Emergent social structure and collective behaviour from individual decision-making in wild birds

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Preface: The Small Fat Bird

In the 1980s, the world was introduced to the small fat bird. Like most birds, this one slept at night and ate during the day. Yet each time it appeared, typically during the winter, this bird faced new challenges. In some cases, patches varied in whether they contained food or not, or at other times they varied in how difficult each food item was to handle. A further challenge that this bird faced was the threat of a skilled predator, forcing it to remain leaner and more agile, but at an increased cost of starving during the long winter nights. Luckily, this bird had an ally: evolution had provided it with the innate ability to make accurate decisions when faced with two unequal options. This bird had evolved an optimal strategy.

Although this small fat bird represented millions of common garden birds faced with surviving harsh winter conditions, it was and remains a modelling abstraction of theoretical biology. Its living counterparts, those that survive and breed year-in year-out, face a much wider range of challenges: where to find food, how to out-compete others for limited resources, or even how to form alliances in order to ensure they can keep warm enough to survive cold nights. Further, their challenges rarely occur in isolation, but then neither are they alone in having to do so. The presence of others can provide a range of benefits, such as providing information about the environment or increasing their chance of escaping attacking predators. Amazingly, groups of birds can solve complex problems by combining their individual abilities. However, in order to achieve all of this, these birds require robust rules, ones that will succeed many more times than they will fail.

Understanding the decisions that the small fat bird made has helped to uncover how animals survive in their physical environment. However, the rules that govern how individuals interact, and the feedback of environmental conditions, still remain largely unknown. In the pages that follow, I explore the social structure of wintering groups of birds and the rules maintaining these. In doing so, I provide a small window for understanding the role that social behaviour plays in evolution, as seen through the decisions of small fat birds.

Abstract

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DPhil thesis by Damien R. Farine, Wolfson College, submitted Michaelmas 2013

Social behaviour is shaped by complex relationships between evolutionary and ecological processes interacting at different scales. Benefits gained from social associations can range from predator dilution to collective sensing, but little is known about how these can be influenced by social structure and phenotypic composition. In this thesis, I investigated how individual decision-making affects phenotypic social structure, and how this mediates social behaviour through emergent properties of collective group behaviour.

First, using mixed-species flocks as a model system, I showed individual tits (*Paridae*, chapter 2) and thornbills (*Acanthizae*, chapter 3) varied significantly in their social positions. Within-species variation in network position was as large as between-species variation, suggesting that prescribing functional roles at the species level may not sufficiently account for potential differences in fitness operating at the individual level. Rather, this suggested that structure may be driven by phenotypic traits, underpinning network structure (chapter 4).

Next, I used an extensive data set of foraging records to explore factors determining the composition, of flocks of great tits (*Parus major*, chapter 5). For example, assortment by dispersal phenotype (immigration status) was the result of spatial disaggregation, and I showed that this may facilitate social selection for breeding territories (chapter 6).

Finally, I investigated how decision-making shaped mixed-species social structure. I found that tits used a common strategy for managing pressures of predation and starvation by shifting from exploration to exploitation at different times of the day (chapter 7). I then found that a very simple interaction rule successfully replicated mixed-species group structure (chapter 8). Strikingly, the same rule was applied to both conspecifics and heterospecifics, potentially playing an important role in the maintenance of flock structure. Through experimental manipulation of ecological conditions, I found that heightened perceived predation resulted in stronger social attraction overall, whereas increased competition led to a reduction in attraction to conspecifics (chapter 9). Simulations suggested this could be one potential mechanism underpinning fission-fusion dynamics in these species.

Together, the results in this thesis form a framework linking social behaviour to individual fitness where natural selection is shaped by the social environment. This approach may prove useful for testing whether following common social rules reduces variance in benefits accrued by individuals, and how within-species variation in social behaviour can impact emergent properties of groups.

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Author Contributions

Main contributors

Damien R. Farine had independent input into all aspects of this thesis, collected two years of 'quad' data, one year of experimental 'quad' data, and contributed to all EGI-collected data (spring breeding season ringing and winter social network). Also, analysed data, wrote first drafts, and incorporated co-author comments to produce final manuscripts.

Ben C. Sheldon (supervisor and co-author of chapters 2, 5, 6, 8, 9) secured funding, provided guidance on experimental design and analysis, and gave comments on all chapters.

Colin J. Garroway (co-supervisor and co-author of chapters 2, 5, 8) had intellectual input and provided detailed comments on all co-authored chapter drafts. Provided guidance or comments on most other chapters.

Additional contributors

Peter J. Milburn (co-author of chapter 3) assisted with data collection and provided minor comments on drafts of the chapter.

Joshua A. Firth (co-author of chapter 5) provided input on conceptual design, performed parts of the analysis, and provided detailed comments on chapter drafts.

Social Network Group (co-authors of chapter 5) performed the field work, contributed to early design and discussion, and provided comments on chapter drafts.

Stephen D. Lang (co-author of chapter 7) performed the field work and provided detailed comments on chapter drafts.

Lucy M. Aplin (co-author of chapter 8) contributed to field work and provided detailed comments on chapter drafts.

Richard P. Mann (co-author of chapter 8) contributed to analytical design and provided detailed comments on chapter drafts.

Contents

CHAPTER 1

Introduction

Introduction

Living in groups: from selfish herds to cooperative societies

Group-living is widespread across the animal kingdom, and encompasses a spectrum of complexity in individual social strategies. At it simplest, individuals may spatially aggregate with others in order to dilute the risk of being attacked. In an attack by a predator each individual in an N-sized group will have a 1/N chance of being killed (Rand, 1954; Alexander, 1974). Within these groups, individuals may further reduce their relative risk by competing for positions closer to the centre of the group, or away from the higher-risk edges, behaving as 'selfish herd' (Hamilton, 1971). Though outwardly simple, this process may result in a rich and complex set of interactions arising from competitive and benefit asymmetries. In this thesis I focus on this, at first sight, deceptively simple issue.

Animals can further benefit from group-living via a number of additional non-exclusive mechanisms. For example, in addition to reducing their predation risk through dilution, individuals can also share vigilance costs with others in their group (the many eyes hypothesis, Powell, 1974). Group vigilance can lead to earlier detection of a predator at the point of the attack (Bednekoff and Lima, 1998), and perhaps more rapid spread of information regarding its presence after discovery (Magrath et al., 2007). Secondly, predators may be less able to make successful kills when attacking larger groups, as it becomes more difficult to efficiently target prey (confusion effect, Landeau and Terborgh, 1986). Finally, groups can benefit from increased foraging success as a consequence of several processes: (i) a reduction in vigilance times per individual in large groups (Bednekoff and Lima, 1998), (ii) more efficient acquisition of food either through beating for insects (Greenberg, 2000) or cooperative hunting (Vail et al., 2013), and (iii) a greater chance of discovering novel food sources either through social links (Aplin et al., 2012) or problem solving (Morand-Ferron and Quinn, 2011). By being close to others, individuals can benefit by gaining access to the information that is produced either intentionally (such as alarm calling, Magrath et al., 2007) or unintentionally (through public information, Danchin et al., 2004; Dall et al., 2005; Valone, 2007).

Mixed-species groups: a cost-mitigating social strategy

Despite the putative benefits of living in groups, processes that bring individuals into greater spatial proximity generally lead to an increase in competition for limited resources. This parallels recent theoretical developments in studies of the evolution of altruism, where structured populations that lead to increased interactions between relatives also increase competition at the same rate (Doncaster et al., 2013). This competition can take two forms: exploitation competition, where individuals deplete a resource and indirectly affect its availability to others; and interference competition, where individuals actively prevent others from accessing a resource (Krause and Ruxton, 2002; Dhondt, 2012). Interference competition, in particular, can negatively impact group members by excluding them completely. Costs incurred should therefore limit the joining rate proportionally with group size (Pulliam and Caraco, 1984). Therefore, in many species, while animals group with related individuals (such as in white-winged choughs *Corcorax melanorhamphos*, Heinsohn and Cockburn, 1994) providing indirect fitness benefits (Hamilton, 1964), this may be not be adaptive if interacting relatives are also competing. One alternative solution to the trade-off between the costs and benefits of grouping is to associate with particular individuals with whom competition is lower, but from which some, or all, of the benefits of grouping might be obtained. In this way, competition from conspecifics is thought to be an important factor leading to the evolution of mixed-species groups (reviewed in Buskirk, 1976; Dhondt, 2012).

By associating with heterospecifics, individuals can continue to gain many grouping benefits (such as dilution of risk or shared vigilance) but with a reduction in the costs that would be incurred from similarly-size groups of conspecifics (Sridhar et al., 2009; Harrison and Whitehouse, 2011). However, in order to gain benefits from these heterospecific groups, there must be some degree of niche overlap between the associating species. For example, in order to gain benefits from predator risk dilution, heterospecifics must share at least one common predator. Furthermore, if the two species do not share any foraging niche overlap, then they will not benefit from shared public information (Goodale et al., 2010). Thus, although the costs of associations increase with higher niche overlap between species, these may be smaller than the loss of benefits incurred if there is no niche overlap. Recent studies support this theory, suggesting that species are not overdispersed as would be expected if competition was alone in driving associations (Powell, 1985; Latta and Wunderle, 1996; Sridhar et al., 2012).

The most widespread and best studied example of multi-species group-living is mixed-species flocking in birds (Greenberg, 2000; Harrison and Whitehouse, 2011). Mixed-species flocks (MSFs) can range from just two species to several dozen (Greenberg, 2000) and are found in almost every habitat on earth. The mechanisms governing the formation of these flocks have attracted extensive ecological investigation, from hypotheses of colour-matching species (Diamond, 1987; Beauchamp and Goodale, 2011) to Diamond's assembly rules (Diamond, 1975). An extensive history of research into interspecific coexistence has demonstrated niche shifts caused by interspecific competition (Lack, 1971; Ekman, 1989; Dhondt, 2012). However, more recent observational evidence has also suggested that niche convergence occurs in mixed-species flocks (Latta and Wunderle, 1996; Hino, 1998, 2000; Thiollay, 2003; Zou et al., 2011; Sridhar et al., 2012), where species forage in closer niche space when associated than when not together. This would suggest that the benefits gained from these associations outweigh the increased costs expected through increased niche-overlap. Despite this, research into MSFs has remained primarily focused on disentangling the hypotheses of predator avoidance and foraging benefits (Sridhar et al., 2009).

Studies testing the competing hypotheses of predation and foraging benefits as drivers of mixed-species flocking have provided the most compelling evidence that environmental conditions affect mixed-species flocking. A number of experimental of studies have manipulated food availability using supplementary feeders and found that flocking propensity decreased when food was abundant (Berner and Grubb, 1985; Grubb, 1987; Szekely et al., 1989). Further, Grubb (1987) found that birds exhibited greater variation in flocking propensity in changing weather conditions when supplementary food was not available, suggesting that mixed-species flocking was a response to enhanced energy stress and the need to forage more efficiently. Manipulation of predation pressure in studies of MSFs are rarer, but the study by Szekely et al. (1989) supported the prediction that flocking propensity increases proportionally with apparent predation pressure. These results were supported in several comparative studies that found that birds in areas with lower predation pressure (islands) flock less (Beauchamp, 2004) and that foraging guilds that are more prone to predation have a higher propensity to flock (Thiollay and Jullien, 1998).

