by either overlapping or alternating broadcast songs with the subjects' songs). At the same time, we radio-tracked a neighbour of the playback subject. Male vocal responses during playback and spatial movements after playback varied according to male explorative behaviour and playback treatment. Males with lower exploration scores approached the loudspeaker less, and sang more songs, shorter songs and songs with slower element rates than did males with higher exploration scores. Moreover, neighbour responses were related to the explorative behaviour of the subject receiving the playback but not to their own explorative behaviour. Our overall findings reveal for the first time how personality traits affect resource defence within a communication network providing new insights on the cause of variation in resource defence behaviour.

Keywords: personality; territorial signalling; radio-tracking; interactive playback; communication networks

1. INTRODUCTION

Individual variation in sexually selected characters is understood to reflect individual variation in quality or motivation (Andersson 1994). Selection on individuals signalling higher quality using elaborate signals will favour the evolution of these signals. Birdsong is an extensively studied secondary sexual character as it is used both for territory maintenance and for mate attraction and stimulation (Catchpole & Slater 2008). Several features of birdsong vary among individuals and such variation can reveal differences in singer motivation or quality (Gil & Gahr 2002). For instance, song rate, song amplitude, song performance, repertoire size or counter-singing patterns (such as song matching or song overlapping) can be relevant indicators of male quality or motivation (Gil & Gahr 2002). Yet not all individual differences can be explained by differences in quality or motivation, so additional individual characteristics need to be considered to understand variation in sexually selected signals and behaviours.

In many species, individual differences in behaviour and physiology are consistent across contexts and are stable over time. Such consistent individual differences

are referred to as behavioural syndromes or personality (Groothuis & Carere 2005; Sih & Bell 2008; Dingemanse *et al.* 2010), and their expression may well also affect sexually selected signals (Schuett *et al.* 2010) and resource defence. Indeed, a previous study on male collared flycatchers (*Ficedula albicollis*) suggests that song post height in birds could reveal personality traits (Garamszegi *et al.* 2008) and song rate in great tits (*Parus major*) was shown to be higher in more explorative males under laboratory conditions (Naguib *et al.* in press). Yet little is known about how individuals with different personality traits vary in signalling behaviour during territorial contests in the wild.

One of the best-studied animals in terms of causes and consequences of personality is the great tit. Several studies have shown that individuals with different explorative behaviour, used as a proxy for personality traits, differ in foraging behaviour (Verbeek *et al.* 1994; Marchetti & Drent 2000; van Oers *et al.* 2004), aggression (Carere *et al.* 2001), mating decisions (van Oers *et al.* 2008), physiology (Fucikova *et al.* 2009), song (Naguib *et al.* in press) and in fitness in the wild (Dingemanse *et al.* 2004; Both *et al.* 2005).

Here, we tested whether variation in territory defence within communication networks during the period of reproduction (i.e. when individual differences may

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specifically surface) is related to explorative behaviour of male great tits. Radio-tagged males with known explorative behaviour were exposed to interactive playbacks simulating the presence of an intruder in their territory. Each male received one of two playback treatments, either simulating an intruder that overlapped the male's song or one that alternated song with the male. An overlapping intruder is considered to be more aggressive, whereas an alternating intruder is considered less aggressive (e.g. Naguib *et al.* 1999; Peake *et al.* 2001; Mennill *et al.* 2002; see Searcy & Beecher 2009; Naguib & Mennill *in press* for a recent discussion). To determine how playback treatment, subjects' responses and exploratory behaviour affect the behaviour of neighbours forming a communication network, we additionally followed radio-tagged neighbours during and after playback to the focal male. Based on previous studies on personality in great tits (Verbeek *et al.* 1996; van Oers *et al.* 2004; Carere *et al.* 2005), we predicted *a priori* that faster-exploring males would respond more aggressively to playback and more so when the intruder represents a stronger threat. Previous studies also showed that relative differences in singing behaviour in communication networks play a major role in female and male decision-making (Peake *et al.* 2001; Mennill *et al.* 2002; Naguib *et al.* 2004). Therefore, if personality traits play a role in communication networks, we predicted that neighbour responses would be related to their own explorative behaviour and that faster-exploring neighbours would respond more aggressively.

