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LETTER

Individual personalities predict social behaviour in wild networks of great tits (*Parus major*)

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Abstract

Social environments have an important effect on a range of ecological processes, and form a crucial component of selection. However, little is known of the link between personality, social behaviour and population structure. We combine a well-understood personality trait with large-scale social networks in wild songbirds, and show that personality underpins multiple aspects of social organisation. First, we demonstrate a relationship between network centrality and personality with ‘proactive’ (fast-exploring) individuals associating weakly with greater numbers of conspecifics and moving between flocks. Second, temporal stability of associations relates to personality: ‘reactive’ (slow-exploring) birds form synergistically stable relationships. Finally, we show that personality influences social structure, with males non-randomly distributed across groups. These results provide strong evidence that songbirds follow alternative social strategies related to personality. This has implications not only for the causes of social network structure but also for the strength and direction of selection on personality in natural populations.

Keywords

Behavioural syndrome, Paridae, personality, social behaviour, social network theory.

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INTRODUCTION

Understanding the causes and consequence of animal personalities has become one of the great challenges for recent research in evolutionary and behavioural ecology (Wolf *et al.* 2007; Dall *et al.* 2012). Consistent behavioural differences between individuals have been demonstrated in multiple taxa, with some individuals repeatedly exhibiting more bold, aggressive or exploratory behaviour across a range of contexts (Sih *et al.* 2004). These consistent differences often have a genetic basis and are likely to be subject to selection, thereby creating the challenge of explaining how such diversity in behavioural traits could arise and persist in natural populations (Dingemanse *et al.* 2004; Dingemanse & Wolf 2010). Most current research has concentrated on individual traits associated with variation in personality, e.g. dispersal (Quinn *et al.* 2011), or on dyadic interactions, e.g. in aggression assays (Carere *et al.* 2005). We thus have little understanding of the relationship between individual-level personality traits such as exploration behaviour and social behaviour (Webster & Ward 2011; Sih *et al.* 2012), or how social structure, group dynamics and personality may interact (Krause *et al.* 2010). This is a major gap, as social interactions are an important aspect of the ecology of almost all animals, and knowledge of the social context of personality is essential when considering potential mechanisms for the evolution and maintenance of personality differences (Wolf *et al.* 2007; Bergmuller & Taborsky 2010; Dingemanse & Wolf 2010).

Social network theory provides a formal framework for describing association patterns, allowing characterisation of social structure that integrates all levels from individual interactions to population processes (Krause *et al.* 2010). If personality affects an individual's

social behaviour, this would be expected to influence its association patterns in the social network (Croft *et al.* 2009). However, the resulting social network structure may in turn change the strength and direction of selection on personality, if individual fitness is dependent on the social environment (Krause *et al.* 2010; Wilson *et al.* 2013). This patterning of social interactions may thus be important for assessing theoretical models for the evolution of personality, most particularly selection driven by negative frequency dependence or social niche specialisation (Wolf *et al.* 2007; Dingemanse & Wolf 2010). Under the first of these two models, payoffs are dependent on trait frequency and network structure should thus show a mixing of personality types (Dall *et al.* 2004; Johnstone & Manica 2011), while a social niche specialisation model selection should favour diversification or character displacement leading to reduced social conflict (Bergmuller & Taborsky 2010).

There have been few empirical studies of the role of personality in social networks. Most notably, Pike *et al.* (2008) found that captive bold sticklebacks (*Gasterosteus aculeatus*) had more social connections, but these interactions were more evenly spread, with shy fish preferring to associate more strongly with fewer individuals. Consequently, shoals of all bold type individuals displayed higher activity levels. A similar result was found in captive water-striders (*Aquarius remigis*), where groups of aggressive males were more active (Sih & Watters 2005), and in shore-crabs (*Carcinus maenas*), where fast-exploring individuals were more likely to make spatial movements between groups (Tanner & Jackson 2012). Only one study has thus far investigated the relationship between social organisation and personality in the wild, with female Trinidadian guppies (*Poecilia reticulata*) more likely to be found in shoals with individuals of the same personality type (Croft *et al.* 2009).

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We studied personality and social behaviour in great tits, *Parus major*, using the reactive-proactive personality axis common to many vertebrate groups. This axis contrasts cautious, shy, slow-exploring (SE) individuals with bold, aggressive, fast-exploring (FE) individuals; it is believed to reflect a trade-off between predator-averse behaviour prioritising survival, and more risk-prone behaviour that enhances productivity (Smith & Blumstein 2008; Quinn *et al.* 2012). In both our population and others, an assay of exploration behaviour in a novel environment (performed on wild birds temporarily taken into captivity) has been demonstrated to be a good proxy of the reactive-proactive axis (Carere *et al.* 2005; Groothuis & Carere 2005; Quinn *et al.* 2009, 2012). Exploration behaviour has further been shown to be repeatable (Carere *et al.* 2005), heritable (van Oers *et al.* 2004), subject to selection (Dingemanse *et al.* 2004; Quinn *et al.* 2009, 2011) and linked to a set of life history traits across several populations (e.g. dispersal behaviour (Groothuis & Carere 2005; Quinn *et al.* 2011)).