Social conditions can also affect the behavioural decisions made by individuals. For example, in his classic studies of ecological communities in New Guinea, Diamond (1975) hypothesised that the presence or absence of mixed-species flocking behaviour on different islands was a result of the composition of species present on any given island. Later studies found similar results by exploring variation in mixed-species flock composition and stability across fragmented landscapes (Maldonado-Coelho and Marini, 2000, 2004). One series of experiments removed all individuals of a focal mixed-species flocking species to observe the effects on other species. In the first experiment, Dolby and Grubb (1998) found that the remaining individuals suffered reduced body condition after the removal of heterospecific flock members. Removal of the same species in the second experiment (Dolby and Grubb, 2000) resulted in a reduction in visits made by the remaining species to high-risk foraging locations. Whilst the authors used this evidence to support the anti-predator hypothesis of mixed-species flocking, the findings also show the important effect of the social environment on individual behaviour.

The body of literature on mixed-species flocking provides compelling evidence that both environmental and social conditions can affect the structure of avian communities. It suggests that this behaviour may be plastic: individuals can alter their flocking propensity according to variation in these conditions. If this is the case, then individuals may be trading-off behavioural state according to some fitness-maximising function. Thus, studying decision-making mechanisms in the context of evolutionary hypotheses for group-living could greatly advance our understanding of when and why individuals join mixed-species flocks.

Selfish social genes: group-living is an individual decision

In his 1970 monograph, Morse (1970) put forward what remains to date the most accepted functional definition (Farley et al., 2008) of social groups in birds:

> Any group of two or more birds, whose formation depends upon positive responses by individuals to members of their own or other species is considered a flock.

However, this definition implies a process of decision-making that is incompatible with most of the analytical approaches used in studies of multi-species groups to date. It suggests that the mechanism by which groups are maintained, a positive response, is inherently individual, hence distinguishing groups from mere passive aggregations (Morse, 1970). Thus, whilst existing research has provided evidence that mixed-species flocking is influenced by various trade-offs (reviewed in Harrison and Whitehouse, 2011), we have little knowledge of the mechanisms that lead to the formation and maintenance of these groups (Farley et al., 2008). Moving to a more bottom-up approach that is consistent with the definition by Morse (1970) opens a wide range of questions that have yet to be considered in heterospecific groups. For example, do dominants make different social decisions than subdominants? How do individuals assess the cost-benefit trade-offs when making the choice of whether to join a group or not? Such an approach reflects recent research into the behavioural ecology of monospecific group-living (Mcfarland, 1977; Dukas, 1998; Couzin and Krause, 2003; Ydenberg, 2010).

Perhaps the best studied examples of monospecific groups, where the relationship between individual social decision-making and social structure is most well known, are in primates (Dunbar, 1988). Widespread studies across many species have enabled powerful comparative work, such as demonstrating how social structure is predicted by the cost and benefit trade-off in group living (Janson and Goldsmith, 1995), and how these can drive population dynamics (Lehmann et al., 2007). Importantly, longitudinal research has provided detailed knowledge of how social relationships (in males, females, and between sexes) influence social structure, and the link between individual decision-making strategies, social position, and fitness (reviewed in Dunbar, 1982; Sterck et al., 1997; Kappeler and van Schaik, 2002). Finally, recent interest on movement dynamics in primates (King and Sueur, 2011) has highlighted the role of individual variation in social position (King et al., 2008), social structure (King and Cowlishaw, 2009; Jacobs, 2010; Sueur et al., 2011b), and social networks (Jacobs et al., 2011; King et al., 2011; Sueur et al., 2011a) in determining collective decision-making.

Social networks: individual variation in social behaviour

Hinde (1976) first proposed a framework whereby societies emerge from the social behaviour of individuals. These societies are based on discrete interactions between individuals. He proposed that a bottom-up approach that focuses on these interactions will better quantify the relationships and subsequent social structure of all interacting individuals. One method of quantifying these interactions across all sampled individuals is social network analysis (Croft et al., 2008; Whitehead, 2008).

In animal social networks, interactions between individuals (nodes) are represented by edges that characterise the strengths, or probability, of interactions occurring. The combined patterns of connections between individuals then provide a description of the overall population structure as well as individual differences in connectivity or position within this structure. In the case of the former, structure is considered to be crucial in mediating population processes (May, 2006). For example, the classic paper by Granovetter (1973) describes the important role that larger-scale aspects of social structure plays in an individual's social experience: edges that link otherwise disconnected components of population structure can greatly reduce the overall number of steps required for information or disease to propagate across all individuals (Newman, 2003). These 'small-world' networks appear to be common across biological systems (Watts and Strogatz, 1998).

As well as being influenced by broader population structure, individuals may also be influenced by their position in their network (Sih et al., 2009). Several studies have demonstrated a possible link between social position and individual fitness. In particular, male long-tailed mannakins (*Chiroxiphia linearis*) that were better connected as juveniles had greater social status as adults, leading to a higher probability that they gained alpha status in their dancing troops (McDonald, 2007). A similar process was found to occur in house finches (*Carpodacus mexicanus*), albeit in a shorter time frame. In this study, juvenile males that were better connected were able to find a social niche whereby they had a higher relative attractiveness with respect to their competitors (Oh and Badyaev, 2010). Central birds in mixed-species flocks of tits were also found to have a higher probability of discovering food resources (Aplin et al., 2012), and the position, strength and maintenance of social links was predicted by personality in great tits (*Parus major*, Aplin et al., 2013).

Social network analysis has been useful for understanding population processes such as disease dynamics (May, 2006), as well as defining the primary building blocks of population structure in a variety of animals, including dolphins (Lusseau, 2003), rodents (Manno, 2008), bats (Fortuna et al., 2009), and fishes (Croft et al., 2004). Yet, despite the examples above, linking social phenotypes, or variation in social decision-making, to individual fitness has remained largely elusive. This is potentially caused by a mismatch in the scale at which typical social network measures are influenced (these usually describe global structure) and the scale at which selection operates (phenotypic or genetic traits). One approach that may resolve this is to use social network analysis to describe local interactions at a phenotypic level.

Interacting phenotypes: the social currency of selection

Historically, evolution by natural selection was considered to be a long-term process where environmental conditions influenced the distribution of traits in populations (Darwin, 1859). Yet recent studies have clearly demonstrated that the selection can operate both very rapidly and be very localised. For example, in the Galapagos finches (*Geospizinae spp.*), rainfall patterns influence food availability, which in turn rapidly changes the distribution of beak sizes and shapes in the population (Boag and Grant, 1981). In the great tit (*Parus major*), localised differences in genetic variance in body mass can arise in response to differences in environmental quality and is maintained via differential dispersal (Garant et al., 2005). However, is it possible that the relationship between individual phenotype and the environment (Lande and Arnold, 1983) could be further influenced by local social conditions (Wolf et al., 1999)? If selection is dependent on local effects (both in terms of the social environment and other aspects of the environment), then a failure to consider this properly is quite a big omission in our understanding of the selection process.

Take, for example, a medium sized individual in a species where size is proportional to dominance. This individual may be able to modulate the selective pressure it experiences by preferentially foraging in an area containing relatively smaller conspecifics. This process, in which the interaction between phenotypes determines the relationship between phenotypes and fitness, is called social selection (Wolf et al., 1999). A good example of this is in the forked fungus beetle (*Bolitotherus cornutus*), in which natural selection operated strongly on body size, but individuals with smaller social partners had correspondingly greater copulation success than expected given their body size (Formica et al., 2011). This process may represent a largely under-appreciated component of selection, particularly in species where individuals can make active decisions about which social groups to join.

The process of group joining and splitting may enable individuals to dynamically vary their group size, optimising their response to different selective pressures (Lehmann and Boesch, 2004). Such fission-fusion dynamics can provide opportunities for individuals to preferentially associate with others that have a specific phenotype (Couzin, 2006). The continuous reformation of groups may also enable individuals to influence their environment through their interactions with others (such as their competitive ability for limited resources). However, the consequences to individuals making these sorts of decisions have rarely been explored (Kerth, 2010).

Collective behaviour: group dynamics emerge from individual decisions

Animal groups often exhibit striking cohesion and coordination in their behaviour. The degree of coordination in schools of fishes or flocks of birds led early ethologists to conclude that this could only have arisen from telepathic communication (Sealous, 1931). More recently, studies have demonstrated that these seemingly complex behaviours can emerge from very simple rules applied by individuals responding to their closest conspecifics (Reynolds, 1987; Couzin and Krause, 2003). In doing so, the field of collective behaviour has clearly demonstrated how group-level behaviour arises as an emergent property of individuals responding to their own selfish needs (note that findings are not always framed in this way), akin to Hamilton's seminal theory of the selfish herd (Hamilton, 1971). For example, plague locusts shift from being solitary to forming mass coordinated migration as a result of individuals shifting their behavioural rules to high movement alignment as a consequence of increasing risk of cannibalism when population densities are high (Bazazi et al., 2008).

Studies of collective animal behaviour have largely focused on highly coherent groups, such as schools of fish (for example Herbert-Read et al., 2011; Ward et al., 2012; Berdahl et al., 2013) or swarms of insects (for example Buhl et al., 2006; Bazazi et al., 2008; Sasaki and Pratt, 2011). However, when population structure is seen as an emergent property of the decision-making by selfish individuals, it opens the possibility that more general collections of animals can be considered using this framework. In this way, the evolutionary signal of natural selection should be detectable in the decisions that the animals use in response to different sets of challenges. That is, selective pressures shape the structure of groups by influencing the behaviour and decision-making process of individuals. For example, live fish predators selected for individual virtual prey found at the edge of shoals and those that were traveling more linearly (Ioannou et al., 2012).

Recent theory suggests that group living in animals is partly driven by the information, or cues that reduce uncertainty about environmental or social conditions, generated by others (Goodale et al., 2010). This information provides individuals with the ability to make decisions in complex environments (including trading-off predation risk, starvation risk, and finding ephemeral food resources). For example, an individual vigorously shaking its head can indicate that it has successfully found food in its current patch, subsequently attracting others. The simple process of attraction, in this case via local enhancement (Poysa, 1992), may then lead to further information use that ranges from predator detection (Ward et al., 2011) to more complex problem solving, such as accessing new food sources (Morand-Ferron and Quinn, 2011; Aplin et al., 2012), or choosing the 'best' foraging locations in response to a combination of cues (Perez-Escudero and de Polavieja, 2011; Arganda et al., 2012; Perez-Escudero et al., 2013). Numerous studies have shown that complex decisions, such as finding optimal navigation pathways, can be achieved using simple quorum-based processes (Sumpter and Pratt, 2009; Sumpter, 2010). Thus, population behaviour can emerge as a consequence of individual strategies, whereby the individuals use information in order to maximise their short-term fitness at each step.

Following the modelling cycle of collective behaviour (Sumpter et al., 2012), which identifies decision rules in an attempt to replicate the patterns we observe in nature, could yield significant insight into the ecology of group-living (Krause and Ruxton, 2010). Mixed-species flocks are an excellent model system for testing evolutionary questions of group living as the value of information from different group members can be assigned *a priori* based on degrees of niche overlap (Goodale et al., 2010). Yet, to date, individual decision-making has rarely been explored in this context.

Overview of study systems

In this thesis, I use bottom-up approaches to explore the social behaviour of birds in mixed-species groups. My primary study system are temperate mixed-species flocks consisting of great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*) and European nuthatches (*Sitta europaea*), in Wytham Woods, Oxfordshire. My second study system (from Chapter 3) uses Australian mixed-species flocks, dominated by buff-rumped thornbills (*Acanthiza reguloides*), yellow-rumped thornbills (*A. chrysorrhoa*), and striated thornbills (*A. lineata*), in Mulligans Flat Nature Reserve near Canberra.