2. MATERIAL AND METHODS

(a) *Study site and study species*

Data were collected in spring 2009 from a nest-box population of colour-ringed great tits in the study area of Westerheide (5°50' E, 52°00' N) near Arnhem, The Netherlands. Westerheide is a mixed wood covering 250 ha with approximately 600 nest-boxes. As part of a long-term project, nest-boxes are routinely checked throughout the breeding season as well as during winter to record roosting birds. All individuals caught for the first time are caged for 1 day in the laboratory and tested for exploration behaviour in a standardized context as a proxy for personality, as described below.

(b) *General experimental protocol*

Twenty-six males were caught at the beginning of March 2009 from nest-boxes at night and brought to the laboratory within 2 h following the capture. Males were weighed and housed in individual cages (0.9 × 0.4 × 0.5 m) in rooms with windows and normal daylight. All cages had a sliding door (20 × 20 cm) through which the birds could access the exploration room by light manipulation without handling. Birds were provided with mealworms, water, sunflower seeds and commercial seed mixture *ad libitum*. The following morning, we determined the subjects' exploratory behaviour (see below). After testing, birds were weighed again and then equipped with radio-tags before they were released in the afternoon well before sunset; subjects were released directly in front of the nest-box at which they were caught. Most males (92%) maintained the territory on which they were caught. We then performed playback experiments (see below) on 19 males between 31 March and

7 April, before the onset of egg laying. Males were radio-tracked during the days preceding the playback, as well as immediately before, during and after the playback (see below). During most playbacks, at least one neighbour was also tracked. Most males (84%) have been used as both neighbour and playback subject, but neighbouring males were never used on the same day as playback subjects.

(c) *Novel environment test*

Exploratory behaviour was measured using the novel environment test as described in Verbeek *et al.* (1994). On the morning after taking males from the wild, they were individually tested in a closed room (4.0 × 2.4 × 2.3 m) with five artificial trees. The room contained no food but all subjects had *ad libitum* access to food and water in their home cage. After birds entered the experimental room by themselves, we recorded the total number of flights (movements between trees) and hops (movements within trees) within the first 2 min, which were subsequently used to calculate an overall exploration score. Only one experimenter performed the novel environment tests (P.d.G.). To avoid a possible bias of the experimenters on playback experiments, the exploration scores of the birds remained unknown to other experimenters until all experiments were completed and data were entered.

Faster explorers have higher exploration scores compared with slower explorers. These exploration scores have been shown to correlate with behaviour in many other contexts, such as latency to approach a novel object (Verbeek *et al.* 1994), foraging strategy (Marchetti & Drent 2000; van Oers *et al.* 2004), aggression (Carere *et al.* 2005), mating decisions (van Oers *et al.* 2008) and singing behaviour (Naguib *et al.* *in press*). Exploration scores have also been shown to correlate with fitness (Dingemanse *et al.* 2004; Quinn *et al.* 2009). For instance, adult survival has been shown to be related to the exploration score, but the effects were different for males and females, and were reversed in different years according to food availability (Dingemanse *et al.* 2004). Also, breeding pairs with similar exploration scores produced offspring in better condition (Both *et al.* 2005).

(d) *Radio-tracking*

Birds were equipped with BD-2 radio-tags (Holohil Systems, Canada; 30 pulses min⁻¹; 0.80 g) using elastic harnesses. Males had a body mass of 17.7 ± 0.2 g (mean ± s.e.) and the weight of radio-tags was below the recommended 5 per cent of body weight (Kenward 2001).