We use new technologies to measure social associations at a large scale and over an extended time period in a wild wintering population of birds. An evenly spaced grid of automated feeding stations fitted with passive integrated transponder (PIT)-tag recording antennae collected 'snap-shots' of the composition and distribution of flocks. Using this spatio-temporal flocking data, we first constructed a wild foraging social network for the entire population of 1017 individuals. Second, we used social network analysis to obtain a measure of the social phenotype of focal individuals assayed for personality, both at the local community and population level. Third, we investigated the temporal stability of associations between focal individuals over the 3 month winter flocking period. Finally, we used two methods to ask whether the distribution of personality types in foraging flocks was non-random, i.e. assorted, and discuss implications for group formation and organisation. We thus present a multi-faceted approach with complementary lines of evidence to understand the link between individual behavioural phenotype, social behaviour and population structure in group-living animals.

MATERIALS AND METHODS

Study system

The study was conducted on a population of great tits at Wytham woods, Oxfordshire (51° 46' N, 01° 20' W). Wytham woods is a 385 ha area of broadleaf deciduous woodland, and is surrounded by farmland (Fig. S1). This population has been the subject of an extensive long-term breeding survey, and there is an ongoing trapping and monitoring effort. Almost all individuals in the study area are fitted with both a British Trust for Ornithology metal leg ring, and a plastic leg ring containing a uniquely identifiable PIT tag (proportion PIT-tagged estimated at over 90%, see S2 and Fig. S2). While pairs of great tits defend territories over the breeding season, this breaks down into loose fission-fusion groups of unrelated individuals over autumn and winter, with roaming flocks congregating on ephemeral and patchy food sources such as beech mast (seeds of *Fagus sylvatica*) (Aplin *et al.* 2012).

Field observations

Adults and nestling great tits were caught in the breeding season prior to data collection (April to June 2011) and from September to

November 2011, when they were aged and sexed based on plumage colour. Birds were also assigned as 'post-breeding' adults or 'pre-breeding' birds (largely juveniles) based on data from previous breeding seasons (2005–2011). From 2nd December 2011 until 27th February 2012, sunflower feeders were deployed at 65 locations throughout the study site, each approximately 250 m apart (Fig. S1). Each feeding station had two access points each fitted with radio-frequency identification antennae and data logging hardware. All feeders automatically opened from dawn to dusk on two consecutive days in every seven, scanning for PIT-tags every 16th of a second. This equated to 26 days of data collection over 13 sampling periods.

Behavioural assays

Assays of exploration behaviour in a novel environment were conducted on wild great tits that were temporarily taken into captivity at the Wytham field station over four winters (October 2009 to October 2012). Most data (55%) were collected from late February to early March 2012. Behavioural assays have been ongoing in this population since 2005 (Quinn *et al.* 2009, 2012), and we followed existing methods, based on a design by Verbeek *et al.* (1994). Birds were caught with mist-nets and housed individually overnight. On the morning after capture, all birds were individually assayed in a novel environment containing five artificial trees, where their movements were recorded for 8 min using a handheld events recorder (Pision Workabout, Noldus Information Technology, Nottingham, UK) (Verbeek *et al.* 1994; Quinn *et al.* 2009). After assays, birds were released at the site of capture. Twelve types of behavioural observation were used to calculate a principal component analysis, including number of flights, flight duration, number of hops, substrates used and area explored (Quinn *et al.* 2009). PC1 described 45% of variation, and the square-root of PC1 was used in a general linear model with individual, time of year and observation number as fixed effects, producing a single exploration score for each individual. In total, personality scores were collected for 221 individuals, representing 24% of all birds observed in at least 5 of 13 field-observation sampling periods, and 32% of all post-breeding adults.

Statistical analysis

Social associations between individuals were calculated using a Gaussian mixture model that inferred group membership by detecting clusters of visits in spatio-temporal data streams (Farine *et al.* 2012; Psorakis *et al.* 2012). This recently developed method allowed us to detect 'waves' of feeding birds, without imposing arbitrary assumptions about temporal boundaries of groups. A gambit of the group approach (Whitehead & Dufault 1999; Franks *et al.* 2010) was then used to calculate association strengths using the simple ratio index, in which associations (or edges) are scaled between 0 (never observed in the same group) to 1 (always observed in the same group) (Cairns & Schwager 1987). Finally, we tested whether the observed patterns of sociality could have arisen by chance, given spatial proximities. Permutation tests were used on the group matrix, controlling for number of observations and group size (Bejder *et al.* 1998), restricting swaps within site and within days (Whitehead 1999, 2008). We then tested if the observed pattern of associations were non-random by calculating the number of randomised networks with a higher proportion of associations and mean association strength (Whitehead 2008).

