



Male great tits assort by personality during the breeding season



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Animal personalities can influence social interactions among individuals, and thus have major implications for population processes and structure. Few studies have investigated the significance of the social context of animal personalities, and such research has largely focused on the social organization of nonterritorial populations. Here we address the question of whether exploratory behaviour, a well-studied personality trait, is related to the social structure of a wild great tit, *Parus major*, population during the breeding season. We assayed the exploration behaviour of wild-caught great tits and then established the phenotypic spatial structure of the population over six consecutive breeding seasons. Network analyses of breeding proximity revealed that males, but not females, show positive assortment by behavioural phenotype, with males breeding closer to those of similar personalities. This assortment was detected when we used networks based on nearest neighbours, but not when we used the Thiessen polygon method where neighbours were defined from inferred territory boundaries. Further analysis found no relationship between personality assortment and local environmental conditions, suggesting that social processes may be more important than environmental variation in influencing male territory choice. This social organization during the breeding season has implications for the strength and direction of both natural and sexual selection on personality in wild animal populations.

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Recent years have seen a growing interest in understanding the causes and consequences of animal ‘personality’ (Dall, Houston, & McNamara, 2004; Sih, Bell, & Johnson, 2004). Although complete behavioural plasticity might be expected to be the optimum strategy, individuals are typically limited in their range of behavioural expression, with variation observed in the population (Sih et al., 2004). These interindividual behavioural differences, which are consistent over time and correlated across different contexts, are referred to as behavioural syndromes or personality traits (Wolf & Weissing, 2012). They often have a genetic basis (Drent, van Oers, & van Noordwijk, 2003; van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005), are linked to a range of life history traits (Groothuis & Carere, 2005) and can have important fitness consequences (Dingemanse, Both, Drent, & Tinbergen, 2004; Smith & Blumstein, 2008). Behavioural phenotypes may therefore be

subject to natural and sexual selection (Dingemanse, Kazem, Réale, & Wright, 2009).

An understanding of the social context of personality is imperative since an organism’s social environment represents a key component of selection (Bergmüller & Taborsky, 2010; Krause, Lusseau, & James, 2009; Oh & Badyaev, 2010; Réale, Dingemanse, Kazem, & Wright, 2010). Indeed, an individual’s fitness is influenced not only by its own phenotype but also by the phenotype of the individuals with which it interacts (Farine & Sheldon, 2015; Formica et al., 2011; West-Eberhard, 1979; Wolf, Brodie, & Moore, 1999). The importance of social structure has often been overlooked as much work assumes a randomly mixed population (Farine et al., 2015). However, social interactions typically occur nonrandomly within populations, with individuals varying in their number and strength of connections (Croft, James, & Krause, 2008). Several studies across vertebrate taxa (including fish, birds and mammals) have found that individuals are nonrandomly distributed within social networks with respect to their personality (Aplin et al., 2013; Best, Blomberg, & Goldizen, 2015; Carter, Lee, Marshall,

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Ticó, & Cowlshaw, 2015; Croft et al., 2009; Snijders et al., 2014). This assortment may have consequences for social functioning (Wolf & Krause, 2014) and for the strength and direction of selection on behavioural phenotypes (Croft et al., 2009; Krause, James, & Croft, 2010; Wilson, Krause, Dingemanse, & Krause, 2013).

While empirical studies exploring the relationship between social structure and personality in wild populations have demonstrated that personality can be an important phenotypic trait influencing social organization, such studies have largely been restricted to foraging groups (Aplin et al., 2013; Best et al., 2015; Carter et al., 2015; Croft et al., 2009). By contrast, little is known about social network structure with respect to personality in territorial populations, such as during the breeding season of many songbirds. Social interactions at this time are likely to be fundamentally different, with less influence of interactions related to foraging (e.g. social information and predator avoidance) and more influence of interactions related to reproduction (e.g. mating opportunities and male–male competition). The only previous investigation of the relationship between personality and social structure in a territorial breeding population showed, via automated tracking, that slow-exploring male great tits, *Parus major*, tended to occupy less central network positions (Snijders et al., 2014).

