



## 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.

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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, & Dingemans, 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 non-grouping 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, 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

birds in the experimental room were subsequently used to calculate an overall exploration score ranging from low (slower explorers) to high (faster explorers; Dingemans et al., 2002).

As we do not have repeated exploration measures, our study design did not permit us to investigate in more detail the between- and within-individual variation in behavioural types, which has recently been suggested as an alternative procedure in the personality literature (Dall & Griffith, 2014; Dingemans & Dochtermann, 2013). However, exploration behaviour in this population is established as a highly repeatable proxy for behavioural traits in wild great tits (Dingemans et al., 2002). Moreover, a similar study using exploration score to explain territory defence (Jacobs et al., 2014) did not find a qualitative difference in the results when comparing the use of the first score with multiple scores of individual exploration behaviour. Therefore we have good evidence that our measurement of exploration behaviour reflects substantial between-individual variation.

### *Reproductive Success*

During the breeding season, using a standardized procedure (van Oers et al., 2008), we checked nestboxes twice a week to identify the breeding birds and quantify their breeding success. The main recorded breeding measures were laying date, clutch size, start of incubation, number of hatchlings and number of fledglings. Adults were caught inside their nestboxes using spring traps (metal doors that close the nest hole when the bird enters the nestbox) on approximately the 7th day after hatching of the chicks. We caught nestlings on the 14th day after hatching. We fitted unringed individuals with uniquely numbered aluminium leg rings and measured body mass and tarsus length.

### *Spatial Network Tracking*

We equipped 34 of 61 caught birds with an Encounternet tag of approximately 1 g, using a leg-looped backpack harness (see [Supplementary material, Fig. S1](#)). This selection was based both on the limited number of available tags and on the location of the caught birds, i.e. birds caught in the outer corners and at lower density areas of the study site were not included. The Encounternet tags are active radiotransmitters, set to transmit every 5 s, and were especially designed to be as light as possible for use on small passerines. Within 24 h after catching, we released birds next to their roosting nestbox. During a subsequent roosting check a few days later we tagged directly at their roosting nestbox an additional five birds and retagged four birds, whose tag had failed to work. In total 29 males and 10 females were tagged. We selected 13 males for social network analysis based on (1) holding nearby territories, (2) having more than 100 localizations and (3) having simultaneous observations with all other males within the analysis. During two complete roost checks in March we identified 27 unique males within an area comprising all nestboxes within a 242 m radius (two times the maximum documented unmanipulated mean territory size; Both & Visser, 2000) of the subject roosting boxes, which thus represented approximately 48% (13/27) of the nearby male population. Tracking data were analysed only from the day following the day of release (9–13 March 2012) to control for birds' behaviour potentially being affected immediately after tagging.

Encounternet (Encounternet LLC, Portland, OR, U.S.A.) consists of roaming nodes (tags fitted to the birds), base nodes (receivers) distributed across the study site and master nodes used to download data from the receivers. We used up to 93 receivers, which were placed in strategic locations throughout the study site. With this novel tracking system the locations of birds are mapped simultaneously and automatically, thus expanding data collection

considerably beyond traditional radiotracking in which single individuals are followed manually (Naguib, Altenkamp & Griessmann, 2001). Tags transmitted a digital ID code every 5 s which was logged by receivers within signal range, along with a time stamp and a received signal strength indicator (RSSI). We GPS-mapped the locations of the receivers (Garmin GPSmap 62st). Using Pymaster software version 22 (Encounternet LLC, Portland, OR, U.S.A.) we downloaded and organized all received signals per individual tag. Subsequently, the RSSI value was used to calculate the distance between the tag and the receivers based on a fixed distance–RSSI curve (Mennill et al., 2012). Tags can be detected up to approximately 90 m from a base node, with the distance–RSSI curve getting less steep around 50 m. We triangulated the locations of each bird by combining all the RSSI values of at least three receivers within the same half-minute, using MATLAB (The MathWorks, Natick, MA, U.S.A.).