Social phenotype was measured using three commonly employed individual network measures; degree centrality, betweenness centrality and average association strength. These, respectively, measure (1) the number of other individuals with which an individual has been observed associating with, (2) the number of shortest path vertices to all other individuals that pass through the focal individual, important for the transmission of information and disease and (3) the average of an individual's edge weights, representing the average proportion of foraging time spent with each of its associates and calculated by dividing an individual's association strength by its degree (Croft *et al.* 2008). All network analyses were conducted in R Core Team (2012), using the *sna* and *igraph* packages (Csardi & Nepusz 2006; Butts 2008).

Linear models were used to compare degree centrality, betweenness centrality and average association strength to personality, while adding as fixed effects the sampling periods observed, age and spatial movements between data-loggers. To avoid biasing results, all individuals that were observed in fewer than 5 of 13 sampling periods were excluded from analysis. Network communities were identified using weighted eigenvector community detection (Newman 2006). Centrality measures were then recalculated for all individuals with network metrics derived independently from eight community-level networks, and linear mixed models rerun with community as a random variable. Rerunning the analysis within network communities in this way allowed the more stable local differences in social behaviour to be isolated from the possibly confounding effects of rare large-scale events, such as large spatial movements.

The temporal stability of relationships over time were measured using lagged association rates, calculated as the probability of being observed associating τ days after each previous association for each dyad [methods described in Whitehead (2008)]. We plotted the lagged association rates as surfaces using R , and the surface calculated for the top third of personality scores (FE) with all other individuals was compared with the surface calculated for the bottom third of personality scores (SE) with all other individuals. Areas of the surfaces significantly different from each other were calculated using permutation tests developed for three-dimensional surfaces. Given that each point on the surface is estimated from a large number of dyads, this test permuted the dyadic values between the two groups of data that were used to generate the same (matching) points on each of the two surfaces with respect to time lag and relative distance away from either edge of the surface (Pantazis *et al.* 2004).

Finally, we gained an understanding of the relationship between personality and social structure by calculating network assortativity, which is a measure of the mixing patterns exhibited by individuals. Network assortment was calculated independently for males and females using Newman's assortative mixing by scalar properties (Newman 2003) in the *igraph* package (Csardi & Nepusz 2006), with personality scores used as a continuous measure. Observed assortment values were compared with the posterior frequency distribution calculated from 1000 node randomisations on the observed association matrix restricted by sex. We then examined the personality composition of flocks using groups inferred from the spatio-temporal data stream. The sexes were analysed separately, and groups including less than three individuals of known personality score were excluded, as an accurate group mean cannot be derived in these cases. The distribution and kurtosis score of mean group personality phenotypes were compared to 1000 randomisations on the group matrix.

RESULTS

Social associations

Between December 2 2011 and February 27 2012 over 3.3 million visits were recorded from 1017 individual PIT-tagged great tits observed in 26 days of data collection. Over 80% of individuals were recorded in both the first and final sampling periods, indicating that winter survival was relatively high, and population turn-over was low. Median winter range encompassed three feeding stations with eight moves between feeders (S1). It has been suggested in previous studies that personality may influence winter range size (van Overveld & Matthysen 2010); however, we observed no evidence for such an effect in our study (LM: $F_{1,203} = 0.82$, $P = 0.37$). There was also no relationship between personality score and number of movements between feeding stations (LM: $F_{1,203} = 0.1$, $P = 0.83$) or number of visits (LM: $F_{1,203} = 0.4$, $P = 0.53$).

A social network was constructed for the whole winter period taking a 'gambit of the group' approach (Franks *et al.* 2010), inferring group membership from visitation patterns (Farine *et al.* 2012; Psorakis *et al.* 2012). The temporal bounds of groups ranged from 1 s (one visit by one individual) to 559 s; median group length 236 s. Permutation tests demonstrated that the network differed significantly from random, even at the most local scale ($P < 0.001$) (Bejder *et al.* 1998; Whitehead 1999, 2008). The network was also fully connected, indicating a contiguous population. There was a clear difference in the behaviour of adults that had already bred at least once previously ('post-breeders'; $N = 285$ observed in at 5 of 13 sampling periods), and birds that were 'pre-breeding' (largely juveniles; $N = 583$ observed in at least 5 of 13 sampling periods). Pre-breeding individuals made much more extensive spatial movements: (GLM: $\xi_{868} = -3.2$, $P = 0.001$); median post-breeding total distance travelled between feeding stations = 1.36 km, median pre-breeding distance travelled between feeding stations = 4.18 km. There was also a difference in social behaviour, with the social associations of pre-breeding individuals only significantly related to movement (greater movement with higher degree centrality; LM: $F_{1,112} = 67.2$, $P < 0.001$). This was unsurprising, as the social network was recorded over the period in which these individuals had not fully established subsequent territories or pair-bonds. Therefore, for the analysis of network centrality and temporal association patterns only post-breeders were considered.