Wytham Woods is a 385 ha area of broadleaf deciduous woodland, that has been the subject of long-term monitoring of a nestbox population of great and blue tits (Charmantier et al., 2008). The majority of the individuals from these two species have been fitted with British Trust for Ornithology (BTO) uniquely coded metal leg rings. In more recent years, captured individuals have also been fitted with passive integrated transponder (PIT) tags. Birds are caught either while breeding in nestboxes, during winter mist-netting, or marked as chicks before fledging. As part of my research, monitoring was extended to include coal tits, marsh tits and nuthatches since 2010.

The spring breeding territories of blue and great tits break down during the summer, with birds forming loose fission-fusion groups of unrelated individuals throughout the autumn and winter. Coal tits, marsh tits and nuthatches are all thought to hold year-round territories, with adult pairs joined by floating juveniles (Ekman, 1979; Enoksson and Nilsson, 1983). All five species together form mixed-species fission-fusion groups, with nuthatches and great tits dominant over blue ties, then marsh tits and coal tits (Morse, 1978).

The Wytham system is based on detection of PIT-tagged birds visiting feeders fitted with radio frequency identification (RFID) antennae. As birds land on the feeders to collect food, a record of the individual's unique identity (which is later cross-referenced to its ring number) is recorded into a log file, along with the time and date. These log files thus form a data stream that captures the time and location of individual visits, from which we can infer group membership. With automated tracking of individuals enabled by PIT-tag technology, this system opportunity to capture the decision-making by individuals across a range of social and environmental contexts. Methods covering the deployment of feeders and data analyses are detailed in each chapter.

Mulligans Flat Nature Reserve, near Canberra, Australia, is a 683 ha reserve of temperate grassy woodland, a critically endangered habitat type. The reserve is almost entirely enclosed by a predator-proof fence in which invasive species, such as foxes and rabbits, have been removed. In 2008, I established a ringing site within this nature sanctuary to investigate the social structure of thornbill-dominated mixed-species flocks. Thornbills are cooperatively-breeding passerines that are considered to be centrally important in mixed-species flocks (Bell, 1980). They breed from late winter until the end of summer, forming large mixed-species flocks comprising of up to 20 species. Since 2010, a large proportion of the birds have been colour-banded in the central part of the study area, and group co-membership recorded during regular surveys. More detailed methods are provided in chapter 3.

Given that all chapters in this thesis are self-contained publications, they each contained detailed methods that are therefore not repeated here.

Thesis outline

This thesis investigates the evolutionary relationship between social structure, individual decision-making, and the environment. In the nine chapters that follow, I i) develop and apply a framework for using social network analysis to investigate mixed-species flocking, ii) develop a method for measuring phenotypic assortment in weighted social networks and use this to investigate social selection in tits, iii) describe a new hypothesis that links different behavioural strategies for managing competing predation and starvation risks, and iv) investigate the decision-making rules that underpin mixed-species flocking and how these are dynamically-linked to environmental conditions. In doing so, I hope to elucidate the decisions that individuals make in order to form and maintain mixed-species flocks, the spatiotemporal scale at which decisions are made, and how these are influenced by social and environmental contexts.

- In **chapter 2**, I propose social network analysis as a new research tool for investigating mixed-species flocking questions. I argue that the top-down approaches that are pervasive in the field may not capture the full complexity of the system, particularly in terms of intraspecific variation in social behaviour. I propose that using a bottom-up approach, where the associations between known individuals are used to form quantitative measures of social behaviour and the position of individuals within the population structure, will open up a rich set of testable hypotheses. I then use foraging data from PIT-tagged tits in Wytham Woods in order to show how dominance relates to foraging network centrality.

- In **chapter 3**, I test the relationship between foraging niche and social associations. The over-arching theory of group-living (both within and between species) has been largely based on the competing hypotheses of competition and predator avoidance. However, many species that join together in mixed-species flocks display a greater degree of niche overlap than expected from the local pool of species, providing greater support for the role of information use in group formation. This suggests that an individual's associations should be stronger with heterospecific individuals with which it shares a greater niche overlap.

- In **chapter 4**, I develop a method for calculating assortment in weighted social networks. Assortment is the preferential attachment of individuals with the same or similar phenotype. I demonstrate the limitations of using the binary (or unweighted) version of the assortativity coefficient, showing that the improved measure is much more robust to sampling noise. I then describe assortment in the networks from the previous two chapters for several phenotypic traits.
- In **chapter 5**, I describe the fission-fusion dynamics of flocks of great tits in order to examine how short-term decisions can modulate long-term dynamics of phenotypic assortment. This chapter demonstrates how assortment can arise from seemingly random movements of birds through both social and spatial processes.
- In **chapter 6**, I demonstrate how phenotypic assortment in an animal population can influence selection operating on phenotypes. Using first-year birds, I calculate the arrival time for each individual into the population, and calculate the relationship between each individual's arrival time, the mean arrival time of its associates, and its success in gaining a breeding territory. Using the measure of assortment by dispersal phenotype, I then calculate the overall strength of selection operating on this trait when mediated by social factors. My results show that by associating with other late dispersing birds, individuals can reduce the strength of selection for early arrival.
- In **chapter 7**, I examine the foraging strategies of wintering birds. Existing theoretical and empirical research on predation risk and starvation risk considered food resources in terms of payoff uncertainty, whereas many species are dealing with spatial uncertainty in food availability. I propose that animals could have developed a simple two-part strategy that deals with the need to discover food as well as avoid predators. I test this new hypothesis by deploying novel foraging sites, showing that individual birds exhibit a marked shift from exploration behaviour in the early parts of the day, before shifting to exploitation of food patches in the later parts of the day.
- In **chapter 8**, I use a novel 'quad' feeder design to determine how individual decision-

making rules vary between conspecifics and heterospecifics. This design is a square consisting of four feeders, providing individuals with an option to either move away or join others while the flock is foraging within this patch. I use a collective decision-making model to mathematically infer the contribution of conspecifics and heterospecifics to individual flocking decisions. I show that individuals use equivalent interaction rules across both conspecifics and heterospecifics, and that a common rule recreates observed flocking behaviour.

- In **chapter 9**, I experimentally manipulate predation risk and competition in each quad to determine the influence of ecological conditions on the interaction rules observed in chapter 8. Although collective behaviour has been widely shown to arise from simple rules, there is little evidence that these are dynamically adjusted in response to environmental change. I find that birds changed their interaction rules under different ecological conditions, and that these could be varied according to different components of the flock.
- Finally, in **chapter 10**, I provide a synthesis of the chapters above, discuss future directions, and formulate general conclusions from this thesis.

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CHAPTER 2

Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour

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Commentary

Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour

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Mixed-species social aggregations are common across taxa. There are two, nonexclusive, hypotheses typically proposed to explain the formation of social groups: increased predator vigilance and greater foraging efficiency. In mixed-species groups, these hypotheses are typically tested with species-level summary measures such as flocking propensity, the assignment of species-level roles, mean body size, and foraging and habitat characteristics. Literature syntheses make it clear that while these hypotheses are important, much about mixed-species groups remains unexplained. We suggest that we can substantially increase our understanding of the evolution and ecology of mixed-species social groups in terms of both traditional and novel hypotheses by shifting the analytical focus to bottom-up approaches common in intraspecific investigations of sociality. Bottom-up approaches to analyses of social structure treat pairwise interactions as the fundamental unit of analysis and social structure as an emergent property rather than relying on a priori assignments of species as units of association. The construction of social networks from pairwise interaction rates allows us to assess the factors that promote group formation on the basis of individuals, a more appropriate level of selection, rather than species groups. We illustrate this approach with data from mixed-species foraging assemblies in tits (Paridae), finding significant effects of dominance on social behaviour within species. This new focus allows us to address questions about active associations among heterospecifics, the role of individuals within mixed-species societies, and the role of environments, which will collectively provide a richer description of the evolution and function of mixed-species societies.

A society is a cohesive group of individuals with organized relationships that impact both survival and fitness. Social groups are distinguishable from random aggregations, for instance when group formation is due to a locally limiting resource, by the presence of nonrandom preferred and avoided interactions between specific individuals over time (Whitehead 2008). Darwin (1871) noted that the tendency to be social is a trait upon which selection can act. Since then benefits to individuals of being social are often cast, and perhaps often best understood, within the context of inclusive fitness (Grafen 2009). Direct fitness benefits can also play an important role in the evolution of sociality but can be difficult to disentangle from indirect kin-based benefits (Clutton-Brock 2002). However, inclusive fitness can be excluded a priori for mixed-species social relationships making mixed-species sociality particularly important for understanding how direct fitness benefits of social relationships can produce complex social structure in the absence of kinship. Mutualism and manipulation are classical explanations for social behaviour among nonkin individuals of the same, or different, species (Clutton-Brock 2009). Mutualistic interactions entail that interacting individuals gain immediate and shared benefits that exceed any costs associated with interacting (e.g. cooperative hunting, foraging and resource defence; Kokko et al. 2001; Clutton-Brock 2009). Although manipulative social behaviours may be selected largely for the benefits accruing to the manipulating individual, both individuals may benefit, albeit disproportionately. An individual mimicking the call of another species in order to attract it to a resource or to mob a predator is a common example of manipulative behaviour.

Despite a long research tradition, particularly in birds (reviewed in Rand 1954; Harrison & Whitehouse 2011), we suggest that our understanding of the evolution of mixed-species sociality can be considerably expanded by a shift in analytical focus. In particular, we suggest that typical conceptual approaches to the studies of mixed-species groups suffer from drawbacks related to a top–down classification scheme when describing heterospecific social structure. First, the typical unit of analysis in the mixed-species flock (MSF) literature is the species. This implicitly imposes a social

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structure (MSFs are structured by species), rather than describing it using social data. Second, selection occurs at the level of individuals and their genes, so the fitness costs and benefits of being social are also best measured at the level of the individual and not the species. Inferences about selection and fitness benefits, and therefore the evolution of MSFs, drawn from top–down examination are consequently constrained to be cursory.

Here we advocate a bottom–up approach, productive in intraspecific studies of animal social structure, for analyses of MSFs (Hinde 1976; Whitehead 2008). Bottom-up studies of sociality have identified substantial variation in the tendency to be social among individuals that is masked by current species-level classifications in typical MSF studies. For example, wild guppies, *Poecilia reticulata*, exhibit greater association strengths that are temporally more stable in higher predation risk environments (Kelley et al. 2011) and exhibit both behavioural (Croft et al. 2009) and physical (Croft et al. 2005) assortment. Similarly, in bats, *Myotis septentrionalis*, associations vary according to age and reproductive stage, with gestating females having fewer associations (Patriquin et al. 2010). Furthermore, a study of meerkats, *Suricata suricatta*, by Madden et al. (2011) describes several levels of social positions according to intrinsic individual characteristics; for example greater body mass determined dominance and males showed assortment. In particular, social network analysis provides a quantitative framework that can integrate across levels, based upon dyadic interactions, from individuals to species. This makes it useful for testing traditional species-level hypotheses as well as additional hypotheses regarding individual variation within MSFs (Croft et al. 2008; Whitehead 2008).

THE BOTTOM–UP APPROACH FOR MIXED-SPECIES FLOCKING RESEARCH

Hinde (1976) proposed an elegant conceptual framework that has been adopted for the study of vertebrate social organization (Whitehead 2008). His insight was to consider dyadic interactions as the fundamental unit of social analysis. The patterning of interactions between pairs can then be used to describe relationships, and social structure inferred from the pattern and persistence of these relationships within the population. At each level the data reveal properties that may not be apparent at the level below; relationships emerge from interactions, and social structure from relationships. Thirty-six years after its publication, Hinde's framework continues to be influential, leading to rich and novel insights into the ecology and evolution of complex and cryptic animal societies (Goodall 1986; Cheney et al. 1987; Dunbar 1988; Whitehead 1997, 2008). The mixed-species flocking literature has largely missed these technical and conceptual advances from individual-based approaches in the social structure literature.