The 13 subject males were on average detected for 2007 (971–4698) half-minutes and triangulated 722 (134–2809) times. Detection numbers vary per bird, depending on the difference in tag life span and birds moving out of the detection range of a base node. There are fewer triangulations than detections as birds were not always in the range of at least three base stations. A simultaneous observation is defined as two individuals both having a triangulated location during the same minute. In calibration tests, in which we placed two tags within 5 m of each other, the system calculated them to be  $7.5 \pm 6.5$  m apart. We therefore decided 10 m apart to be a good cutoff point (approximation) for an encounter as it would capture most of the real encounters between individuals (birds being aware of each other), while taking into account the inaccuracy of the localization. An encounter was thus a priori (before analysis) defined as two triangulated individuals being within 10 m of each other. The association strength between two individuals was defined by the number of times two individuals were within 10 m of each other divided by the total number of times they were observed simultaneously. Individuals in our analysis had on average 472 (173–1129) simultaneous observations. A unique combination of two males was observed on average 39 times simultaneously and 68 (87%) of the 78 ( $(12 \times 13)/2$ ) possible pair combinations were observed more than 10 times simultaneously. Thus with all possible pair combinations we mean to say that the 13 males could each meet 12 of the other males. We divided this number by 2 as in a spatial association we cannot distinguish between male A meeting male B and male B meeting male A.

### *Statistical Analysis*

#### *Spatial network tracking*

Using an unprecedentedly large data set of individual locations, a total of 9380 localizations, 3066 simultaneous observations and 70 encounters within 10 m ([Appendix Fig. A1](#)), we calculated and visualized the social network properties with the software programs UCINET (Borgatti, Everett, & Freeman, 2002) and SOCPROG (Whitehead, 2009). The individual network properties analysed were Strength (the sum of association strengths per individual), Eigenvector centrality (this measure of connectivity takes into account how well an individual is connected to other well-connected individuals) and Degree (the number of unique connections per individual). We used the linear permutation model in the *lmPerm* package (Wheeler, 2010) version 1.1-2 in R 2.15.2 (R Core Team, Vienna, Austria) for statistical analysis of dependent data. For all other analyses, unless mentioned otherwise, we used SPSS 19.0 (IBM Corp., Armonk, NY, U.S.A.). Because values for significance in permutation models are based on approximation, significance levels are shown using '<' or '>'. The 'Prob' method of *lmPerm* was employed, which approximates the permutation distribution by

randomly exchanging pairs of dependent values and iterations are stopped when the estimated standard error of the estimated proportion  $p$  is less than  $p \times 0.1$  (Wheeler, 2010). Every 10 cycles a complete random permutation was performed.

All the linear permutation models for the effect of exploration score on the individual network properties were controlled for the average nestbox distance of the individual (the average of the distances between the subject roosting box to the other 12 individuals) as a continuous variable, age of the individual as a categorical factor (younger or older than 1 year) and condition of the individual calculated as the residual of the function of weight against tarsus (continuous). Because birds in the centre of the study area would have a higher chance of encountering other individuals at random than birds on the edge of the study area we controlled for this using the average territory distance. Males with territories more towards the edge of the study area also had the largest average territory distance (independent  $t$  test:  $t_{11} = -4.245$ ,  $P = 0.001$ ). Thus to correct for spatial dependence in a territorial species at all times and because there was a nonsignificant trend for Degree to be larger with a smaller average territory distance, we kept average territory distance (an approximation of spatial dependence) as a control in all the final models. We used backward model selection for age and condition and removed them when there was less than a trend effect ( $P > 0.1$ ), starting with the least significant term.

Results were checked for possible systematic biases, that is, biases introduced by the systematic data collection itself which could consequently be driving the results we found. We tested with approximate Spearman correlation tests (9999 permutations) in the R Coin package (Hothorn, Hornik, Van de Wiel, & Zeileis, 2008) whether exploration score, Strength, Eigenvector centrality and Degree were correlated with average territory distance (only for exploration score to check for possible collinearity between exploration score and average territory distance), number of localizations, detectability (locations/h) and number of simultaneous observations. There was only a trend for an effect ( $Z = 1.8335$ ,  $P < 0.08$ ) for number of simultaneous observations on Degree; however, controlling for this in the linear model did not significantly change the outcome and it was therefore left out of the final model. Additionally, birds with territories more towards the edge of the study area were not characterized by a significantly higher or lower exploration score (independent  $t$  test:  $t_{11} = -0.142$ ,  $P = 0.89$ ).