Personality and network centrality measures

Personality score in post-breeders showed a positive relationship with degree centrality; individuals with higher exploration behaviour scores (FE) had a larger number of social associates than individuals with lower exploration behaviour scores ($N = 90$), (LM: $F_{1,86} = 6.1$, $P = 0.01$, Fig. 1a). This remained significant when controlling for the number of spatial movements between data-loggers over the winter (LM: $F_{1,85} = 6.3$, $P = 0.01$), see Table S3. In contrast, exploration behaviour was negatively correlated with average association strength, with more FE birds having on average weaker social connections than more SE birds (LM: $F_{1,86} = 4.3$, $P = 0.04$, Fig. 1b), and when controlling for spatial movements (LM: $F_{1,85} = 4.0$, $P = 0.05$). Finally, more FE individuals were significantly more likely to move between foraging flocks, with a higher betweenness centrality (LM: $F_{1,86} = 5.2$, $P = 0.02$). Three outliers exerted undue leverage on the model fit; however, when these were removed the relationship was similar (LM:

$F_{1,83} = 5.7$, $P = 0.02$, Fig. 1c), and remained significant when controlling for spatial movements (LM: $F_{1,82} = 5.0$, $P = 0.03$) (Table S3).

To test for whether this connection between social interaction patterns and personality occurred within 'social cliques' as well as at the population level, we identified eleven cohesive network communities within the population (Newman 2006), Fig. S4. Eight of these communities contained focal individuals. Network metrics derived at the community-level revealed the same overall relationships between personality and centrality measures (Table S4). Therefore, at both the population level and within social cliques, proactive (FE) birds were more likely to connect with other individuals, but did so with a weaker association strength.

Temporal dynamics

We quantified the temporal stability of social relationships by estimating the lagged association rates of all post-breeding individuals with all other post-breeding individuals over the 3-month sampling period (Whitehead 2008). More SE birds had a significantly higher

likelihood of re-associating with other individuals, and their probability of re-association was highest with other SE birds, for which associations were maintained at a relatively high rate over time ($N = 90$; Fig. 2a and b). In contrast, more FE birds were much less likely to re-associate, and had lower lagged association rates over the 3 month winter period (Fig. 2c and d). Association rates were lowest in FE-FE interactions (Fig. 2c). The effect was synergistic, with the most ephemeral relationships being between pairs of more proactive (FE) birds (Fig. 2c), and the most stable between pairs of more reactive (SE) birds (Fig. 2a; Table S5).

Social structure

We tested whether individuals of similar personality were more likely to be observed together, influencing the composition of groups and emergent social structure. Post-breeders and pre-breeders were analysed together, as groups were comprised of a mix of ages that did not show strong differences in mixing patterns. Preliminary analysis did, however, reveal contrasting results for mixing patterns among males and females, and the sexes were analysed separately. Social structure was then inves-