During radio-tracking sessions, the location of the birds was assessed with a three-element Yagi antenna connected to a receiver (ICOM IC-R20). We recorded the location of the focal bird every minute on a detailed map of the study area (1:2500 scale). The subjects were radio-tracked at least 15 min (mean ± s.e.: 18 ± 1 min) directly preceding playback, during playback and 30 min (mean ± s.e.: 32 ± 1 min) after playback. During most playbacks, at least one neighbour was also tracked so that usually at least three observers were involved in each playback: one running the playback (M.A.), one tracking the subject (M.N.) and one tracking a neighbour (P.S. or a field assistant, H.W.). Moreover, each of the 19 playback subjects was tracked seven to eight times (duration 30 min) on 7 different days preceding the playback, resulting in a total tracking time of 224 ± 11 min (mean ± s.e.) per bird. These tracking sessions before the playback allowed us to determine the ranges

used by males. Males were radio-tracked between 06.30 and 17.30 using interval sampling to mark every minute whether or not a bird had been singing at a given location. We always tried to avoid disturbing the birds by staying as far away from them as we could, about 15–20 m distance, when determining their position.

(e) Playback stimuli

Playback songs were constructed from great tit songs recorded the preceding year in Westerheide by using a Sennheiser ME66/K6 or ME67/K6 microphone connected to a Marantz PMD660 digital recorder (sample frequency: 44.1 kHz; resolution: 16 bit). We used 22 experimental songs constructed with Avisoft SASLAB PRO software (Raimund Specht, Berlin, Germany) from songs of 22 different males recorded the previous year. All songs were filtered (2000 Hz high-pass filter) and adjusted to the same peak amplitude. Each song was composed of six identical phrases (with two or three elements) at the natural rate typical for the respective song. Songs ($n = 22$) had a duration of 2.7 ± 0.10 s (mean \pm s.e.).

(f) Playback protocol

Playback tests were conducted between 09.00 and 15.00. Loudspeakers were placed near the centre of a male's home range as determined by the radio-tracking data. Each playback session had two phases: a lure phase and an interactive phase. Songs were broadcast by Yamaha NX-U10 loudspeakers connected to a digital player (Creative Zen), allowing an interactive playback mode by playing songs stored as wav files separately. Songs were broadcast at a sound pressure level of 85 dB SPL at 1 m (Voltcraft digital sound-level meter 322). Each loudspeaker was fixed at a height of 1.5–2 m on the branches of a tree. The lure loudspeaker was placed at 18.4 ± 0.7 m (mean \pm s.e.) from the interactive loudspeaker as measured with an infrared device (Leica Rangemaster CRF 800). One loudspeaker was used for the lure playback and the other loudspeaker was used for the interactive playback. We used two loudspeakers to standardize the distance between the subject and the interactive playback speaker. A lure song and an interactive song were randomly assigned to each bird.

We started the lure phase only when the focal male was within 40 m of the loudspeaker, as determined by radio-tracking. Thus, the precise location and identity of all subjects was always known at the onset of playback. The lure stage consisted of a 1 min non-interactive playback of a song (a song every 5 s) to alert the territorial male and incite it to sing. After this lure phase, one of the two treatments (alternating or overlapping) of the interactive phase was initiated. In the alternating treatment, we broadcast a song only after the focal male had finished a song. In the overlapping playback, we broadcast a song as soon as the focal male started to sing a song. If the male stopped singing altogether, we continued to broadcast a song every 5 s until it resumed singing. In the alternating treatment, playback duration of the interactive phase was 134 ± 11 s (mean \pm s.e.). In the overlapping treatment, playback duration of the interactive phase was 138 ± 9 s (mean \pm s.e.). The duration of the interactive playback did not significantly differ between the treatments ($T = 82$; $p = 0.791$; Mann–Whitney rank-sum test). During the interactive playback, the proportion of subject songs that were overlapped differed between the