To check whether individual social connectivity was not just driven by individual activity, we calculated the median speed (m/s) for each individual by calculating the distances moved between two consecutive (half a minute apart) locations (31–193 values per individual). The median of speed was used to account for non-normality. To account for the variation in sample size we randomly drew 10 000 times 31 samples from each individual (without replacement) and calculated the median speed for all of them (thus 10 000 times per individual). Subsequently, we performed a Spearman correlation test between exploration and these median speeds 10 000 times.

#### *Reproductive success*

Linear models were used to analyse the relationship between the number of fledged offspring and the breeding male's Eigenvector centrality (excluding one failed nest). Age of the birds (younger or older than 1 year) did not have a significant effect and was left out of the final model. Including the nest in which none of the chicks fledged did not significantly change the outcome.

#### *Ethical Note*

Within 1.5 h after being caught the birds were transported by car from the field to the institute (maximum 20 min). The exact

duration between catch and transport ranged from approximately 10 min to 1.5 h between individuals, depending on when they were removed from their roosting box. During this time, and during transport to the institute, birds were individually housed in standard darkened wooden carriers containing 10 compartments (10 × 10 × 10 cm). There were no apparent effects of the transport on health (no visual injuries or mortality). When moved from carrier to indoor cage, and vice versa, birds were caught by hand. Before being housed in individual standard indoor cages (see *Novel Environment Test*), tarsus and weight were measured (maximum duration of handling was 5 min). In the laboratory, birds were provided with mealworms, fat balls, apple, sunflower seeds and water ad libitum. The exploration test is part of an established routine procedure and was conducted between 0800 and 1200 hours. During this procedure birds commonly do not lose weight outside their natural range (Dingemanse et al., 2002). Individual cages are connected to the novel environment room (see *Novel Environment Test*) via a 20–20 cm sliding door and the individual cage was darkened, so a bird could enter the room without being handled. When the test was terminated, after at most 10 min, the room was darkened (birds stay perched then) and the bird was caught by hand and released back to its cage within 1 min. None of the birds died in captivity. After being tested for exploration behaviour and tagging (see *Spatial Network Tracking*), which lasted a maximum of 5 min, birds were released back in the field close to their nestbox within 24 h. After these procedures, birds usually stay on their territory and breed, as evidenced by yearly breeding records and also by radiotracking (Amy et al., 2010). Tags had a weight of, on average, 5.6% of body weight (maximum 6.2%). We are aware that 5% of body weight is often recommended as an upper limit and we agree that transmitters should be as least disruptive and stressful as possible. However, a meta-analysis on avian transmitter effects (Barron, Brawn, & Weatherhead, 2010) did not find greater transmitter effects when proportionally heavier devices were used. Additionally, to maximally reduce the possibility of a negative effect of the transmitter on the birds, the Encounternet tags were especially designed to be as light as possible for use on small passerines, while still allowing for the use of this novel technology (simultaneous observation of multiple individuals). Of the 34 birds caught and tagged on 7 March 2012, 25 individuals were later found breeding (73%), similarly to the 10 of the 15 birds we checked that same night but that we left in their nestbox and were later found breeding (67%). Additionally, tagged parents did not have fewer fledged chicks when comparing parent birds that only differed in receiving an Encounternet tag on 7 March (median = 6 chicks) to birds that did not (median = 5 chicks). These data indicate that during the time between tagging and provisioning the chicks (approximately 2 months) birds with tags did not have a higher risk of mortality, for example by increased vulnerability to predation, or impaired parental abilities. Tagged birds were found breeding in the same nestbox in which they were caught or in a nestbox within 200 m. Only one male bred more than 200 m away from the place of catching. Birds lose their Encounternet tags, including the harness, usually within 3 months, because the harness wears out. Breeding birds that had not lost their tag were trapped as parents in their nestbox during chick feeding using spring traps, as part of a routine procedure to establish the identity of the breeding birds. These birds had their tag removed and were released within a few minutes. Birds were not trapped inside their nestbox for longer than 15 min. It is unknown how long birds took to go back to their broods after trapping, as we left the area to avoid disturbing the birds; however, the trapping, for parent identification, was done following a standard protocol and our data did not suggest that trapping had any profound effect on chick mortality or brood desertion. Permission for this study was granted by the