The bottom–up framework of interindividual interactions within mixed-species flocking provides an opportunity for measuring the indirect genetic effects of the social environment. An indirect genetic effect is the phenotypic expression of an individual's trait that is affected by their interactions with other individuals (Moore et al. 1997; Wolf & Moore 2010). Furthermore, fitness consequences of interspecific indirect genetic effects have been suggested as being important in community structure and provide evidence for community-level selection (Shuster et al. 2006; Whitham et al. 2006). Harrison & Whitehouse (2011) suggested that by participating in MSFs, species are able to alter the selective pressures they experience through the process of niche construction, an ecoevolutionary feedback modifying community-level selection. The pattern of interactions between pairs of individuals provides a measure of social phenotype that can be assessed against morphological traits and reproductive success in order to determine the effects of selection operating within populations, and how selection varies according to social conditions. Applying a bottom–up approach to MSFs can provide the basis for exploring the interplay between community-level selection and cooperation based on mutualism.

While this framework will not be suitable for all questions (for example landscape variation in species guilds), the shift of mixed-species flocking research towards a bottom–up approach will provide a quantitative interface between the social behaviour of individuals and population-level phenomena (Croft et al. 2008). This will enable our understanding of MSFs to be explored in the context of theoretical advances in sociality, as well as better informing classical evolutionary theories of group living such as predation risk minimization and foraging benefits. One tool that has proved particularly useful for investigating sociality from a bottom–up perspective is social network analysis (Croft et al. 2008; Whitehead 2008; Newman 2010).

SOCIAL NETWORK ANALYSIS

Social network analysis is a tool for studying the social organization of groups based on the associations or interactions between individuals. Its utility for studying animal populations has been to explore the variations in individual sociality, and the consequences of such variation (e.g. Lusseau 2003; Croft et al. 2004). Thus, while social network analysis methods to test differences between individuals in populations are not novel, their application to MSFs have as yet received little attention. One study has so far used social networks in multispecies groups. Beyer et al. (2010) measured association rates between classes of different fish species, using a network approach to show differential social associations between native and invasive fish. This study, however, was at the level of the species (species were nodes in the network) as opposed to the associations between individually identified animals.

Methods for gathering social network data of animal groups are well described and easily applied to mixed-species populations (Whitehead 2008). These involve recording associations or interactions between known or marked individuals repeatedly over time in order to describe connections between individuals, and, preferably, the interaction rate and stability of each dyadic pair. In the context of MSFs, each individual would be treated equally, irrespective of its species category. The collective dyadic links between individuals produces a network on which metrics can be calculated describing various aspects of an individual's tendency to be social. These measures can be statistically assessed along with both intrinsic traits and extrinsic factors. For example we can measure individual gregariousness (the sum of their associations) and test whether associations are related to species or rather to individual traits (see Whitehead 2008; Croft et al. 2011 for further details and caveats on statistical tests for nonindependent network metrics).

In Fig. 1, we show two simple hypothetical interspecific social networks. Mixed-species populations can be made up of very different species, and the participation of individuals in the social network could be based primarily on species (Fig. 1a) or individual-level characteristics (Fig. 1b). Thus, whereas the position of individual nodes in Fig. 1a is comparable to the results of existing top–down approaches (where all individuals could be replaced by one node representing species), the social structure of Fig. 1b represents a radical departure from anything that could be quantifiably assessed, or even detected, with species-level analyses.

Social network analysis provides a catalogue of quantitative metrics that can be calculated for an observed population (Newman 2010). These span three scales: the individual, the dyadic pair and the population. At each level, comparisons can be made with null models of randomized networks (Bejder et al. 1998; Whitehead 2008; Croft et al. 2011) to test for nonrandom characteristics of the observed social structure. At the dyadic level, variations in link

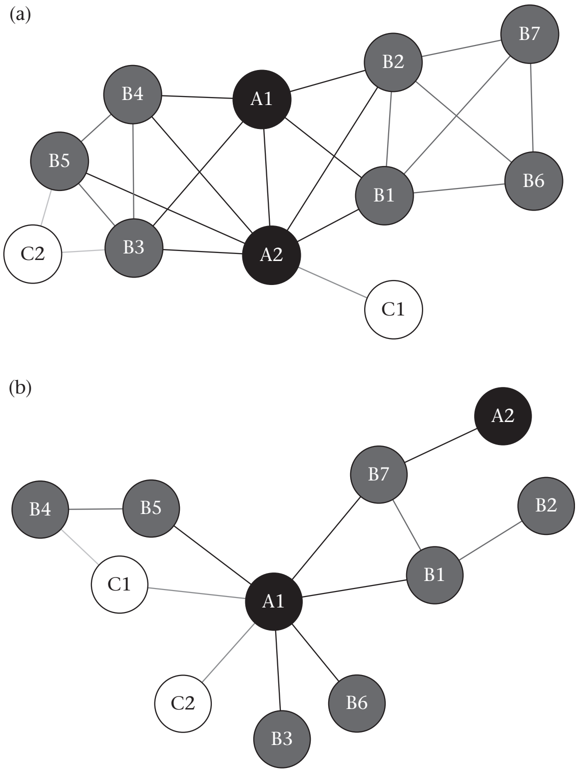

Figure 1. Example interspecific social networks showing different network structures. In (a) the network shows clear species assortment, at least for species A and B. This would indicate stronger attraction with conspecifics, where, for example, species A may be a resident monogamous species, B a cooperative breeder and C perhaps a migratory species. The social participation of individuals in this network is homogeneous within species. In contrast, (b) shows a network with greater individual variation that is not necessarily attributable to species. For example, node A1 has a highly central role, whereas A2 is poorly connected.

strengths (preferred associations) can be tested against morphological, ecological and environmental factors. Individual differences can then be related to biological features, such as personality or genotype, to understand their impacts on social behaviour.

APPLICATIONS TO MIXED-SPECIES FLOCKING

Here we discuss some key questions in mixed-species flocking to which social network analysis could be readily applied, and explore how doing this might in turn advance our understanding of the evolution of social behaviour more generally.

Are There Active Associations Among Heterospecific Individuals?

One outstanding question in mixed-species flocking is whether preferential, or avoided, associations exist between heterospecific pairs of individuals. Nonrandom associations between individuals within species have been shown in a wide range of taxa and specifically tested for in wild populations of, for example, dolphins (Lusseau 2003), ungulates (Sundaresan et al. 2007) and guppies (Morrell et al. 2008). In the case of mixed-species flocking, being familiar with associates may provide benefits over socializing with random individuals. Stable associations can lower uncertainty, thereby increasing payoff of mutualistic interactions through reduced costs of competition (stable dominance hierarchy) and predation. For example, Blumstein et al. (2004) showed that individuals can discriminate the identity of alarm callers in order to ascertain the level of vigilance that is required. Stable associations can also provide more opportunity for information transfer through social learning or other mechanisms (Krebs 1973). A population containing both resident territorial flocks and transient associates would be ideal for exploring benefits of long-term cooperation over random associations. Permutation tests of pairwise associations can be used to determine preferred or avoided individuals (Whitehead 2008) and lagged association rates to measure their persistence over time, which is important as benefits may be delayed or reciprocal (Clutton-Brock 2002).

What are the Social Roles of Individuals in MSFs?

The mixed-species flocking environment has been suggested as having the potential to modify selection on within-species variation (Harrison & Whitehouse 2011) but the adaptive significance of variation must be analysed at the level of individuals rather than species. Juvenile connectivity in birds has been shown to increase social status in the short term (house finches, *Carpodacus mexicanus*: Oh & Badyaev 2010) and the long term (long-tailed Manakin, *Chiroxiphia linearis*: McDonald 2007), providing subsequent fitness benefits. Individuals may also interact both mutualistically and manipulatively. In nonrandomly associating flocks different individuals may therefore gain different direct fitness benefits from their position relative to others as the benefits to cooperation can be asymmetrical (Gibson et al. 2002; Magrath et al. 2009; Nolen & Lucas 2009). This potentially leads to preferences for active, passive and avoided associations in dyadic pairs, and hence enables emergent self-organization and sociality. Social network analysis provides many different measures that can evaluate the social phenotype of individuals. However, empirical studies may require support from simulation results to provide an a priori classification of network measures and roles.

How Does the Physical Environment Affect Mixed-Species Flocking?

Community composition is influenced by habitat characteristics at several scales. Understanding the differing roles that individuals and species play in different habitats can provide insight into mutualistic interactions that may allow their habitat tolerability to be greater than their niche otherwise permits. The best evidence (Harrison & Whitehouse 2011) that flocking can be mediated by community composition comes from Diamond (1975) who found that New Guinean islands lacking key species did not have any mixed-species flocking in those that remained, and Maldonado-Coelho & Marini (2000) who found that the absence of one nuclear species from forest fragments in Brazil led to the loss of mixed-species flocking occurring in those fragments. These examples point to manipulation by the flocking species underlying the evolution of flocking within those communities. Furthermore, variations in the relative proportions of syntopic species may affect not just social structure but also social roles. For example, the fitness benefits of mixed-species flocking to individuals from a scarce species may be much greater where its population density is low than where it is high. In such cases, there might be selection for more interspecifically gregarious phenotypes to colonize or maintain presence in less preferred habitats or at the edge of their range. The social network of populations would be structurally very different in the presence of relative changes in species abundances, and therefore whole network structure can be used to relate these differences to environmental conditions. This has, to our knowledge, remained unexplored.

How can mixed-species flocking evolve?

The best supported hypotheses for the evolution of MSFs have been that they lead to increased foraging success and predation risk dilution. However, the presence of preferred and nonrandom associations within these flocks suggests the existence of some higher-level processes. This would support the hypothesis that MSFs are mutualistic, albeit providing a range of benefits that may not be identical for all participants (Clutton-Brock 2002). For example, sentinel species may gain better access to food resources while other species benefit from more rapid detection of predators (Satischandra et al. 2007). By cooperating, organisms can alter their selection pressure (such as through niche construction as suggested by Harrison & Whitehouse 2011). Competition costs may be incurred by both species, and these will be outweighed by the benefits (at least approximately equalled in cases of manipulated species). Maintained associations can enable long-term benefits or potentially enhance them through reciprocity.

EMPIRICAL EXAMPLE: MIXED-SPECIES TIT FLOCKS

The benefits of participating in MSFs are unlikely to be experienced equally by all individuals. Dominant individuals can supplant subdominants from the safest foraging positions, in turn reducing flocking benefits to subordinates (Morse 1978; Ekman 1989). Morse (1978) examined the social dominance hierarchy of tits (*Parus* spp.) in Wytham Woods finding that larger species were dominant over smaller species. Despite significant mixed-species associations, agonistic interactions occurred most often between conspecifics rather than heterospecifics (Morse 1978). Larger more dominant individuals in general can have a larger optimal group size as they incur lower competitive costs and can supplant subdominants from safer and more profitable resources (Krause & Ruxton 2002). This should lead to dominants having a larger number of associates than subdominants regardless of species composition. Mixed-species groups may be more important for subdominants by enabling them to increase their group size either with individuals that are even more subdominant than they are or with those from species that use a different feeding niche. By choosing to flock with heterospecifics of a smaller species, subdominants might thereby increase their relative rank within their flock, increasing their individual benefits of flock participation (Gosler & Carruthers 1999). Subdominants should therefore have a relatively greater number of heterospecific associates than dominants. Finally, dominant individuals have been shown to maintain more central group positions than subdominants in both fish and birds (reviewed in Krause & Ruxton 2002). A central individual is likely to have access to better information on predators or food resources, and be safer from attacks, but incur larger competition costs which may be offset by dominance. As an example of the application of social network analysis to mixed-species flocking, we used social network analysis to test for effects of dominance on associations within and between species. We hypothesized that dominants should have a greater number of associates, that subdominants should flock with more heterospecifics, and that dominants should be found in positions of greater centrality than subdominants.