treatments (alternating treatment: 0.10 ± 0.02 ; $n = 8$; overlapping treatment: 0.68 ± 0.08 ; $n = 9$; $T = 36$; $p < 0.001$; Mann–Whitney rank-sum test). Moreover, in the overlapping treatment, we broadcast our song with a latency of 1.6 ± 0.1 s from the onset of a subject's song and 0.6 ± 0.1 s before the end of the subject's song, whereas in the alternating treatment songs were broadcast with a latency of 5.6 ± 0.8 s from the onset of a subject's song and 1.2 ± 0.2 s after the end of the song. There was a significant difference between treatments in timing of the broadcast of songs (latency from the onset of the subject's song: $t_{1,17} = 5.360$; $p < 0.001$; t -test; latency from the end of the subject's song: $T = 108$; $p < 0.001$; Mann–Whitney rank-sum test). The exploration score of the subjects, as a proxy for personality traits, did not differ between the treatments (exploration score of subjects was 19 ± 3 in the alternating treatment ($n = 10$) and 19 ± 3 in the overlapping treatment ($n = 9$); $t_{1,17} = 0.090$; $p = 0.930$; t -test).

During interactive playback, songs of the focal bird were recorded using a Sennheiser ME 66/K6 microphone connected to one channel of a Marantz PMD660 digital recorder (sample frequency: 44.1 kHz; resolution: 16 bit) and additional information was spoken into a microphone connected to the other channel. No neighbours or males within hearing range were tested on the same day.

(g) Measures of responses

From the recordings made during the interactive playback, we determined for each bird (i) the song rate (no. of songs per s), (ii) the mean element rate within a song (number of elements), (iii) the mean song duration (s), (iv) the number of song type switches and (v) the proportion of playback songs overlapped by subjects using Avisoft SASLAB PRO software. We further extracted (vi) the time spent within 5 m and (vii) the latency to their closest approach. From the radio-tracking data, we extracted the following variables for the playback subjects: (viii) total distance moved after playback, (ix) distance moved away from the loudspeaker after playback, (x) distance covered after playback relative to the distance covered before playback and (xi) time spent outside the range where the subjects were tracked in the days preceding playback. For the neighbours, we extracted (xiii) the closest distance they approached to the loudspeaker, (xiv) their closest song post, (xv) the latency to reach the closest song post and (xvi) the number of song posts to which males flew.

(h) Statistical analysis

Data analysis was done using R v. 2.7.1 (R Development Core Team 2008). We used Pearson's correlations to assess whether male exploration score was related to male body mass and male condition, measured as the residuals on the regression of tarsus size on weight. To analyse the responses to playback, we used linear models (LMs) for each dependent variable, with exploration score and male condition as continuous variables and playback treatment (overlapping versus alternating) as factor, as well as the interaction between exploration score and playback treatment. For model simplification, we used backward selection following Crawley (2007). We removed non-significant ($p > 0.05$) terms from the maximal models that included all factors, covariates and the interaction, starting with the interaction. One bird was not radio-tracked during playback as it had lost the radio-tag, and because of technical problems the behaviour and the

songs of another bird were not registered during the playback. Therefore, sample size varies depending on the variable analysed. In order to test whether neighbour responses were affected by the strength of response of the subject, we combined subjects' vocal responses (variables i–v) into one score using a principal component analysis (SPSS 17.1). We also used these scores as combined measure of response by the subjects themselves. We only selected the vocal responses as a neighbour could eavesdrop on these responses whereas not on silent movement patterns. We used the scores on the first principal component (no rotation; eigenvalue: 2.5; variance explained: 50.6 per cent; loadings of variables: song rate 0.72, element rate 0.53, song duration 0.89, song type switches 0.89, songs overlapped 0.40) as a combined measure or a response intensity.

3. RESULTS

The exploration score obtained prior to the breeding season was not correlated with body mass on the day of capture (Pearson: $r = 0.225$, $p = 0.327$, $n = 19$) nor with body condition ($r = 0.213$, $p = 0.381$, $n = 19$).