Dutch legal entity: KNAW Dier Experimenten Commissie (DEC) no. NIOO-10.05 to M.N. and K.v.O.

## RESULTS

### Spatial Network Position

Strength, a measure of how much time a male spends close to the other males relative to the time he spent alone, was lower for slower exploring males (Table 1). As a consequence, slower explorers also occupied the least central positions in the network (Fig. 1a), reflected by a lower Eigenvector centrality (Fig. 1b, Table 1). Interestingly for a territorial species, some of the males did encounter up to nine of the 12 other tagged males, with a trend for slower males to have the fewest unique contacts, also called Degree (Fig. 1c, Table 1). Males that had the fewest unique contacts were characterized by the lowest Strength (linear permutation model: estimate = 0.048, iterations = 5000,  $N = 13$ ,  $P < 0.005$  and Eigenvector centrality linear permutation model: estimate = 0.036, iterations = 5000,  $N = 13$ ,  $P < 0.005$ ). In all final models we included the average territory distance for each male to all other 12 males as a control variable, but only the number of unique contacts (Degree) tended to decrease when the average territory distance between males became larger (Table 1).

### Movement Speed

Slower explorers were not slower during tracking, and thus when they were in their natural environment, as 98.3% of the 10 000 correlation tests of exploration score and median speed, based on randomly drawn samples of equal sample sizes for each individual, were not significant (Fig. 2). This indicates that the lower social connectivity of slower explorers was not a side-effect of lower spatial activity.

### Reproductive Success

There was no relationship between the number of fledged offspring (range 2–6) and the Eigenvector centrality of breeding males (linear model:  $F_{1,7} = 0.76$ ,  $N = 9$ ,  $P = 0.41$ ).

**Table 1**  
Permutation model statistics for social network position

Social network position		Estimate	Iterations	<i>P</i>	<i>N</i>	
Strength	<b>Exploration score</b>	0.008	3996	<b>&lt;0.03</b>	13	
	<b>Average territory distance (km)</b>	−0.703	103	<b>&gt;0.40</b>	13	
	Condition	−0.005	51	>0.90	13	
	Age	0.048	141	>0.20	13	
	Eigenvector centrality	0.007	5000	<b>&lt;0.02</b>	13	
Eigenvector centrality	<b>Average territory distance (km)</b>	−0.440	77	<b>&gt;0.50</b>	13	
	Condition	0.000	51	>0.90	13	
	Age	−0.070	323	>0.20	13	
	Degree	<b>Exploration score</b>	0.101	1801	<b>&lt;0.06</b>	13
		<b>Average territory distance (km)</b>	−29.335	1340	<b>&lt;0.08</b>	13
Condition		−0.126	51	>0.70	13	
	Age	0.102	51	>0.90	13	