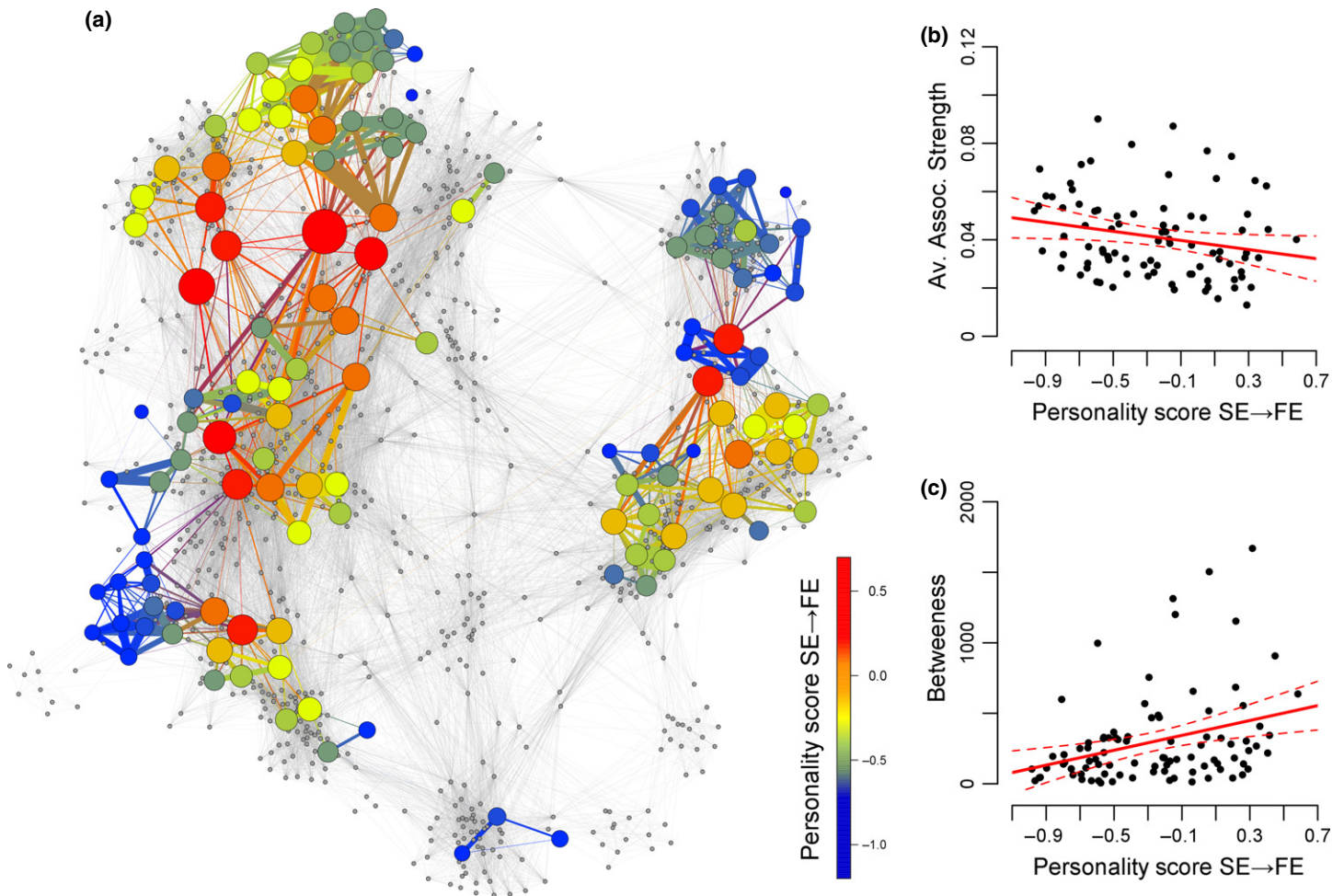


Figure 1 The relationship between personality and social network position in wild great tits. (a) Social network where colour represents personality score ranging from most reactive (SE) phenotypes in blue to most proactive (FE) phenotypes in red; the range of the colour distribution has been slightly exaggerated at the ends of the distribution to emphasise more extreme phenotypes. Grey nodes are individuals of unknown phenotype. Size of coloured nodes represents degree. More proactive (FE) phenotypes tend to have a larger degree centrality. (b) Average association strength decreases with personality score. (c) Positive relationship between personality and betweenness centrality (figure is shown with 3 outliers removed; see text for analysis). Analysis was conducted on all post-breeders present in at least 5 of 13 sampling periods ($N = 90$) and dashed lines represent 95% confidence intervals.

