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Social networking in territorial great tits: slow explorers have the least central social network positions

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In various animal species individuals differ consistently in their behaviour, often referred to as personality. In several species these personality differences also correlate with differences in social behaviour. This is important as the social environment is a key selection pressure in many animal populations, mediated, for example, via competition or access to social information. Using social network analysis, recent studies have furthered our understanding of the role of personality in the social environment, usually by focusing on swarming or flocking populations. However, social associations in such populations are fundamentally different from those in territorial populations, where individuals meet less frequently and where the costs and benefits of spatial associations differ from those for swarming or flocking species. In this study we therefore tested whether social network position is related to individual differences in exploration behaviour, an established measure of an avian personality trait, using a wild, territorial, personality-typed great tit, *Parus major*, population. By means of novel, large-scale, automated tracking (Encounternet) we show, while controlling for average territory distance, that slower exploring males had less central social network positions. Yet, slower explorers overall did not travel shorter distances than faster explorers, indicating that a less central social network position was not merely a consequence of lower activity. Finally, males with less central social network positions did not have reduced breeding success compared to males with more central positions. Our results suggest that territorial individuals influence the structuring of their own social environment in relation to their personality. This is relevant, because the establishment of social relations and familiarity with possible competitors is predicted to be important in many territorial populations.

The social environment in animal populations imposes a fundamental selection pressure on the fitness of individuals (see Smith & Parker, 1976; Wolf, Brodie, & Moore, 1999). Thus, it is relevant to understand whether and how individuals influence the structure of this social environment. Socially relevant behaviours have been found to vary in relation to personality, defined as consistent individual differences in behaviour (Amy, Sprau, de Goede, & Naguib, 2010; Groothuis & Carere, 2005; Pike, Samanta, Lindström, & Royle, 2008), and personality-dependent behaviour can, vice versa, vary depending on the social context (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; van Oers, Klunder, & Drent, 2005; Webster & Ward, 2011; Wolf & Krause, 2014). For example, in great tits, *Parus major*, a species in which boldness correlates positively with exploration behaviour (Groothuis & Carere, 2005), slow explorers are more strongly affected by social stress (Carere, Groothuis, Möstl, Daan, & Koolhaas, 2003) and differ from fast explorers in the strength of their response to social confrontations (Amy et al., 2010; Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005). Additionally, slow exploring males are found to adjust risk-taking behaviour to the behaviour of a companion, whereas fast males do not (van Oers et al., 2005). Personality differences are thus likely to have an influence on the social structuring of a population (Krause, James, & Croft, 2010; Wolf & Krause, 2014).

A relatively novel approach in animal behaviour for investigating the role of specific individual characteristics within the structuring of the social environment is social network analysis (Croft, James, & Krause, 2008). In a social network individuals are represented as nodes that can be connected to each other via social associations or interactions, represented by edges. By using social network analysis, the position of an individual within the social structure can be quantified. Consequently, it can be analysed

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whether this social network position is related to a certain characteristic of an individual, such as its personality. A limited number of studies have examined how personality differences could affect the social network structuring in animal populations. In a study of guppies, *Poecilia reticulata*, social associations were assorted in relation to individual boldness (Croft et al., 2009). Also, in a study analysing winter feeder visits of nonterritorial great tits, the most central network positions were occupied by the faster exploring individuals (Aplin et al., 2013). Findings on the relationship between personality and social network position are very relevant for understanding the costs and benefits of personality types, as social network studies have revealed that an individual's social network position can predict social rank (McDonald, 2007), discovery of new foraging patches (Aplin, Farine, Morand-Ferron, & Sheldon, 2012), acquisition of novel feeding strategies (Allen, Weinrich, Hoppitt, & Rendell, 2013) and mating success (Oh & Badyaev, 2010).

These social network studies have greatly advanced our knowledge of social network dynamics but have primarily focused on swarming or flocking populations (Aplin et al., 2013, 2012; Croft et al., 2009; Krause, Lusseau, & James, 2009; Oh & Badyaev, 2010). However, social associations are highly relevant also in nongrouping contexts such as in territorial populations (Getty, 1987), yet very little is known about the social network structuring of such populations. Territorial individuals are often limited in having many spatial associations with conspecifics, yet these spatial associations with conspecifics can increase access to social information, such as on local resources, competition and threats (Amrhein, Kunc, & Naguib, 2004; Aplin et al., 2012; Krama et al., 2012), information that is similarly relevant for territory owners. Additionally, spatial associations at the start of the territorial season may allow territory owners to familiarize themselves with each other. When individuals, later in the season, recognize each other as territory owners instead of as strangers, who could be trying to take over a territory, they are predicted not to escalate interactions among each other, as the payoff from winning would not balance the energetic costs and risks of injury (Smith & Parker, 1976). Indeed, territorial songbirds have the ability to remember and distinguish between familiar and unfamiliar neighbours (Akçay et al., 2009; Godard, 1991; Grabowska-Zhang, Sheldon, & Hinde, 2012) and neighbour familiarity has been found to correlate positively with reproductive success in several territorial songbirds (Beletsky & Orians, 1989; Grabowska-Zhang, Wilkin, & Sheldon, 2011).