(a) Effects of male exploration score on responses to playback

During playback, all 19 males approached the loudspeakers and 80 per cent of them approached within 5 m of the interactive loudspeaker. Only one male did not sing during the interactive playback. Exploration score and playback treatment both showed a significant relation with the scores on the first principal component (see table 1) which summarized vocal responses to the interactive playback. Exploration score showed a significant relationship with song rate, song duration and element rate (table 1 and figure 1*a–c*). Males with higher exploration scores sang at a lower rate, longer songs and songs with higher element rates than did males with lower exploration scores. Also, males with higher exploration scores stayed for a significantly longer period near the loudspeaker than did males with lower exploration scores (table 1 and figure 1*d*). In contrast, males with lower exploration scores sang at a higher song rate, shorter songs and songs with slower element rates (table 1 and figure 1*a–c*). Males with lower exploration scores spent less time near the loudspeaker compared with males with higher exploration scores (table 1 and figure 1*d*).

After playback, the distance moved away from the loudspeaker and the time spent outside the range used prior to playback were significantly related to the exploration score of the birds. Males with slower exploration scores moved farther away from the playback site (table 2 and figure 1*f*) and spent more time outside the area in which we radio-tracked them on the days prior to playback (table 2). The distance covered after playback and the distance covered after playback relative to before playback were not affected by male exploration score (table 2).

(b) Effects of playback treatment on response

Males responded differently to playback overlapping their songs compared with playback alternating with their songs. Males sang at a higher song rate and with shorter songs in response to overlapping playback compared

Table 1. Results of the LMs for subject responses during playback. Significant values are printed in bold.

responses during playback	test statistic	<i>p</i> -value
song rate		
exploration score	$F_{1,14} = 5.467$	0.035
treatment	$F_{1,14} = 5.730$	0.031
exploration × treatment	$F_{1,13} = 1.051$	0.324
condition	$F_{1,13} = 0.991$	0.338
element rate (mean)		
exploration score	$F_{1,15} = 6.730$	0.020
treatment	$F_{1,14} = 0.223$	0.644
exploration × treatment	$F_{1,13} = 0.071$	0.794
condition	$F_{1,14} = 0.002$	0.970
song duration (mean)		
exploration score	$F_{1,14} = 7.244$	0.018
treatment	$F_{1,14} = 8.674$	0.011
exploration × treatment	$F_{1,13} = 3.096$	0.102
condition	$F_{1,13} = 0.656$	0.433
song type switches		
exploration score	$F_{1,14} = 1.187$	0.295
treatment	$F_{1,15} = 7.941$	0.013
exploration × treatment	$F_{1,13} = 0.828$	0.380
condition	$F_{1,14} = 0.235$	0.635
proportion of songs overlapped		
by subject		
exploration score	$F_{1,13} = 0.063$	0.806
treatment	$F_{1,13} = 9.192$	0.010
exploration × treatment	$F_{1,13} = 8.052$	0.014
condition	$F_{1,12} = 1.385$	0.262
time spent within 5 m		
exploration score	$F_{1,14} = 6.797$	0.021
treatment	$F_{1,13} = 0.320$	0.581
exploration × treatment	$F_{1,12} = 0.037$	0.850
condition	$F_{1,13} = 0.204$	0.659
latency to the closest approach		
exploration score	$F_{1,12} = 0.148$	0.708
treatment	$F_{1,12} = 0.329$	0.577
exploration × treatment	$F_{1,12} = 0.820$	0.383
condition	$F_{1,15} = 1.418$	0.252
principal component analysis		
exploration score	$F_{1,14} = 10.594$	0.006
treatment	$F_{1,14} = 16.627$	0.001
exploration × treatment	$F_{1,13} = 1.918$	0.189
condition	$F_{1,13} = 0.709$	0.415

with alternating playback (table 1 and figure 1*a,b*). Males also used more song types in the alternating playback compared with the overlapping playback (table 1).

The interaction between male exploration score and playback treatment was significant for only one variable (i.e. the number of songs a subject overlapped). During the overlapping playback, the higher exploration score the males had, the less they overlapped playback songs, whereas in the alternating playback, the higher exploration score they had, the more songs they overlapped. Males with a lower exploration score overlapped playback songs to a similar intermediate extent in response to both treatments (table 1 and figure 1*e*).