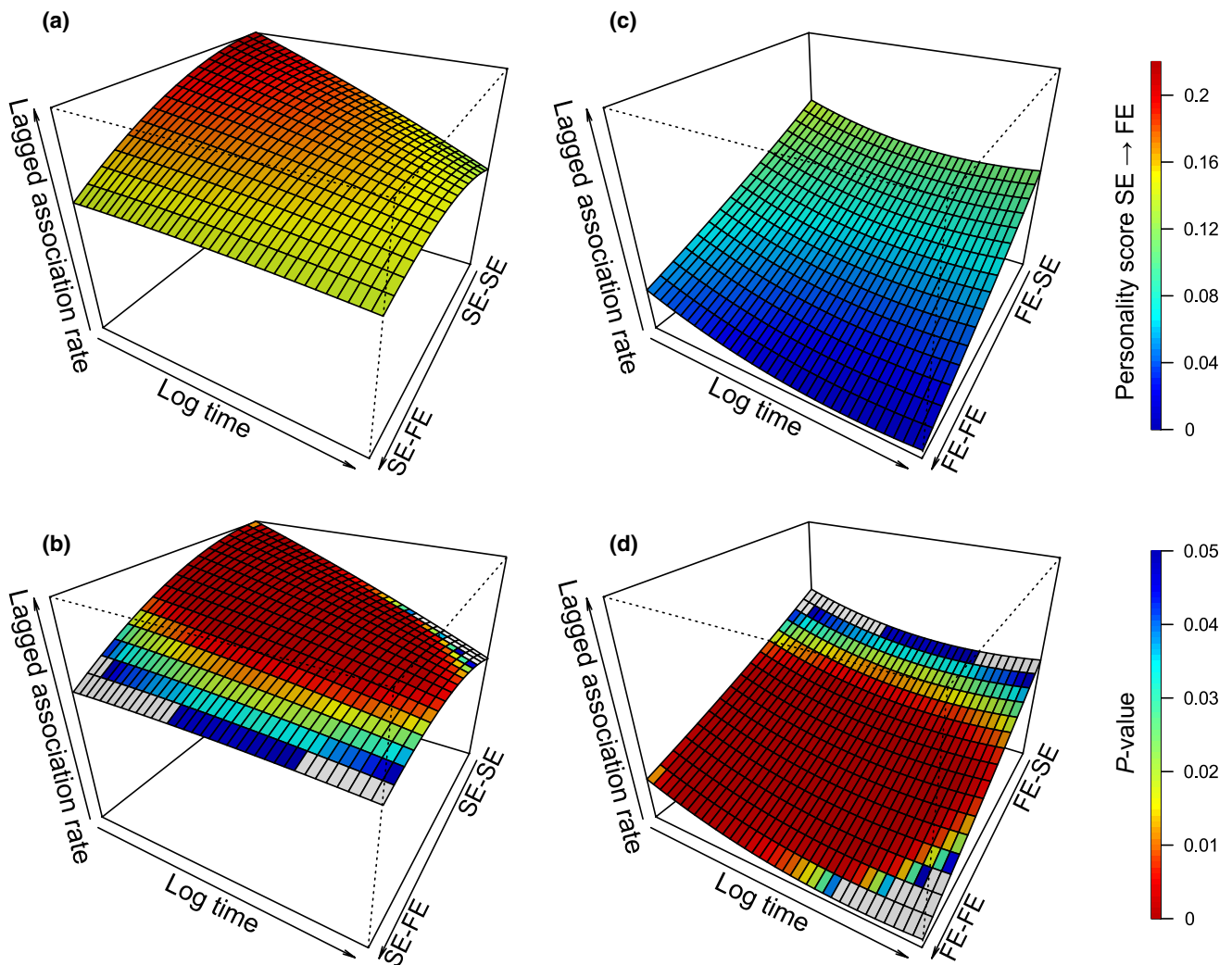


Figure 2 Lagged association rates between individuals of differing personality. (a) Directed re-association rates between individuals with bottom third of personality scores (SE) and all other individuals from most SE at back of plot to FE at front. Lagged association rates vary from blue (no probability of re-association between days) to red (re-association rate of 0.2 after τ days). Legend is shown at upper right. (b) Parts of plot A that significantly differ from surface in plot C; estimated from the proportion of permuted data points where the difference between two surfaces was larger than observed. Colours show increasing significance from $P = 0.05$ (blue) to $P < 0.001$ (red); grey cells are non-significant. Legend is shown at lower right. (c) Directed re-association rates between individuals with top third of personality scores (FE) with all other individuals, shown with SE at back to FE at front. (d) Significance surfaces for plot C.

tigated using two complementary approaches. First, Newman's assortment measure was computed on the social network (Newman 2003). Males tended to associate with other males of similar personality type ($N = 97$; $r = 0.07$; $P = 0.03$ from 1000 node-randomisations; Fig. 3a). Females showed no such positive assortment, with any trend in the opposite direction to that observed in males ($N = 99$; $r = -0.05$, $P = 0.18$, Fig. 3b). Second, we identified all of the discrete groups observed at the feeding stations over winter using the spatio-temporal data streams ($N = 73\,455$, and generated a distribution of the mean personality scores from these groups. To test whether personality phenotypes were non-randomly distributed between groups, we calculated the kurtosis of the distribution of mean phenotype of each group. If groups were assorted by phenotype, then the distribution of mean group scores should be wider, resulting in a lower kurtosis score. We then compared this score with the distribution of the kurtosis scores from 1000 randomisations of the group matrix.

The observed distribution of personality types in groups recorded at the data-loggers was not different from expected under random

mixing in females (no. of females = 110; Fig. 3c), with a kurtosis score inside the distribution of kurtosis scores obtained from randomised data (Fig. 3c inset). Males, however, showed a significantly different kurtosis (no. of males = 111; Fig. 3d inset), with an observed distribution of mean group phenotypes that fell outside of the 95% CI of randomised data for a large part of its range (Fig. 3d). Therefore, males within individual flocks tend to be skewed towards particular personality types, and this supports evidence from the network assortment measures that males are grouping with individuals of similar personality. Our two alternative analyses demonstrate this non-random mixing occurs both in the composition of short-term flocks and over the entire winter network.

DISCUSSION

Using standard behavioural assays and automated monitoring of foraging flocks, we show that individual-level differences in behaviour predict the frequency, stability and distribution of social associ-

