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

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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.

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

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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, Rytkönen, 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, Kazek, 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