Methods

We generated four social networks based on the feeding associations of a population of wild birds. Four feeders were placed in a square 300 m apart for the month of January 2012 at Wytham Woods, Oxford, U.K. (51°46′00N, 01°20′00W). Food was available over four consecutive weekends (2 days each, total 8 days) with the feeders closed at other times and not recording visits. Feeders were fitted with RFID antennae in place of the perch for both access holes (Dorset ID, Aalten, Netherlands). These detected visits to each feeder by blue tits, *Cyanistes caeruleus*, coal tits, *Parus ater*, great tits, *Parus major*, marsh tits, *Poecile palustris*, and nuthatches, *Sitta europaea*, fitted with passive integrative transponder (PIT) tags (IB Technology, Aylesbury, U.K.) recording the time, date, location and identity of each individual.

The social network was inferred using a recently developed method utilizing a Gaussian mixture model to detect clusters of visits in time (Psorakis et al. 2012). Mixture models are typically probabilistic models used to represent the presence of subpopulations, but are used here to represent the presence of bursts of arrivals at a feeder within the data stream. Instead of fixing time limits of associations, it allowed us to detect temporally focused bursts in activity, or ‘waves’, of feeding birds. Observations are then assigned to a group according to the temporal burst in which it occurs. We applied the simple ratio (Whitehead 2008) method for weighting associations to describe the proportion of visits made by individuals within the same group. We used randomization tests, following Bejder et al. (1998), to test for nonrandom associations among individuals. This randomization method controls for important features of the data such as the number of observations, gregariousness and group size. If the standard deviation of the observed association matrix is greater than that of the randomized association matrix then it is likely that there are nonrandom preferred and avoided associations (Whitehead 2008).

Wing length was used as a proxy for expected dominance status. In great tits, wing length is a predictor of dominance within species, with long-winged adults and males being categorically dominant over juveniles and females (Sandell & Smith 1991). The distribution of wing length across species follows the dominance hierarchy described by Morse (1978).

To describe quantitatively the participation of each individual in the network, we calculated the number of associates (unweighted degree) as a measure of gregariousness. We calculated eigenvector centrality which is a measure of an individual’s centrality within the entire network. Finally, we split the number of associates into interspecific and intraspecific components, converting the measure into the proportion, or density, of each in order to account for different species population sizes.

We used generalized nonlinear mixed models (GLMMs) with random effects to estimate the effect of individual wing length on each network parameter. Binomial and Poisson error distributions were used in models with proportional and count values, respectively. We accounted for the lack of independence in social network measures by analysing four replicates of the social network (Croft et al. 2011), including sampling period (network number) and ring number as random effects. Finally, we tested our models by comparing parameter estimates to randomizations of the dependent variable. If parameter estimates were greater or less than 95% of the randomly generated parameter estimates we considered that variable to have nonrandom effects.

Ethical Note

All work was subject to review by the Department of Zoology (University of Oxford) ethical committee and adhered to U.K. standard requirements. Birds were caught using mist nets and ringed with a uniquely numbered British Trust for Ornithology (BTO) ring on one leg and a PIT tag on the other under BTO licence C5714. PIT tags were fully moulded into an 8 mm plastic ring with no protrusions and supplied by IB Technology. This work was conducted as part of a large ongoing research project at Wytham Woods (for example see Morand-Ferron & Quinn 2011). Previous work found no evidence of and impact of PIT tags on behaviour (Patrick & Browning 2011) or survival (Nicolaus et al. 2008) in great tits, and no adverse effects on fitness (Schroeder et al. 2011) in passerines.

Results

We detected 234 295 visits to the feeders, and inferred 11 586 gathering events across all four sampling periods. These were used to generate four networks with a total of 272 individuals (185–222 per weekend) across all species (a full network for all periods combined is shown in Fig. 2). Each network was tested for nonrandom associations and in all had significantly greater standard deviation of association weights than the null expectation (one-tailed $P < 0.001$ in all cases). These networks also exhibited significant within-species variation in network measures (Fig. 3). Together, these results indicate that individuals interacted nonrandomly.

We analysed the networks in a GLMM to test the effects of individual wing length on network metrics and account for temporal variation (results in Appendix Table A1). Across species, wing length was significantly related to the number of associates (group size) with larger birds having more associates than small birds (coefficient ± SE: 0.02 ± 0.003; $P < 0.001$). Large birds also had a greater proportion of intraspecific associates (coefficient ± SE: 0.03 ± 0.01; $P < 0.05$), whereas there was no effect of wing size on the proportion of interspecific associates, indicating that subdominants did not have more heterospecific associates (coefficient ± SE: 0.008 ± 0.01; $P = 0.5$). Finally, there was no relationship between eigenvector centrality and wing length (coefficient ± SE: 0.026 ± 0.024; $P = 0.2$). Sampling period (random effect) explained very little of the variance in these models, indicating that the patterns were consistent across all four replicates at this timescale.

Discussion

We found that body size was an important determinant of social behaviour in MSFs. As we predicted, large birds had a greater number of associates overall than smaller individuals. Large birds associated

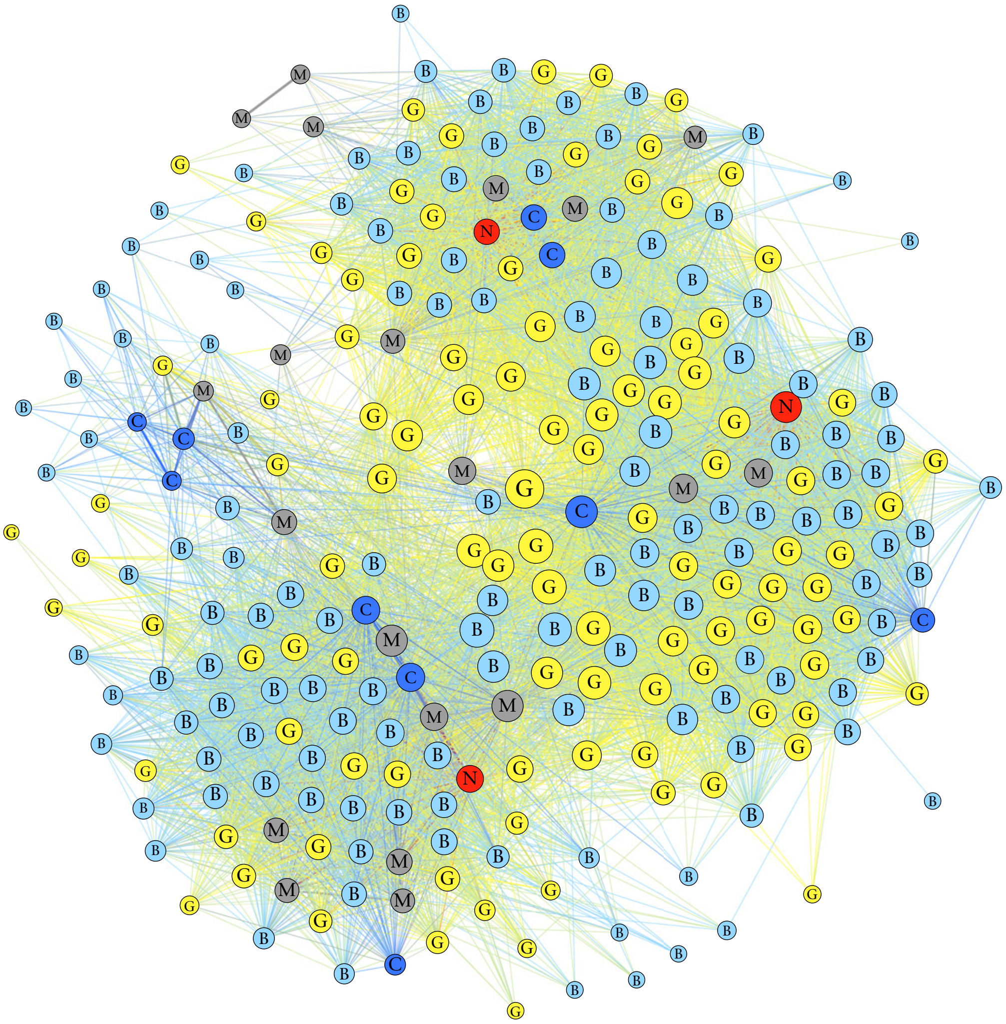

Figure 2. Social network of 136 blue tits (B), 10 coal tits (C), 103 great tits (G), 20 marsh tits (M) and three nuthatches (N) combined over the four periods of data collection. Nodes are coloured according to species and sized according to degree. Edge thickness, or weight, represents association strength between nodes. Node position was determined as the product of the attraction to connected nodes and repulsion from others, using the Fruchterman–Reingold algorithm in GEPHI (Bastian & Heymann 2010). Note that all individuals are connected; however, the edge weight of peripheral individuals is small and may not be visible.

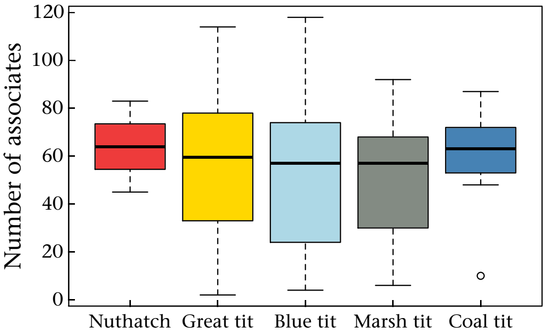

Figure 3. Summary of the number of associates by species for the first period of data collection (7 and 8 January 2012) indicating the presence of overlapping variation in social characteristics within species and overlaps between species. Species are ordered left to right by decreasing wing length and dominance rank as defined by Morse (1978). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circle is an outlier.

with more conspecifics than did smaller birds whereas there was no difference in the number of heterospecific associations between small birds and large birds. This suggests that all individuals aim to achieve a large group size, but that subdominants are limited in their ability to associate with conspecifics, perhaps because of the competitive costs that these associations incur. Thus, unlike our prediction that smaller birds would have more heterospecific associates, there was no effect on the number of heterospecific associates across dominance ranks. This uniform rate of interspecific associations may indicate a benefit in avoiding predation as experimental evidence has shown that information is unlikely to be an important proximal mechanism of mixed-species flocking with regards to feeding (Waite & Grubb 1988). In contrast, larger birds may be attracted to conspecifics in order to gain access to better problem solving (Morand-Ferron & Quinn 2011) or opportunities for scrounging (Giraldeau & Caraco 2000).

However, unlike our prediction that dominant birds should be more central, we found that eigenvector centrality was not linked to wing size. This indicates that dominance had little effect on individuals' positions within the whole network. By associating with heterospecifics, subdominants may be able to maintain central positions in their social groups, whereas in single-species flocks they would become peripheral. Hence, the ability of subdominants to maintain central positions in a population may be a previously undetected benefit of mixed-species flocking. Although we found that dominant individuals had a greater number of conspecific associates, there was no effect of dominance on the number of heterospecific associates. Since there are usually more heterospecific than monospecific links in a network, this can result in subdominants reducing the effect of dominance on their global social position. This may bring significant benefits to subdominants, as while local associations are important, it is likely to be the global network characteristics of individuals that most affect lifetime fitness (McDonald 2007).