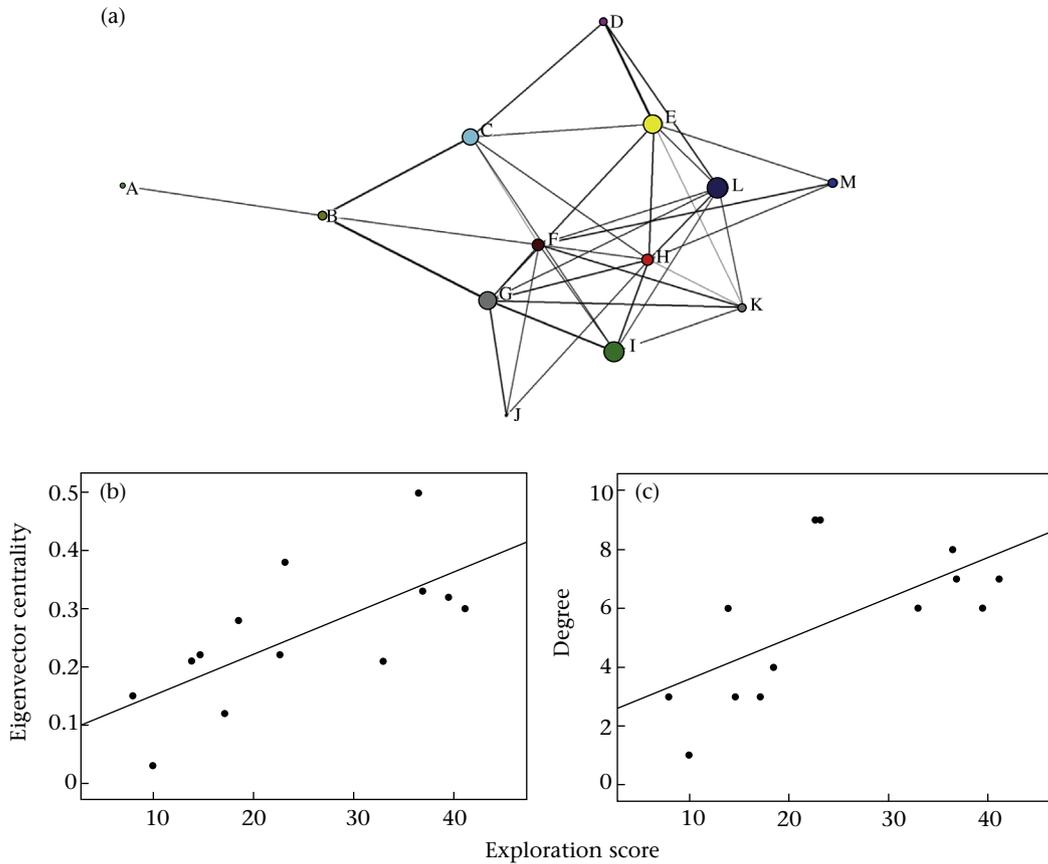
Values are based on the last model still including the variable, using backward model selection. Variables in bold were kept in the final model.

## DISCUSSION

The automated tracking of male territorial great tits revealed that slower exploring males showed an overall weaker social connectivity, in terms of less central spatial social network positions, than faster exploring males. Moreover, our findings suggest that higher connectivity in the wild is an active process and does not result from a generally higher activity of faster explorers, as the median distance travelled did not correlate with individual exploration behaviour. Finally, we found no evidence that a weaker social network position was correlated with lower breeding success.

Our finding that territorial males differed in social network position in relation to their exploration behaviour has important implications. Slower explorers spent relatively the least time in the vicinity of other males (lower Strength) and this was strongly related to the number of unique contacts (lower Degree) of individuals. When individuals spend less time near other conspecifics this will presumably lead to less familiarity among conspecifics. This is relevant, because familiarity, mediated by repeated encounters among individuals, can lead to a general decrease in the level of aggressive interactions (Geffroy, Bru, Dossou-Gbété, Tentelier, & Bardonnnet, 2014; Ward & Hart, 2003). Familiarity between individuals, which exhibit consistent behavioural differences (personality), is predicted to promote social responsiveness, as it makes individuals predictable and so allows individuals to match their behaviour to that of their interaction partner (McNamara, Barta, & Houston, 2004; Wolf, Van Doorn, & Weissing, 2011). This can mediate the use of tit-for-tat strategies (Akçay et al., 2009), reducing unnecessary aggressive interactions and allowing for cooperative alliances (Booksmythe, Jennions, & Backwell, 2010; Elfström, 1997; Goodwin & Podos, 2014; Grabowska-Zhang et al., 2012). For example, neighbouring great tits that shared a territory boundary the previous year were more likely to join each other in nest defence than neighbours that had not shared a boundary (Grabowska-Zhang et al., 2012). However, individuals that are already generally less aggressive, such as slower explorers (Carere et al., 2005; Verbeek, Boon, & Drent, 1996), might also have fewer benefits from increasing familiarity with conspecifics, as they are anyway less likely to escalate territorial defence interactions. Indeed, slower exploring male great tits showed a weaker approach during territory defence when confronted with a simulated intruder (Amy et al., 2010). Additionally, a similar trend has also been found in other species, such as rainbowfish, *Melanotaenia duboulayi*, in which lower ranked males, which were less aggressive, were also less social (Colléter & Brown, 2011).