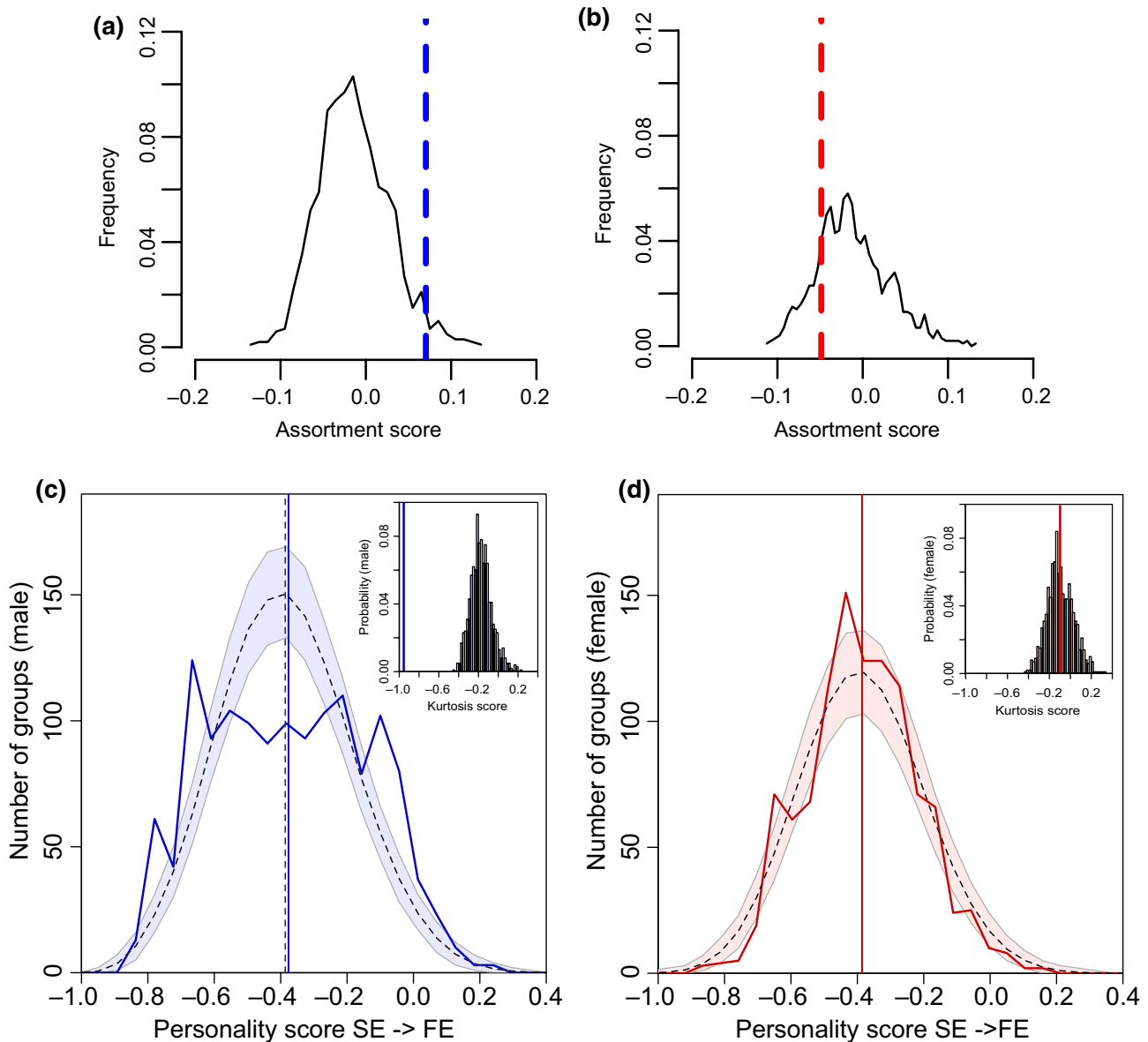


Figure 3 Within group mixing patterns in relation to personality and sex. (a) Assortment in males is significantly higher than expected from data node-randomised 1000 times. Assortment scores of node-randomised data are shown by the distribution, assortment score of observed data is given by vertical blue dashed line (b) Assortment score for females does not differ from that expected under random-mixing. (c) In males, fewer groups with intermediate personality types were found than expected under random mixing. Observed data are shown as solid line, randomised data are shown dashed with a 95% CI shaded area. Solid vertical line is observed mean group-level personality score; dashed vertical line is mean group-level personality score for randomised data. Insert shows posterior distribution of kurtosis scores for randomised data in comparison to observed kurtosis score (blue vertical line). (d) Distribution of group-level personality in females does not significantly differ from that expected under random mixing.

ations in a wild songbird. In particular, we demonstrate that individual-level variation in exploration behaviour (a proxy for the reactive-proactive axis) is associated with both social phenotype and patterns of group organisation in adult great tits. Individuals with slow-explorer personalities tend to have strong associations with a few other individuals, maintaining these associations over a relatively long period of time. In contrast, animals with fast-explorer personalities have more social associations, but these tend to be weak and persist over a relatively short time period. The higher betweenness centrality observed in fast-explorers further suggests that they are more likely to 'hop' between foraging flocks, foraging with several groups. They are thus likely to be more important in ecological

processes such as the spread of information or disease (Lusseau & Newman 2004; Aplin *et al.* 2012). Interestingly, whether these processes rely on the strength or number of connections may change the relative importance of different personality types in diffusion dynamics; this largely remains to be investigated.