(c) Effects of male condition on responses

Male condition did not affect any response variable and was dropped from all models (tables 1 and 2). However,

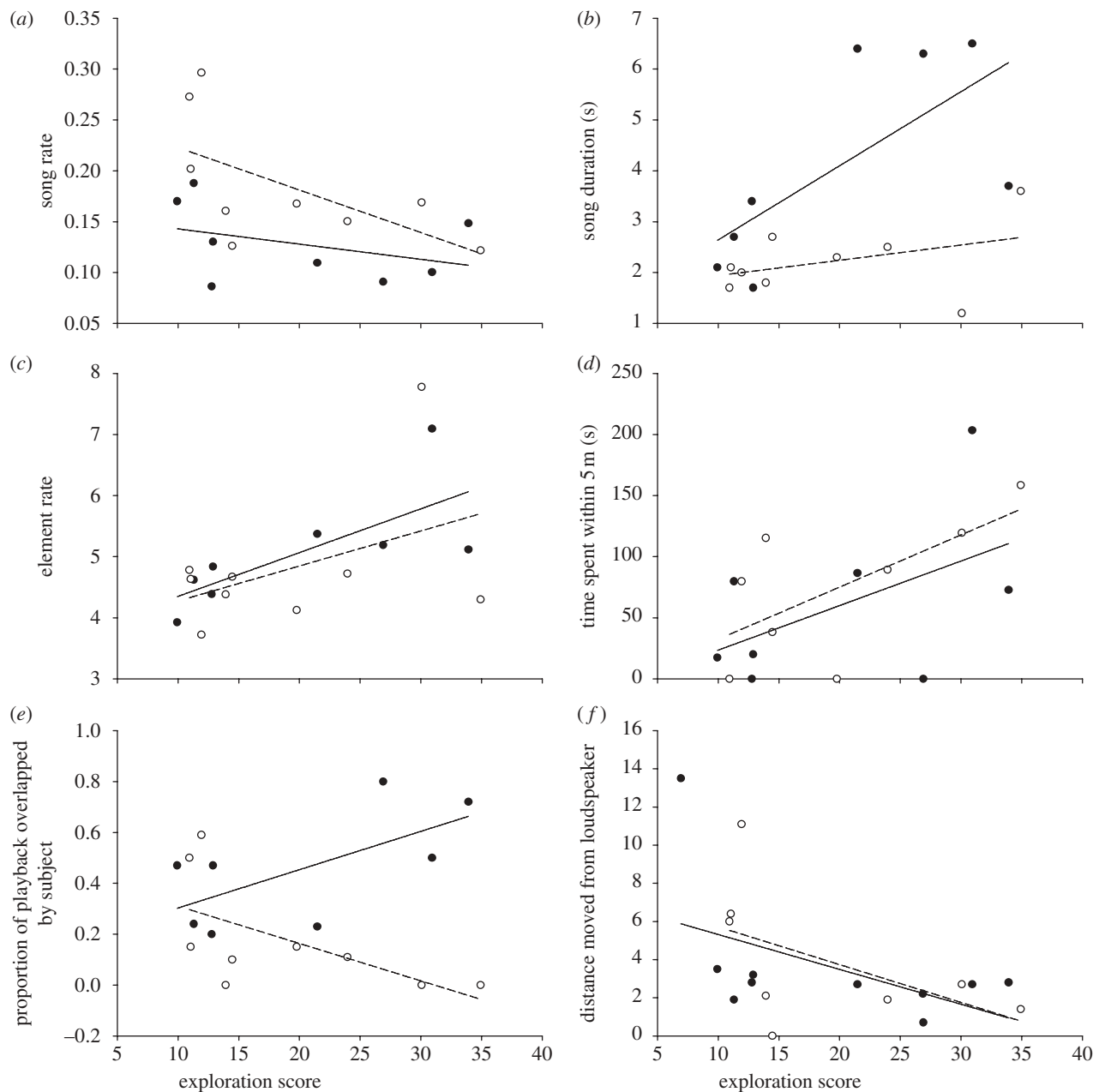


Figure 1. Subject responses (*a–e*) during playback and (*f*) after playback, according to their exploration score. Open circles: overlapping treatment. Filled circles: alternating treatment. Lines are regression lines for each playback condition. (*a*) Song rate (number of songs), (*b*) song duration (s), (*c*) element rate (number of elements), (*d*) time spent within 5 m (s), (*e*) proportion of songs overlapped by the subject and (*f*) maximal distance moved away from the loudspeaker (1/25 of a metre).

males of lower condition tended to move farther away after playback than did males in better condition ($F_{1,15} = 4.028, p = 0.063$).

(d) Effects of playback on movements by neighbours

Movements by neighbours were not affected by either playback treatment or their own exploration score. Yet neighbour responses were affected by the exploration score of the subject that received the playback. The latency to reach the closest song post to the loudspeaker by the neighbours, as well as the number of song posts