Still, social connectivity also relates to how much an individual is exposed to public information about potential food resources and feeding techniques (Allen et al., 2013; Aplin et al., 2012), competitors (Amrhein et al., 2004; Gil & Gahr, 2002) and mates (Mennill et al., 2012; Oh & Badyaev, 2010), all components that directly affect individual fitness. For example, in songbirds and whales spatial associations led to new feeding opportunities (Allen et al., 2013; Aplin et al., 2012) and for some songbirds also to better mating opportunities (Oh & Badyaev, 2010). Nevertheless, we did not find an effect of spatial network centrality on breeding success, which could be the result of several factors. First, it is certainly possible that our sample size was too small to detect a correlation between spatial network position and breeding success. A larger sample size would be necessary to rule out this hypothesis. Second, the lack of an effect on breeding success could be related to personality-dependent social responsiveness and use of social information: for example, slow exploring male great tits were shown to be more socially responsive, by adjusted their risk-taking behaviour in response to a companion's behaviour (van Oers et al., 2005) and in barnacle geese, *Branta leucopsis*, shy



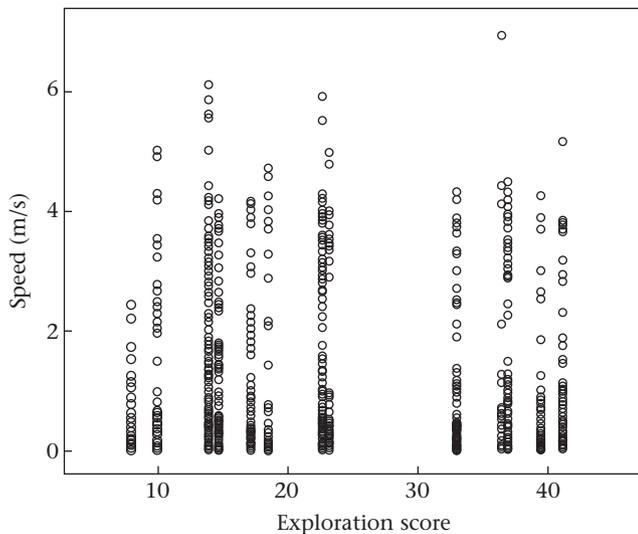
**Figure 1.** (a) Visualization of the social network with NetDraw (Borgatti, 2002) using a spring embedded layout based on distances, node repulsion and equal edge length. The size of the nodes reflects the relative exploration score of individuals (different letters) and the thickness of the lines represents the relative association strength between each pair. (b) A bird's Eigenvector centrality, a network position measure including direct and indirect connectedness, according to its exploration behaviour. (c) Degree, the number of direct connections per individual, according to the bird's exploration score. Lines are regression lines.

individuals were more inclined to use social information than bolder individuals (Kurvers et al., 2010). Finally, it might be that, for slower explorers, the costs of a more central social network position outweigh the benefits of increased access to social information. It can also be risky to be close to a conspecific, as it might result in a

fight (Carere et al., 2005; Rowell, 1974), increased social stress (Carere et al., 2003; Rowell, 1974) and more exposure to parasites (Croft et al., 2011) and predators (Grabowska-Zhang et al., 2012; Krama et al., 2012). If the costs of a stronger social network position indeed vary with personality it would explain both why slower explorers, which are more risk-averse (Réale et al., 2007) and more vulnerable to social stress (Carere et al., 2003), showed weaker social connectivity, but also why we did not find a correlation between social network position and breeding success.