This study demonstrates the strength of the bottom–up approach. Morse (1978) could identify the presence of interspecific dominance hierarchies aligned with body size with his observations at the species level. Here, we found that these dominance hierarchies led to social effects at the individual level, and that these were not always aligned with the predictions we made based on studies of sociality in monospecific systems.

CONCLUSION

We think social network analysis will be a useful tool for refining our knowledge of mixed-species societies. Relative to more typical top–down approaches this line of questioning is well suited for exploring interspecific interactions among individuals that are likely to be highly complex (Goodale et al. 2010), and may elucidate advances to theories about group living in general. In particular, quantifying interactions between individuals and relating them to direct fitness benefits arising from mutualism or manipulation will open a large number of pertinent and unexplored questions.

The application of social network analysis is valid for a wide range of hypotheses across all contexts, from ecology to evolution to conservation, and entirely compatible with pre-existing paradigms. However, most current work remains focused on exploring patterns of social structure, and the challenge will be to use this approach to understand social processes better (Croft et al. 2008). It may be that mixed-species flocking will be useful for questioning sociality and cooperation theory more generally by simplifying some effects (such as dominance) and eliminating others (such as mate choice), from the measured social affinity. We hope that this paper will stimulate new focus and continued interest in mixed-species flocking.

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Appendix

Table A1
Output of generalized linear mixed models

Dependent variable	Wing	Ring number	Date
No. of associates	0.0189 (0.005)	0.2585 (0.5085)	0.0123 (0.1108)
No. of conspecific associates	0.0265 (0.0118)	0.0138 (0.1173)	0.0005 (0.0241)
No. of heterospecific associates	0.0077 (0.0119)	0.0100 (0.1002)	0.0001 (0.01044)
Eigenvector centrality	−0.0004 (0.0120)	0.0000 (0.0000)	0.0000 (0.0000)

Wing length was a fixed effect and we give the effect size with SE. Ring number and date were random effects, and the variance is given with SD. We used a Poisson error distribution for the number of associates model, and a binomial error distribution for the other three models.

CHAPTER 3

Social organisation of thornbill-dominated mixed-species flocks using social network analysis

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ORIGINAL PAPER

Social organisation of thornbill-dominated mixed-species flocks using social network analysis

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Abstract Mixed-species associations are a widespread phenomenon, comprising interacting heterospecific individuals which gain predator, foraging or social benefits. Avian flocks have traditionally been classified as monolithic species units, with species-wide functional roles, such as nuclear, active, passive, or follower. It has also been suggested that flocks are mutualistic interactions, where niches of participating species converge. However the species-level perspective has limited previous studies, because both interactions and benefits occur at the level of the individual. Social network analysis provides a set of tools for quantitative assessment of individual participation. We used mark-resighting methods to develop networks of nodes (colour-marked individuals) and edges (their interactions within flocks). We found that variation in flock participation across individuals within species, especially in the buff-rumped thornbill, encompassed virtually the entire range of variation across all individuals in the entire set of species. For example, female, but not male, buff-rumped thornbills had high network betweenness, indicating that they interact with multiple flocks, likely as part of a female-specific dispersal strategy. Finally, we provide new evidence that mixed-species flocking is mutualistic, by quantifying an active shift in individual foraging niches towards those of their individual associates, with implications for trade-off between costs and benefits to individuals derived from participating in mixed-species flocks. This study is, to our knowledge, the first instance of a heterospecific social network built on pairwise interactions.

Keywords Social network analysis · Mixed-species flock · Group living · Foraging niche · Individual variation

Introduction

One striking feature of many animal communities around the world is the presence of mixed-species associations. These consist of individuals of two or more species that maintain cohesion through time and space (Morse 1970; Greenberg 2000) in order to gain benefits such as predator dilution and increased foraging success (Waite and Grubb 1988; Szekely et al. 1989; Dolby and Grubb 1998; Thiollay and Jullien 1998; Thiollay 1999). Whereas many animals rely on cohesive interactions with conspecifics, individuals in multi-species groups may respond equally to heterospecific associates (Krause and Ruxton 2002). Yet no study has investigated heterospecific social interactions between marked individuals (Wascher et al. 2012). Social interactions can occur between of individuals from very different taxonomic groups such as monkeys and birds (Boinski and Scott 1988), seabirds and cetaceans (Evans 1982), and even across different trophic levels (Oommen and Shanker 2010). However, the most common and widely studied interspecific associations are avian mixed-species flocks (MSFs) (Greenberg 2000; Harrison and Whitehouse 2011).

The traditional approach to describing avian MSFs has been to categorize species into functional roles. Species are classified as either central to the formation and maintenance of flocks (nucleus) or peripheral followers (satellite) that associate more loosely with passing flocks (Winterbottom 1943; Powell 1985; Hutto 1994; Farley et al. 2008; Srinivasan

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et al. 2010). Further classifications have been made according to status as leaders or followers in flocks (Moynihan 1962), and integrated into nuclear and peripheral roles (Morse 1970; Farley et al. 2008). However, whilst rigorous definitions of these roles remain elusive (Greenberg 2000), studies have shown that the heterospecific social landscape can have important impacts on the behaviour of focal species. These include risk-taking during foraging by peripheral species in the absence of flock leaders (Dolby and Grubb 2000) and the total absence of flocking without the presence of nuclear species (Diamond 1975; Maldonado-Coelho and Marini 2004).

In addition to categorizing species roles in MSFs, several recent studies on interspecific interactions have reported shifts in the foraging location of species determined by their participation in, and the composition of, MFS. These have shown differences in foraging niche of one or more species whilst in MFS versus when foraging alone (Buskirk 1976; Valburg 1992; Latta and Wunderle 1996; Hino 1998, 2000; Thiollay 2003; Zou et al. 2011). This is in contrast to the classic theory on niche differentiation that argues that species remain in sympatry by diverging in their diet and habitat use (Hutchinson 1957; Lack 1971; Schoener 1974). Experimental evidence supporting the niche segregation hypothesis has shown increased niche divergence in the presence of interspecific competition (reviewed in Schoener 1983; Dhondt 2012). So why would individuals preferentially shift away from their monospecific foraging niche and converge with associates at the cost of increased competition when joining MFS? Predation is likely to be a critical factor in determining fitness in small passerines and leads to two potential explanations. First, the risk of predation may exclude species from accessing a particular feeding niche when in small conspecific flocks (Valburg 1992). Alternatively, reduced predation when flocking in larger groups may outweigh the costs of sub-optimal foraging, such as through decreased vigilance. This can enable more time to be spent on finding and handling difficult food items.

Mixed-species flocking has generally not been considered in the context of the individual participants in each flock. Theory on cooperation (Clutton-Brock 2009) suggests that in order to maximise beneficial return, and therefore in the case of mixed-species flocking to offset the costs arising from competition, heterospecific interactions should occur between non-random individuals. Further, the recent study by Wascher et al. (2012) showed the existence of individual recognition of heterospecifics living in the same environment. It is such non-random social interactions that lead to emergent and complex population structure (sensu Hinde 1976).

In this study, we investigate the social structure of wild MFS dominated by thornbills (*Acanthiza* spp.), small passerines common across the southern half of the Australian continent (del Hoyo et al. 2007). These were described by Bell (1980) as being nuclear in MFS, which they join regularly outside of breeding season, in the Canberra region of Australia. Of the 13 species of thornbills, nine are cooperative breeders, which is thought to be ancestral in the genus and sub-family (Acanthizinae), having arisen from male philopatry (Nicholls et al. 2000). All species are insectivores, sedentary, conspicuous in their song and frequently mimic. There is no described dimorphism in plumage in any species, though most are slightly dimorphic in size (larger males, del Hoyo et al. 2007).

Here, we use social network theory (Croft et al. 2008; Whitehead 2008; Newman 2010) to ask the following questions: (1) are associations between heterospecific individuals in MSFs non-random, (2) do individuals vary in their social behaviour and flock participation, and (3) does mixed-species flocking by individual thornbills result in a shift in their foraging niche?

Methods

Study area

This study was conducted in the Mulligan's Flat Sanctuary (Manning et al. 2011), part of the Canberra Nature Park. It is situated on the outskirts of Canberra in south-eastern Australia, centered at 35°09′56″, 149°10′18″. The nature reserve was established in 1994 in order to protect 683 ha of temperate grassy woodlands, a critically endangered habitat type, with a predator-free sanctuary completed in 2009. It has an elevation range of 650–700 m altitude with a mean annual rainfall of approximately 650 mm (for further details, see Lepschi 1993; McIntyre et al. 2010). The predominant vegetation type in the reserve is open grassy eucalyptus woodland comprised of Yellow Box (*Eucalyptus melliodora*) and Blakely's Red Gum (*Eucalyptus blakelyi*).

Colour marking

Individuals of eight species were captured and uniquely colour-marked within one two hectare (200 × 100 m) area over 6 days in late April 2011. The colour-band schema consisted of a single anodised alloy band on each leg with the right leg being an anodised numbered band supplied by the Australian Bird and Bat Banding Scheme (ABBBS). This simple schema limited the unique number of colour combinations to 36 per species, but was adopted as other studies have found that injuries such as broken legs may occur in plastic colour-banded thornbills (ABBBS, personal communication). In order to mark an even proportion in each flock with this limited supply of unique combinations (rather than mark a few strongly connected family groups), colour bands were allocated to captured thornbills as follows: (1) individuals in the same net (or two contiguous nets) at the same time were colour-banded up to a maximum of four individuals per species, (2) the order of individuals banded were randomly picked from the bags (captures from one net), (3) older re-trapped birds (first banded 2 or 3 years previously) were always colour-banded. As we would not be able to mark a very high proportion of the population, this strategy aimed to achieve an even proportion of colour-banded birds and a proportionate representation of each species within in each flock, and to avoid biasing our sample to young birds as these were easier to capture. Individuals were sexed according to the presence of brood patches, or by total head length and wing length (P. Milburn and D. Farine, unpublished data) where possible.

Observations

We defined an area of approximately 67 ha surrounding the capture area to search for colour-banded birds. Daily observations of individual flock membership were made in May and June 2011. We initially defined flocks as two or more birds within 10 meters of each other maintaining spatial cohesion for at least 1 min, but found that identifying co-membership was very clear due to frequent interactions between (such as 'beating' for insects) and large gaps between flocks, ensuring that this artificial threshold was not required. Upon encountering a flock, individuals were located and their identity recorded. Each observation of an individual was assigned a unique flock number that commenced at 1 on the first study day. All birds observed within the same flock were therefore associated by their flock number. Observations were not limited to flocks, though single colour-banded birds were rarely encountered. The location of the observation was marked on map from which coordinates were later extracted using Google Earth™ (Google Inc.). Due to the high-resolution imaging available, heterogeneity of the habitat, and our knowledge of the area, we could assign coordinates of the exact tree recorded to four decimal places. This method was found to be less time-consuming and less prone to transcription errors than using a GPS. We recorded the foraging height of the focal bird using the following strata categorisations: top (canopy), mid (small tree, lower branches), and lower (shrub, ground) in order to detect any preferential shift dependent on flock composition. Flocks were clearly dominated by associations between either buff-rumped thornbills (*Acanthiza reguloides*) and yellow-rumped thornbills (*A. chrysorrhoa*), or between buff-rumped thornbills and striated thornbills (*A. lineata*). Flocks were followed for up to 1 h (Farley et al. 2008), or until it was deemed unlikely to have further colour-banded birds (i.e., all observations were of previously seen individuals). In cases when flocks split into two separate groups, we chose a random group to follow and a new flock number was allocated. Three hours was chosen as it marked the point at which the entire area had been searched and the same flocks were being re-encountered. These periods were spread evenly across daylight hours for the duration of the study.