used, was significantly affected by the exploration score of the subject that had received the playback (latency: $F_{1,11} = 6.542, p = 0.027$; song posts: $F_{1,11} = 6.102, p = 0.031$; figure 2*a,b*). Neighbours approached their closest

song post faster if the subject had a lower exploration score (figure 2*a*). Moreover, they used fewer song posts when the subject had lower exploration scores (figure 2*b*). Neighbour approach distances were not affected by any variable. However, neighbours tended to move a greater distance after playback compared with before playback if the subject displayed a strong vocal response (subjects' response strength (PC scores): $F_{1,10} = 4.00, p = 0.073$).

4. DISCUSSION

The experiments revealed that males with different exploration scores responded differently to playback and thus provide new insights into strategies used in resource defence. Faster explorers stayed longer near the loudspeaker and sang longer but fewer songs than did slower

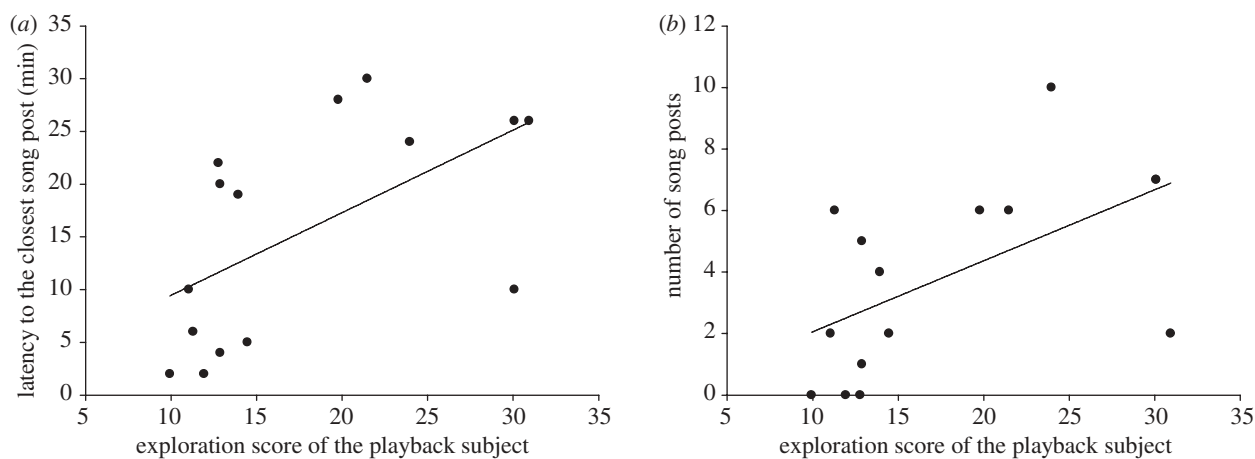


Figure 2. Neighbour responses according to the exploration score of the playback subjects. Lines are regression lines. (a) Latency (min) to the closest song post and (b) the number of song posts.