In this study, we used data from a wild great tit population spanning 6 years to examine whether individuals show spatial assortment by personality type during the breeding season. In particular, we assessed exploration behaviour (the degree to which individuals explore a novel environment) since this is commonly used as a proxy for the reactive–proactive axis, including in our study species (Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). This behavioural axis contrasts shy, slow-exploring individuals with bolder, fast-exploring individuals (Quinn, Cole, Bates, Payne, & Cresswell, 2012). The continuous variation along this axis is hypothesized to result from the inherent trade-off between predator-averse behaviour favouring survival and risk-prone behaviour prioritizing productivity (Biro & Stamps, 2008; Wolf, van Doorn, Leimar, & Weissing, 2007). Previous work on our study population has demonstrated positive assortment among males by this measure of personality type in winter foraging flocks (Aplin et al., 2013). This suggests that shy birds may actively modify their social environment by avoiding bolder, more aggressive individuals (Aplin et al., 2013). Indeed, aggressive interactions between males are more intense during the territorial period and aggression is known to be positively correlated with exploratory behaviour in this species (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005). We therefore hypothesized that birds may also demonstrate positive assortment by personality with respect to their choice of breeding location.

METHODS

Study System

Data were collected from a wild great tit population at Wytham Woods, Oxfordshire, U.K. (51°46'N, 01°20'W), which is a mixed deciduous woodland of 385 ha, bordered by farmland. This population is part of a continued long-term breeding survey, which began in 1947 and monitors the location and identity of nesting pairs (Savill, Perrins, Kirby, & Fisher, 2010). The majority of great tits at this study site have a unique metal leg ring and they generally nest in one of the 1018 nestboxes in the woodland (Aplin, Farine, Morand-Ferron, Cockburn, Thornton, & Sheldon, 2014). The population exhibits fission–fusion dynamics over autumn and winter, whereas the social structure changes in the breeding season (Psorakis, Roberts, Rezek, & Sheldon, 2012). During this period,

typically from March to June, socially monogamous pairs hold and defend territories around the nestboxes (Hinde, 1952).

Personality Assays

An individual's position along the shy–bold personality axis was estimated using an assay of exploration behaviour in a novel environment. These assays were first conducted in 2005 and have been carried out in subsequent years according to the same methodology (Quinn et al., 2009). Great tits were captured via mist netting during winter and kept in individual indoor aviaries overnight. Birds were assayed individually the following morning for 8 min in a novel environment room with five perches. The frequency and location of their movements were recorded with a handheld computer. These observations were incorporated into a principal component analysis to generate an exploration score for each bird on a continuous scale, such that individuals visiting each of the five perches and each of the five areas, and with a greater frequency of hops and duration of flights, were assigned a higher exploration score (Quinn et al., 2009). Exploration behaviour was moderately repeatable within and between our assaying seasons (Quinn et al., 2009) and has been shown to correlate with a wide range of functional behaviours in our wild population (Aplin, Farine, Mann, & Sheldon, 2014; Aplin et al., 2013; Cole & Quinn, 2012, 2014; Patrick, Chapman, Dugdale, Quinn, & Sheldon, 2012; Quinn, Cole, Patrick, & Sheldon, 2011; Quinn et al., 2012).

Social Networks During Breeding Season

Associations between individuals were inferred based on the spatial proximity of occupied nestboxes. By connecting individuals (nodes) via associations (edges), social network analysis provides a means to assess fine-scale population structure (Farine & Whitehead, 2015; Krause et al., 2010). Network analyses and all associated statistics were performed in R 3.2.3 (R Development Core Team, 2015). Networks were constructed for six consecutive breeding seasons from 2005 to 2010. To account for local breeding densities, we classified individuals as associated with their k nearest neighbours for a range of values of k (where $k = 3, 5$ or 7). As weighted networks provide more robust estimates of assortment (Farine, 2014), we also assigned weights to each edge e_{ij} , where $e_{ij} = \frac{1}{\ln(d)}$ and d is the Euclidean distance between the nestboxes in which individuals i and j are breeding (but where $e_{ij} = 0$ if j is not a k th nearest neighbour of i). This measure of proximity is particularly relevant, as the slope of decline in extrapair paternity with distance follows a log-linear relationship (Hadfield, 2012) and so it is reasonable to assume that territorial interactions may occur on a comparable spatial scale. Since nearest-neighbour networks are not necessarily symmetrical (as one individual may be another's nearest neighbour but not vice versa), this method generates directed networks. For comparison, networks were also constructed using the Thiessen polygon method to approximate neighbours. Associations were assigned based on which individuals shared a boundary when Thiessen polygons were created around each occupied nestbox to predict territories (Schlicht, Valcu, & Kempenaers, 2014). The polygons were generated using the packages spatstat (Baddeley & Turner, 2005), spdep (Bivand, 2016), mapproj (Bivand & Lewin-Koh, 2012) and rgdal (Bivand, Keitt, Rowlingson, & Pebesma, 2012). These Thiessen polygon networks are undirected, but individuals can vary in their number of neighbours based on the geometry of their territory. We use the term neighbour throughout to describe any two individuals that are connected in a network, although with the nearest-neighbour method, this may not necessarily equate to sharing a territory boundary.

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