Social network analysis

All analyses and statistical tests were conducted in the statistical package R (R Development Core Team 2010). The gambit of the group approach (Whitehead 1995; Franks et al. 2010) was used to generate a group-by-individual matrix. We calculated association strength of each dyad using the simple ratio index (Whitehead 1995), which is the proportion of time a dyad co-occurred, as a proportion of the total time that the individuals were observed. Edges in the network were not filtered; however, individuals were discarded if they had been observed on less than 3 distinct sampling days (Franks et al. 2010). This subset included all the individuals with maximum association rates that fell outside of the 5th and 95th percentile of the population distribution, indicating that they were inadequately sampled in order to generate accurate values.

The observed network was compared to a null model using permutations tests described by Bejder et al. (1998) and improved by Whitehead (2008) and Sundaresan et al. (2009). Here, randomly selected observations of two individuals in different groups were swapped, and the proportion of non-zero association indices and mean association index were calculated after each swap (Whitehead et al. 2005). The process was repeated 10,000 times and the distribution of values from the permutations compared to the observed values. This method controls for group size, number of observations, and gregariousness of each individual. Further, in order to control for possible spatial effects we subdivided the area into 36 equivalent 1.9 ha cells and constrained swaps between groups that were recorded in the same grid. As all individuals were present and alive in the study area for the duration of the study, we did not have to control for time.

As measures of social behaviour, the network statistics betweenness and degree were calculated using the sna library for R (Butts 2010). Home range analysis was performed in order to test if network measures were correlated to spatial range, and calculated using the Brownian Bridge movement model (Horne et al. 2007). Assortment was calculated using the method described by Newman (2003).

We re-calculated the weighted network to test for foraging height preferences. The foraging height of individuals with each of its associates was scored from 1 (bottom) to 3 (top) and averaged across all their observed interactions. This provided a standard directed network allowing comparisons to be made between groups (Croft et al. 2011) and we used general linear models (GLMs) to compare the foraging stratum of individuals in monospecific and heterospecifics dyads (using the out-degree with identity and species of associate as fixed effects). We used the DIP test for unimodality (Hartigan and Hartigan 1985; Hartigan 1985) to test for differences in buff-rumped thornbills' degree distributions with striated and yellow-rumped thornbills, where a bimodal distribution would indicate a social preference by individuals to associate with one species over another. The degree distribution was calculated by subtracting each individual's mean degree with one species by the mean degree of the other, where an even association with both species by individuals would yield a normally distributed degree with a mean of zero. Visualization of the network was performed using the open-source Gephi program (Bastian and Heymann 2010).

Box 1. Social network measures

Degree: Sum of the weights of all the focal node's connections.

Betweenness: Importance of the focal node in connecting groups or components of the network (the number of shortest paths between other dyads that pass through it).

Association Rate: Proportion of time a dyad co-occurred, as a proportion of the total time that the individuals were observed.

Density: The proportion of observed edges to all possible edges.

Results

We recorded associations between 80 individuals, of which 17 did not satisfy the minimum number of observations and were not included. Our marking schema was successful in achieving a high level of coverage within an area of 67 ha around the banding site where individuals had largely overlapping home-ranges. Figure 1 shows the home-range polygons for the 11 most frequently observed individuals (the estimated combined home-range of all individuals was 32 ha, see Online Resource 1) and are typically large in the open woodland habitats in which the study took place. Approximately 80 % of flocks in this area contained marked individuals and an even proportion of individuals were marked in each of these flocks (estimated at 40 % from observations). By marking one to two individuals in any family group, we were able to representatively mark individuals in proportion with the species representation in almost every flock encountered. The bulk of the discarded individuals were from a group of yellow-rumped thornbills which principally resided outside the study area and were only observed once subsequent to being colour-marked. This left 4098 observed associations between 63 individuals on which the analysis was conducted, summarised by species in Table 1. These interactions were used to generate the weighted social network (Fig. 2).

Non-random flock structure

The proportion of non-zero association indices and the mean association index was calculated for 10,000 permutations of the observed data. These values were significantly lower than those from the observed data when controlling for space and other social factors ($p<0.001$ in both cases). This indicates that significant non-random, or preferential, associations were present in the population even when home-ranges largely overlap (Fig. 1, see also Online Resource 1 for selectable home-range polygons of all individuals in the study).

However, we found no significant assortment by species present in the network ($r=0.013$), indicating a high level of interspecific mixing. Figure 3 shows that edge density was at least as great between heterospecifics as between conspecifics for most species and roughly equal for all species. Individuals in these flock had an equal number of conspecific and heterospecific associates. In contrast, the rate of associations between buff-rumped thornbills, yellow-rumped thornbills and scarlet robins was generally higher than between most other species pairs. For example, the strongest connections (with association rates between 0.5 and 0.6, or seen together approximately half the time) were between two buff-rumped and two yellow-rumped thornbills. There were also four buff-rumped thornbill dyads and two yellow-rumped thornbill dyads with association rates just above 0.5, and the pair of scarlet robins with an association rate of 0.78.

Individual variation in social behaviour

Betweenness was measured for each individual in the population (Fig. 4). In order to verify that the observed betweenness was not related to home-range size, we tested their correlation, finding it weak but significant ($r=0.276$, $p=0.045$, $n=53$). However, this disappeared if the values of area below 10 ha are omitted ($r=0.170$, $p=0.248$, $n=50$). This indicates an underlying mechanism for social behaviour that is not related to spatial distribution. Figure 4 shows the individual scores for betweenness, and the variation in buff-rumped thornbills is as large as that across the entire set of individuals in all species. Furthermore, the five highest-ranked individuals in the population were all female buff-rumped thornbills.

Foraging niche

Foraging height of individual buff-rumped thornbills was recorded in flocks associating with either striated thornbills or yellow-rumped thornbills (Fig. 5). When foraging with conspecifics, over 70 % of foraging associations were in the middle stratum. In contrast, when foraging with yellow-rumped thornbills, individual buff-rumped thornbills were found on average 68 % of the time in the bottom lower third

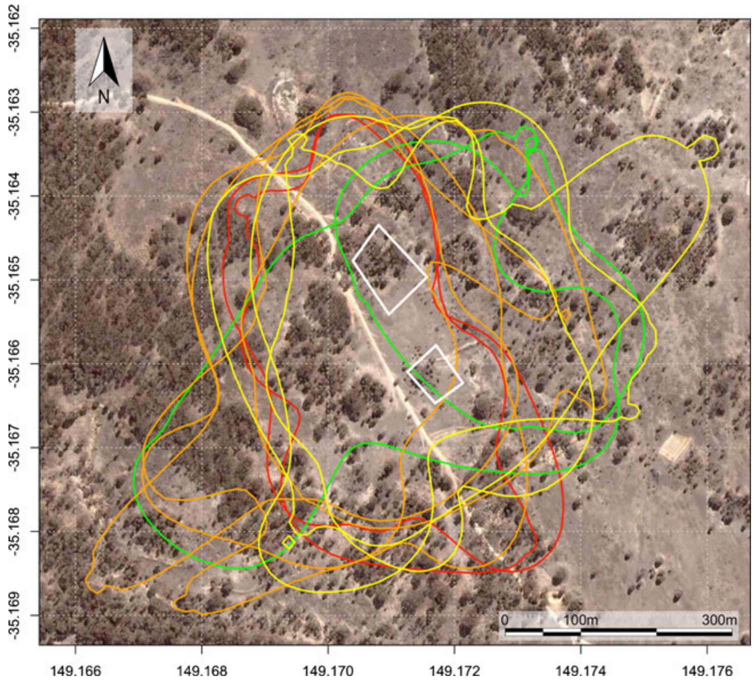

Fig. 1 Home-range polygons for the 11 most frequently encountered individuals shows that these individuals had largely overlapping ranges. *Polygon*s are coloured by species (*two red*: scarlet robins, *two green*: striated thornbills, *four orange*: buff-rumped thornbills, *three yellow*: yellow-rumped thornbills). Also shown are the habitat patches in which all birds were captured (*two white polygons*). Full set of interactive individual polygons can be found in Online Resource 1

of the habitat, as opposed to just 11 % in the top third. This was a significant shift in foraging height of individuals according to their associates (GLM $t=-5.92$, $p<0.001$). Further, while associating with striated thornbills, individuals were found on average 40 % of the time in the middle stratum and 58 % in the top stratum, significantly shifting their foraging niche in the opposite direction (GLM $t=4.27$, $p<0.001$). In other species, we found strong preferences for striated thornbills to forage high, and yellow-rumped thornbills to forage low, the former showing some preference for shifting to lower heights when associating with the latter (GLM $t=-5.49$, $p<0.001$). We tested whether our results were due to individual buff-rumped thornbills preferentially associating with one leading species over another (Fig. 6). The mean and median of the distribution were slightly biased towards yellow-rumped thornbills (−0.27 and −0.10, respectively); however, the DIP test statistic detected no divergence from unimodal distribution of social preference between the two species (dip=0.064, $n=26$, $p=0.55$), indicating that individual buff-rumped thornbills did not preferentially associate with either species.

Discussion

Australian thornbills are well-known members of MFS, and are often described as behaving in a tit-like fashion (referring to the classic flocking behaviour of the genus *Parus* which are not represented in the Australo-papuan avifauna, del Hoyo et al. 2007). We found that individuals associate non-randomly

Table 1 Species included in the study, including the number of uniquely colour-marked individuals and those satisfying minimum criteria for inclusion into the analysis. We also include the fundamental stratum for each species. White-throated treecreepers were restricted entirely to the trunk and main limbs of trees

Abbreviations	Species name	Scientific name	Marked	Analysis	Stratum
SCRO/SR	Scarlet robin	*Petroica boodang*	3	2	2
STTB/ST	Striated thornbill	*Acanthiza lineata*	15	13	3
BRTB/BR	Buff-rumped thornbill	*Acanthiza reguloides*	27	26	2
YRTB/YR	Yellow-rumped thornbill	*Acanthiza chrysorrhoa*	24	14	1
	Golden whistler	*Pachycephala pectoralis*	2	0	
SPWA/SW	Speckled warbler	*Chthonicola sagittatus*	4	4	1
WTTC/WT	White-throated treecreeper	*Cormobates leucophaea*	2	2	2
WEHE/WH	White-eared honeyeater	*Lichenostomus leucotis*	3	2	3

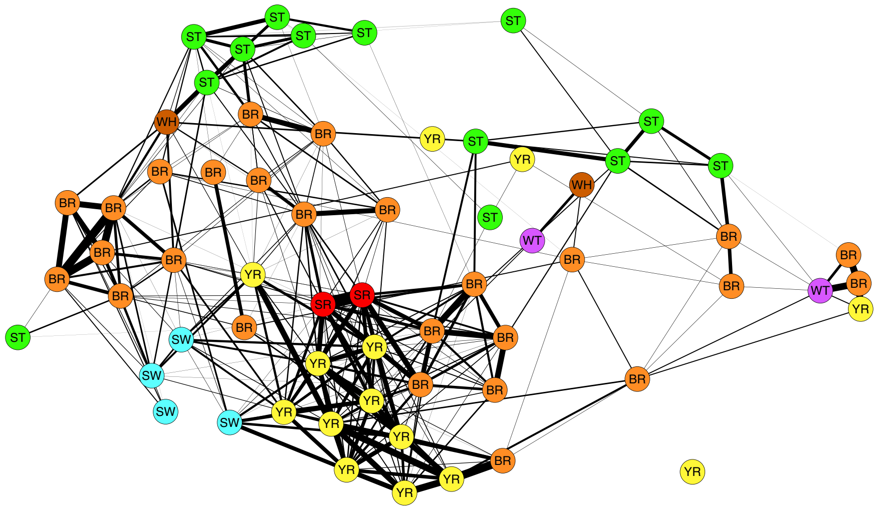

Fig. 2 Social network from the observation of colour-marked individuals shows significant mixing between heterospecifics based around a central cluster of strongly associating buff-rumped thornbills (*BR*), yellow-rumped thornbills (*YR*) and a pair of scarlet robins (*SR*). Nodes are colored according to species with weighted edges between nodes representing the rate of association (calculated using the simple ratio, see text). For visual clarity, the network is filtered to display only edges between individuals that associated more than 15 % of the time (edge densities are summarised in Fig. 3). Individual yellow-rumped thornbill in the lower-right was not isolated but was weakly associated to 15 others (maximum association strength was 0.09). See Table 1 for abbreviations

in MFS rather than mix evenly with all individuals in their range. Such non-random associations have been shown to provide important fitness benefits in group-living species (Krause et al. 2007) and may form the basis of cooperative alliances. For example non-randomly associating wild guppies were often found to cooperate during predator inspections (Croft et al. 2006). The social structure in the flocks we observed also suggests that individuals partake differentially in flocking behaviour. It is therefore unlikely that the species-level role paradigm accurately captures the range of behavioural participation of individuals in MFS (Hino 2000).