Our study therefore employs multiple lines of evidence to demonstrate that wild great tits with different exploratory personalities also interact socially in quite different ways. We are the first to quantify this relationship in a fission-fusion population over a large spatial scale and extended time period. Results from previous studies have begun to suggest an emergent pattern; bold individuals showing higher activity and larger spatial movements than shy individuals,

leading to a higher degree but lower association strength (Sih & Watters 2005; Pike *et al.* 2008; Tanner & Jackson 2012). Our results are consistent with these findings, but expand the scope and impact of an area of study which, outside of research on humans, has had very limited investigation to date. We make a further important contribution in providing evidence that differences in sociality are not solely driven by individual differences in movement or space use (Krause *et al.* 2010), but may also represent active preferences for within-site movements between flocks. In contrast to research in animal groups, the role of personality in human social networks has been well studied, with a strong link identified between extroversion and network centrality (Schaefer *et al.* 2008). These findings are thus also broadly consistent with sociological research.

As a proxy for the reactive-proactive axis, exploration behaviour is thought to be connected to risk-taking, with individuals consistently tending to engage in behaviour that ranges from risk averse (but with low rewards) to potentially high payoff actions with an associated higher risk (Dingemanse & Wolf 2010; Quinn *et al.* 2012). Variation in social behaviour may reflect an extension of this risk-taking trade-off. Smaller social networks may lower risk by reducing exposure to pathogens (Cote & Poulin 1995) and potentially improving efficiency of group defences against predation, including co-ordinated group movement and alarm calling (Micheletta *et al.* 2012). Stable social networks may also facilitate the evolution of cooperative behaviour through repeated interactions (Micheletta *et al.* 2012; van Doorn & Taborsky 2012). Given this, there must be potentially high payoffs associated with the alternative social behaviour observed in more proactive (FE) individuals. In a previous study, we found that a higher network centrality and betweenness in great tits improved access to information, which was advantageous for the acquisition of food resources (Aplin *et al.* 2012). In addition, FE individuals suffer disproportionately in repeated contests (Carere *et al.* 2001; Dingemanse & de Goede 2004), and moving between groups may provide opportunities for FE birds to improve their relative dominance.

We observed an emergent social structure arising from interactions between personality and group formation, with males preferentially associating with others of similar personality. Such assortment by personality has only before been observed in Trinidadian guppies (Croft *et al.* 2009). In this case, it was hypothesised to have emerged from passive mechanisms related to similarities in individual behaviour, or alternatively from a 'behavioural-oddity' effect, in which individuals group with others of similar phenotype to reduce their conspicuousness to predators. Neither effect seems likely in this system, because assortment was confined to males. Rather we hypothesise that, as most aggressive interactions occur between males (Dingemanse & de Goede 2004), and more proactive (FE) individuals tend to be more aggressive (Carere *et al.* 2005; Groothuis & Carere 2005), reactive (SE) males may be actively modifying their social environment by avoiding FE individuals. If so, this has important implications for the operation of frequency-dependent selection on personality (Dall *et al.* 2004), and for the evolution of personalities through social niche specialisation (Bergmuller & Taborsky 2010).

Evolutionary models for the evolution and maintenance of consistent personality differences have used game theory to propose that negative frequency-dependent selection on personality traits could maintain variation, with payoffs dependent on the frequency of such traits in a population (Dall *et al.* 2004). However, with non-random mixing, as in our population, the strength and direction of selection on personality is also likely to be partly dependent on social network

structure (Oh & Badyaev 2010). Theoretical work has suggested that optimal foraging groups may comprise a mix of personality types, e.g. with proactive players acting as 'leaders' and reactive individuals as 'followers' (Johnstone & Manica 2011). However, we found no evidence for heterophily in our social network, but rather positive network assortment (i.e. homophily) among males, similar to that often observed in human personality research (McPherson *et al.* 2001). This may instead allow individuals of certain personality types to modify selective pressures; for example grouping together in temporally stable associations might allow SE birds to engage in risk-taking behaviour that would otherwise be avoided (Webster & Ward 2011). However, it is difficult to conclusively assign causation, with possible feedback between the evolution and ontology of social behaviour and personality. Further research should aim to further understand the mechanisms driving emergent population structure, and attempt to establish the directionality of the relationship between social behaviour and personality traits such as exploration behaviour (Wilson *et al.* 2013).

We have demonstrated a relationship between individual behaviour, flock-level sociality and population structure, using automated technologies to study personality in social networks of a wild songbird. This relationship is likely to interact with ecological processes, with important implications for transmission of information and disease, and for individual variation in the acquisition of resources (Aplin *et al.* 2012). However, even if the relationship between personality and social organisation proves to be broadly consistent across context and taxa, it is likely to be informed by ecological factors such as food availability and predation risk. It may also vary under different population densities and levels of social conflict (Bergmuller & Taborsky 2010). A future challenge will be to advance the understanding of the ecology and evolution of personality by quantifying the role of personality in social networks across fluctuating spatial and temporal gradients.

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AUTHORSHIP

LMA, JMF and BCS designed research; LMA, EFC and JMF collected data; LMA and DRF analysed data; LMA, DRF, AC and BCS wrote the manuscript.

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