Table 2. Results of the LMs for the subject responses after playback. Significant values are printed in bold. Trends are printed in italics.

responses after playback	test statistic	<i>p</i> -value
total distance covered		
exploration score	$F_{1,14} = 0.160$	0.695
treatment	$F_{1,14} = 0.361$	0.563
exploration \times treatment	$F_{1,13} = 0.208$	0.656
condition	$F_{1,14} = 0.660$	0.428
distance moved from loudspeaker		
exploration score	$F_{1,15} = 6.916$	0.019
treatment	$F_{1,14} = 0.049$	0.829
exploration \times treatment	$F_{1,13} = 0.017$	0.897
condition	$F_{1,15} = 4.028$	<i>0.063</i>
distance covered before/after		
exploration score	$F_{1,15} = 0.253$	0.622
treatment	$F_{1,15} = 2.575$	0.129
exploration \times treatment	$F_{1,13} = 0.518$	0.484
condition	$F_{1,15} = 2.308$	0.150
time spent outside range		
exploration score	$F_{1,16} = 5.618$	0.031
treatment	$F_{1,15} = 0.324$	0.578
exploration \times treatment	$F_{1,14} = 0.324$	0.578
condition	$F_{1,15} = 2.346$	0.146

males. Slower explorers, in contrast, sang more songs but stayed farther away and eventually left the playback site for longer and covered a larger distance after playback than did faster males. Moreover, in line with previous experiments, males in general responded more strongly to the overlapping playback than to alternating playback (Dabelsteen *et al.* 1997; Mennill & Ratcliffe 2004; Naguib & Kipper 2006; Schmidt *et al.* 2007). Yet these overall differences in behaviour reveal not only quantitative differences but different strategies. Males with high song rates spent less time close to the playback intruder and also sang shorter songs, indicating that scaled measures of single response variables such as of song rate (e.g. Peake *et al.* 2002) capture only a part of the overall response strategy. Even though response intensity can usually be scaled due to a correlation of various measures of response (McGregor 1992, 2000), our findings highlight that other dimensions of an

individual—such as explorative behaviour (as proxy for personality traits)—can explain substantial additional variation in response strategies.

Our experiments further show that the neighbours' responses depended in rather striking ways on the subject that had received the playback. Neighbour responses depended on the subject's behaviour, as well as on its explorative behaviour, rather than on their own explorative behaviour. Neighbours tended to adjust their responsiveness to the strength of the subjects' responsiveness, suggesting that they paid attention to the level of arousal of threatened neighbours. These findings expand on previous studies showing that birds attend to singing interactions involving the neighbour (Naguib *et al.* 2004; Fitzsimmons *et al.* 2008). Males apparently not only know who their neighbours are, as previously shown (Becker 1982; Godard 1991; Naguib & Todt 1998), but our findings suggest that they also know the personality of their neighbour and adjust their responses accordingly. This is particularly interesting as it suggests that the neighbourhood, and specifically the personality traits of neighbours, can have fundamental implications for territorial behaviour. These findings thus highlight that individuals in a territorial system forming a communication network have more individualized relations than shown previously, and that understanding strategies in territory acquisition and defence requires a wider approach than commonly taken (see also Croft *et al.* 2009).

There are theoretical considerations and empirical evidence that variation in territorial signalling is related to quality (review in ten Cate *et al.* 2002). For instance, in nightingales (*Luscinia megarhynchos*), more aggressive singing males have higher pairing success (Kunc *et al.* 2006). However, in light of this view, male condition did not affect any response in our experiment. Therefore, our study reveals a new pattern, as individual variation in behaviour was better explained by exploration behaviour than by measures of condition.

Overall, the present study shows that exploration behaviour, as proxy for personality traits, explains not only territorial behaviour in response to a threat, but also that an individual's personality is related to the territorial behaviour of their neighbours. The latter

emphasizes that territorial communities and communication networks can be better understood by including individual specific characteristics, such as personality.

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