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Personality-dependent response to field playback in great tits: slow explorers can be strong responders

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Animal personalities can play an important role in how individuals deal with specific social situations, which may have important fitness consequences. A link between personality and social skills seems obvious from a human perspective and it is therefore surprising that relatively few studies have looked at the effect of animal personality on communicative interactions. In this study we tested the evidence for personality-related variation in birds during vocal interactions in the field. We scored individual variation in exploratory behaviour of great tits, *Parus major*, in repeated trials of a novel environment test in the laboratory and related this score to approach and vocal behaviour in response to playback of conspecific songs in the field. Contrary to our expectation, we found males with low exploration scores approached the speaker more closely than birds with high exploration scores. Birds with high exploration scores seemed to respond less aggressively while dealing with the simulated intruder vocally by switching song types more often. Our results suggest that slow-exploring birds in the laboratory respond more strongly during natural interactions in the field. An independent and very similar study also revealed a correlation between personality score and playback response, but with a seemingly contrasting outcome. A comparison of the two studies provides insights into the complexity of interpreting playback results and territorial response patterns in general.

Studies on animal personalities have addressed the biological relevance of consistent individual variation of specific behaviours in a wide variety of taxa and contexts (Dingemanse, Kazem, Reale, & Wright, 2010; Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih & Bell, 2008). In addition, human personality is a well-studied subject and is frequently associated with individual variation in social skills and verbal interactions (McCroskey, 1998; Wilson, Clark, Coleman, & Dearstyne, 1994). This link between personality and interactive performance seems obvious from a human perspective and it is therefore surprising that only a few studies have looked at the effect of animal personality on otherwise well-studied communicative interactions (Hauser & Konishi, 1999; Marler & Slabbekoorn, 2004; Narins, Feng, Fay, & Popper, 2006; Peters, 1980). We believe this disparity is unfortunate as insight into variable styles of vocal mediation during social interactions is important for a better understanding of how avian personalities may affect fitness under natural conditions (Sih, Hanser, & McHugh, 2009; Smith & Blumstein, 2008) and of how to interpret results from playback experiments (de Kort, Eldermire, Cramer, & Vehrencamp, 2009; McGregor, 1992; Searcy & Nowicki, 2000).

As personality traits are typically quantified under standardized laboratory conditions the ecological relevance of these alternative behavioural strategies are still poorly understood. Variation in personality scores is generally linked to individual responses to challenging or novel situations and to rather basal behavioural traits such as aggressiveness, exploratory behaviour and boldness (Reale et al., 2007; Sih, Bell, Johnson, & Ziemba, 2004). Although personalities vary along a continuum, individuals at the ends of these behavioural axes are often categorized as behavioural phenotypes having a more proactive or reactive coping strategy (Coppens, de Boer, & Koolhaas, 2010; Groothuis & Carere, 2005; Koolhaas et al., 1999). Reactive individuals tend to be slow, but more thorough in exploration, cautious and shy, while proactive individuals are fast, but superficial in exploration, bold and risk-prone (Groothuis & Carere, 2005). Studies on free-ranging animals have indicated that personality traits may be correlated with individual behaviour that may be critical to fitness (for reviews see Careau & Garland, 2012; Reale, Dingemanse, Kazem, & Wright, 2010), but most studies have focused on short-range

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antagonistic interactions (i.e. dominance: Cole & Quinn, 2012; competitive abilities: Dingemanse & de Goede, 2004; Kurvers et al., 2010). The consequences of personality when animals are still some distance apart but in communicative contact are poorly known. Only a handful of studies have addressed potential associations between personality and acoustic signalling, despite its importance in providing insights into how personality may affect social relationships (Amy, Sprau, de Goede, & Naguib, 2010; Garamszegi, Eens, & Török, 2008; Naguib, Kazek, Schaper, van Oers, & Visser, 2010).

Birds commonly use acoustic signals for repelling rivals and attracting mates, which provides ample opportunity to study personality-related variation in vocal interactions and the potential impact on fitness. For example, in the collared flycatcher, *Ficedula albicollis*, no personality-related acoustic song features were found, but bold males took more risks during singing bouts by persistently using lower perches than shy males in the presence of a human observer (Garamszegi et al., 2008). In great tits, *Parus major*, a model species for research on avian personalities (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Dingemanse & de Goede, 2004; Drent, van Oers, & van Noordwijk, 2003; Verbeek, Boon, & Drent, 1996), recent studies have revealed a number of correlations between individual personality and vocal behaviour. For example, fast-exploring great tits moved less, but gave more alarm calls during nest defence compared to slow-exploring birds (Hollander, Van Overveld, Tokka, & Matthysen, 2008). Fast birds were also shown to sing more than slow birds (Naguib et al., 2010). Increased vocal output in fast birds was also found in another bird species but only after playback (Guillette & Sturdy, 2011).