Songbirds can also connect to each other via signal interactions, often referred to as communication networks (McGregor, 2005). Great tits have been found to differ in relation to exploration behaviour in using stronger spatial or signal responses when confronted with conspecifics (Amy et al., 2010; Carere et al., 2005; Verbeek et al., 1996). Slower exploring males confronted with a male conspecific showed a longer latency and frequency of attacks (Carere et al., 2005; Verbeek et al., 1996), spent less time close to a simulated intruder (Amy et al., 2010) and showed a longer latency to approach when confronted with a female (Carere et al., 2005). However, slow males did show a higher frequency of agonistic displays during the male to male confrontation in Carere et al.'s study (2005) and sang with a higher song rate during the simulated intrusion in Amy et al.'s study (2010). Connectivity in terms of spatial associations might thus not equal social connectivity.

Our findings expand on a previous study on wintering (non-territorial) great tits visiting artificial feeding stations (Aplin et al., 2013), also showing that slower birds have a weaker social connectivity. Social encounters during the territorial period, however, could be expected to differ from winter encounters since there is



**Figure 2.** Median speed (m/s) according to individual exploration score. Each visualized single speed measurement represents the distance moved between two consecutive, half a minute apart, locations (31–193 values per individual).

less effect of flock composition and use of shared resource locations. Encounters by territorial birds are more likely to reflect direct social interactions among neighbouring birds in competition for space and reproduction. This is relevant, because when certain personality types prefer to avoid social confrontations (Wolf et al., 2011), as the results of this study suggest, this could lead to different personality types thriving better under different population densities (Sih, Cote, Evans, Fogarty, & Pruitt, 2012), especially in a territorial system.

Moreover, a personality type is also likely to be partly shaped by the specific social environment of an individual (Bergmüller & Taborsky, 2010; Wolf & Krause, 2014). Experimental studies would be necessary to confirm the causes and consequences of the correlation between personality and social network position. Still, irrespective of this, we reveal here that individuals in a territorial songbird system do not merely encounter each other at random.

Taken together, our results suggest that territorial individuals influence, and consequently differ in, the structuring of their social environment in relation to their personality. This is important, because the establishment of social relations and familiarity with possible competitors is predicted to be significant in many territorial populations.

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## Supplementary Material

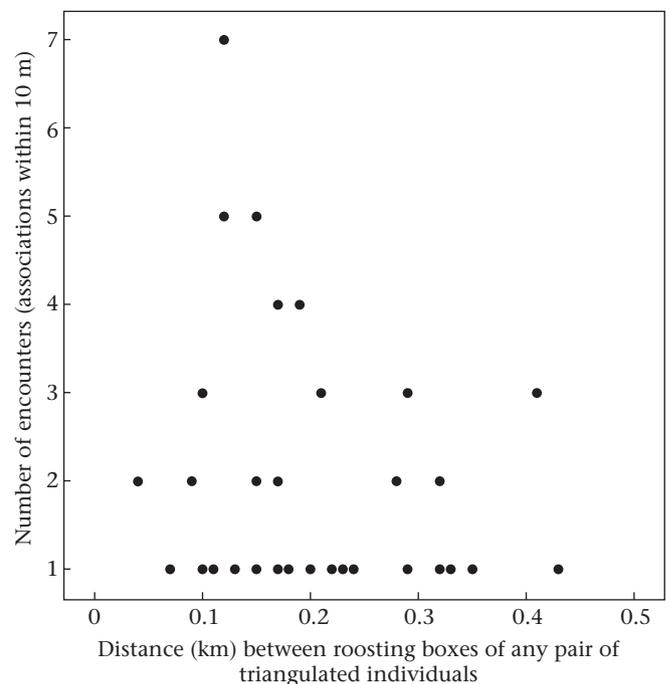
Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.anbehav.2014.09.029>.

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## APPENDIX I



**Figure A1.** The number of encounters between any possible pair combination of the 13 tracked great tit males in relation to the distance (km) between their roosting boxes.