Thus, if certain personality types associate less with surrounding conspecifics, as a result of a general weaker tendency to approach other individuals (Carere et al., 2005), this could have consequences for finding local resources, because of decreased access to social information (Allen et al., 2013; Aplin et al., 2012) and for individual energy expenditure on territory defence, because of reduced familiarity with nearby territory owners (Getty, 1987; Temeles, 1994). Nevertheless, it is not well understood whether and how personality and social network position are correlated within territorial systems. Knowing whether such a relationship exists will provide insights into the social consequences of personality differences (Wilson, Krause, Dingemanse, & Krause, 2013) as well as into the social structuring of territorial populations (Wolf & Krause, 2014).

Hence, in this study we tested, at the start of the breeding and territory season, whether male great tits differ in spatial social network position depending on their exploration behaviour, an established operational measure for a personality trait (Groothuis & Carere, 2005; Réale et al., 2007). Exploration behaviour in great tits not only relates to social behaviour (Amy et al., 2010; Carere et al., 2005, 2003), it also explains substantial variation in a wide range of other behaviours and life history traits, including general risk-taking behaviour (van Oers, Drent, de Goede, & van Noordwijk, 2004), cognitive performance (Titulaer, van Oers, & Naguib, 2012), behavioural response to stressors (Naguib et al., 2013), extrapair paternity (van Oers, Drent, Dingemanse, & Kempenaers, 2008), reproductive success (Both, Dingemanse, Drent, & Tinbergen, 2005) and survival (Dingemanse, Both, Drent, & Tinbergen, 2004). Furthermore, slower explorers show a faster and higher endocrine stress response to standardized stressors (Baugh, van Oers, Naguib, & Hau, 2013). Therefore, as slow explorers are known to take fewer risks (van Oers et al., 2004) and spatial associations in territorial populations are probably not without risk, we predicted that slower exploring territorial males would have less central social network positions. This prediction is also in line with results from earlier studies, such as Amy et al. (2010), in which fast exploring male great tits showed a closer approach to a simulated territory intruder and a more recent study measuring spatial associations at feeding stations of great tits in winter feeding flocks (Aplin et al., 2013), which showed that slower individuals had fewer unique contacts.

To determine spatial social network position, we used a novel automatized tracking system (Encounternet) at the initiation of the breeding season to track wild territorial male great tits, which had been tested earlier for exploration behaviour. By simultaneously tracking neighbouring birds we quantified close-range encounters between these individuals. Additionally, we quantified breeding success at the end of the breeding season to test whether strength of social network position is linked to components of fitness. A more central social network position could lead to increased access to social information about potential food sources and the whereabouts of aggressive competitors, which may be important for efficiently providing food to offspring, leading to a higher breeding success.

METHODS

Study System

We conducted this study at our long-term study population of great tits at Westerheide near Arnhem, The Netherlands (5°50′E, 52°00′N). Westerheide is a mixed pine–deciduous wood with approximately 200 nestboxes distributed within a 1000 m × 1200 m area (see Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002 for details). Using a routine procedure, we tested birds for exploration behaviour (Verbeek, Drent, & Wiepkema, 1994), an established operational measure for personality traits (Réale et al., 2007), using a novel environment test (Dingemanse et al., 2002; Groothuis & Carere, 2005).

Novel Environment Test

In a routine procedure, 61 great tits were taken from their roosting boxes, after sunset, in March 2012 and transported to the bird housing facilities at the Netherlands Institute of Ecology, where they were weighed and housed individually in cages (0.9 × 0.4 m and 0.5 m high), with a solid bottom and top, solid side and rear wall, a wire-mesh front and three perches. We provided food and water ad libitum. The following morning, exploration behaviour of 22 untested birds was measured using the novel environment test following Verbeek et al. (1994). Because birds are tested only when they are caught for the first time (as the test would no longer be testing the reaction towards a novel environment when retesting), only 22 of 61 birds were tested, since 39 birds had already been tested earlier. Birds were individually tested in a room (4.0 × 2.4 m and 2.3 m high) with five artificial trees. After they entered the experimental room, we recorded the total number of flights (movements between trees) and hops (movements within trees) within the first 2 min. The movements of the