Here we report on a playback study on great tits in natural territories to test personality-dependent response strategies during vocal interactions. We tested for a correlation between repeated measures of exploratory behaviour as our personality index with different measures of response intensity and with acoustic variation in song types and singing style. We expected fast birds to respond more strongly than slow birds by approaching the speaker more closely and to sing at a higher rate (Naguib et al., 2010) and for longer (Weary, Krebs, Eddyshaw, McGregor, & Horn, 1988), while switching song types (Peake, Matessi, McGregor, & Dabelsteen, 2005; Searcy & Beecher, 2009; Searcy, Nowicki, & Hogan, 2000), and by overlapping playback songs (Naguib & Mennill, 2010). These expectations were largely in line with the findings of a similar study in great tits by Amy et al. (2010). However, we had some unexpected results for which we provide an explanation using the outcome of both studies.

METHODS

Species and Field Site of Study

Great tits are small passerines, which establish and defend territories before and during the breeding season in spring (Krebs, Ashcroft, & Webber, 1978). Male–male competition is common and the species has an elaborate behavioural repertoire of agonistic displays (Wilson, 1992). Great tits not only use a variety of call types, but also exhibit an elaborate acoustic repertoire of one to nine song types that are repeated in a stereotypic way (Franco & Slabbekoorn, 2009; Lambrechts & Dhondt, 1990; McGregor, Krebs, & Perrins, 1981). Song types usually contain two or three notes, but sometimes also one or four (and exceptionally even more). The group of notes that is repeated is called a phrase and the group of phrases sung in the same sequence is a strophe (Fig. 1). Great tits were studied in a fragmented woodland area called 'Boshoek', to the southeast of Antwerp, Belgium (51°08′N, 4°32′E). The wooded fragments (1–12 ha) are surrounded by roads, residential areas and agricultural areas (see Matthysen, 2002; Nour, Currie, Matthysen, Van Damme, & Dhondt, 1998 for details). The vegetation in these fragments is dominated by mature oak, *Quercus robur*, with some prominent stands of common beech, *Fagus sylvatica*. All plots contain standard nestboxes at a similar density, which are monitored year-round and from which birds are colour-banded for individual recognition. Territorial birds in five different forest fragments were used for the current study and their territories were characterized as being 'oak' or 'beech' type, dependent on the dominant tree species.

Exploratory Behaviour Assessment

Exploratory behaviour of each individual was assessed by a novel environment test (Dingemanse et al., 2012) as part of ongoing studies (exploration tests performed by T.O.). During this test, individual birds are released into an observation room containing five artificial wooden trees each with four short horizontal branches (following Verbeek, Drent, & Wiepkema, 1994). Protocols for housing birds and obtaining personality scores were based on the procedures used by Dingemanse, Both, Drent, Van Oers, and Van Noordwijk (2002). Birds were captured in the field between July and March (outside their breeding season) and were transported to the laboratory (about 10 km away) within 1 h (if caught by mist net) or 2 h (if caught as roosting birds in the evening). They were transported by car in a wooden box consisting of 12 separate compartments (15 × 10 cm and 8 cm high), with a single bird in each compartment. Thus, no more than 12 birds were transported at the same time. In the laboratory, birds were housed individually under a natural daylight regime in cages (0.8 × 0.4 m and 0.5 m high) with a solid bottom and top. During the winter the temperature in the laboratory was kept at 10 °C and during the summer at 15 °C. Birds had ad libitum access to food (mealworms and peanuts) and water, and human disturbance was kept to a minimum. Birds were kept in individual cages for one night and the next morning between 0900 and 1200 hours, each bird was introduced individually into the observation room through a sliding door, without being handled. During the following 2 min, we counted all movements among the different artificial trees (flights) and among the branches of individual trees (hops), including movements towards and from the lamps, sliding doors or the floor, but not including movements on a single branch. The sum of all movements was used as a measure of exploratory behaviour (Dingemanse et al., 2002). After the novel environment test the birds were released at the place of capture. The average weight loss of the birds between arrival at and departure from the laboratory was within their natural range (mean ± SD $= 1.39 \pm 0.68$ g, $N = 242$; Vanbalen, 1967). Observations during the playback experiment and data processing were done 'blind' to individual personality as the exploration scores remained unknown to the experimenter (C.G.C.J.) until the phase of data merging and statistical testing. Only the playback results of birds with known exploration score were used in this study.

Field Data Collection

Data were collected from 10 April to 9 May 2008 preceding and during the egg-laying phase of the breeding cycle. All data were collected before eggs hatched with one exception in which the bird had 1-day-old offspring during the playback experiment. We performed playback experiments from approximately 60 min after sunrise until noon. Individual identification of focal animals was done by occasional reading of colour band codes, but more often by associating birds with a particular territory and nestbox. All breeding birds were typically caught, identified and measured (weight, tarsus length) during the stage of feeding nestlings, which was shortly after our playbacks.

We performed playback experiments on 27 individuals of known personality. Recordings were taken using a Sennheizer