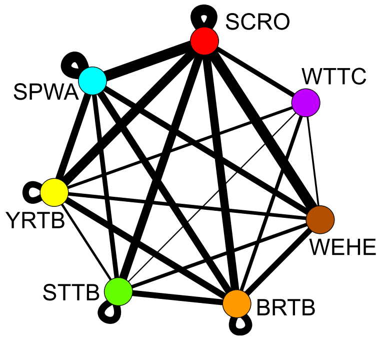

Fig. 3 Inter- and intra-specific edge densities highlight the low levels of associations between individuals with distant niches. Yellow-rumped thornbills (*YRTB*) fed on the ground, striated thornbills (*STTB*) in the crow and white-throated treecreepers (*WTTC*) exclusively on the trunks of trees. Scarlet robins (*SCRO*) and buff-rumped thornbills (*BRTB*), which showed the greatest flexibility in foraging niche, were densely connected with all species. White-throated treecreepers and white-eared honeyeaters (*WEHE*) had no intraspecific edges. Line width of scarlet robin with itself represents 100 % density. The high densities of interspecific links resulted in a very low value of species assortment (see text)

When conceptualizing living in mixed-species groups as a benefit/cost trade-off to individuals, it becomes clear that associating with known heterospecifics should provide greater positive benefits than with unknown random individuals. Our study clearly shows that such associations are present in avian MFS. There is also increasing evidence in the literature that complex interactions take place between individuals in MSFs, including interspecific communication (Goodale et al. 2010) and public information transfer (Schmidt et al. 2010). Communication may be used both for the initial formation of flocks (Goodale and Kotagama 2005b) or in alerting others of the presence of a predator (Goodale and Kotagama 2005a; Magrath et al. 2007; Schmidt et al. 2010). Thornbill flocks are highly vocal, which suggests that individuals can relax the need for being alert due to group vigilance. In this case, being familiar with the caller benefits the receiver, which can then assess the reliability of the signal when deciding how to react to it (Wascher et al. 2012). Evidence already exists that such behaviours occur at the species level (Goodale and Kotagama 2008; Magrath et al. 2009).

In addition, it is unlikely that all heterospecific associations provide equivalent benefits. Nor can one safely assume that all members of a species receive the same qualitative or

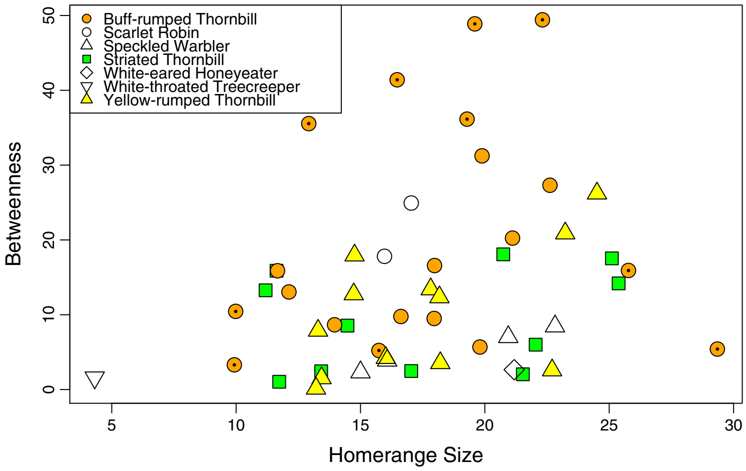

Fig. 4 Betweenness of individuals was not strongly correlated with home-range size (ha). Note that high within-species variation in betweenness, especially in the buff-rumped thornbill, almost entirely encompasses the variation across the entire set of individuals of the entire set of species. Female buff-rumped thornbills (*dotted orange spots*) showed two distinct strategies, high betweenness which indicates frequent swapping of groups, and low betweenness that indicates high group fidelity

quantitative benefits from heterospecific associations. We found that variation in betweenness among individual buff-rumped thornbills encompassed the entire spectrum of values across all individuals in all the species. Individuals of this species therefore participate in flocks in individually distinct ways. In this study, we found that the variation in betweenness within buff-rumped thornbills was almost as great as the population-wide variation. This indicates different participation by individuals of this species. Betweenness is a measure of between-individual connections, and high values can be interpreted to mean that those individuals are brokers of information or as potential spreaders of pathogens (Croft et al. 2008). In this study, the five individuals with the highest betweenness values were all females (Fig. 4), suggesting that social roles differ between the sexes. In their long-term study of buff-rumped thornbills, Bell and Ford (1986) found that young females would delay dispersing until immediately prior to the breeding season. That period coincided entirely with the time during which our study took place; thus the high betweenness observed here may represent female movement among different groups. On the other hand, males remain on or close to their natal territories, and therefore associate primarily with their parents and brothers. This strategy may be for social rather than foraging or predation benefits whereby young females are searching for potential territory openings and go beyond just the broad male–female dichotomy, to a much more individualized evidence of strategic considerations. Although we could not age individuals conclusively, all females with high betweenness were newly banded. If these were all juvenile birds, then social flocking could play an important role in female dispersal of cooperatively breeding species by allowing individuals from multiple family groups to interact non-agonistically. This strategy has been

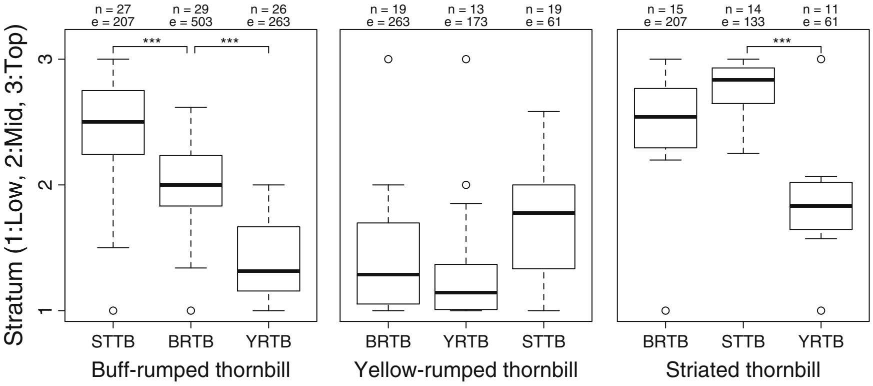

Fig. 5 Foraging strata of individuals was predicted by their social associates both within and between species. Note the full range of stratum expansion by buff-rumped thornbills (*BRTB*) compared to expansion only to the adjacent stratum in yellow-rumped (*YRTB*) and striated thornbills (*STTB*). We assigned values of 1 to 3 for low to high foraging heights, and generated a directed network with edge weights as the mean foraging height for observations of the focal individual with its associate. Significance scores (all $p<0.001$ where significant) were calculated using GLMs. Values of *n* represent the number of nodes of that type included in the analysis, and values of *e* represent the number of edges between the focal nodes and the associates (in the *left panel*, 29 BRTBs associated with 27 STTBs)

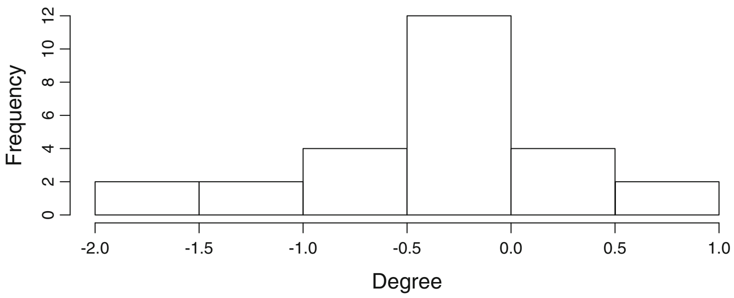

Fig. 6 Distribution of mean interspecific degree of buff-rumped thornbills. Positive values indicate individual preference for flocking with striated thornbills, whereas negative values indicate individual preference for flocking with yellow-rumped thornbills. Distribution of male and female interspecific degree does not significantly differ (Kruskal–Wallis χ^2=25, p=0.46). Thus, although female buff-rumped thornbills had higher betweenness than did males, indicating more inter-flock movements, the sexes did not differ in interspecific interactions, suggesting that for female buff-rumped thornbills a major consideration is the potential intraspecific social benefit, as well as, or instead of, any potential predation or foraging benefit gained from interspecific associations

observed in male house finches (*Carpodacus mexicanus*) where dispersing males that joined more groups had greater breeding success by finding the group where they had the highest relative sexual ornamentation (Oh and Badyaev 2010) and in male long-tailed manakins (*Chiroxiphia linearis*) that rose through the social ranks more successfully after long-term widespread associations (McDonald 2007). Whether individuals consistently vary in their network metrics throughout their lifetimes remains an open question in these species, but the presence of variation suggests individually tuned and perhaps learnt responses to the opportunities available in MSFs.

In order to participate in MFS, individuals may need to forage away from their preferred niche and shift structurally closer to heterospecifics. In doing so, they should suffer reduced foraging efficiency. One of the strengths of the network approach is that we were able to demonstrate that this was an active shift by individuals. Nevertheless, the question remains as to why this shift is generally much more prominent in the autumn and winter (Bell 1980). Bell and Ford (1986) found little difference in the seasonality of food resources of either striated or buff-rumped thornbills, or their close non-flocking relative the brown thornbill (*A. pusilla*). Thus, the primary benefit accrued is probably reduced predation risk from their main predator, the collared sparrowhawk (*Accipiter cirrocephalus*) at a time when the food resource is nonetheless depressed (Bell and Ford 1986). Furthermore, resource overlap can reduce fitness in coexisting species during the breeding season through increased predation (Martin 1996) thereby reducing the benefits of associating.

Alternatively, the literature widely reports benefits of mixed-species flocking that include niche expansion (Hino 1998; Zou et al. 2011) and subsequently increased foraging success (Hino 2000; Sridhar et al. 2009). Most authors suggest that foraging benefits are facilitated by existing niche overlap (Srinivasan et al. 2010; Hsieh and Chen 2011). In contrast, the study by Graves and Gotelli (1993) found that MFS were composed of fewer species with niche overlap than expected. This was supported by our data which showed little niche overlap yet strong associations between the three thornbill species in our study. Further, Valburg (1992) found that common bush-tanagers (*Chlorospingus ophthalmicus*) switched from a frugivorous diet when foraging in single-species flocks to an insectivorous diet whilst foraging with heterospecifics, indicating clearly non-overlapping niches. It therefore remains unclear whether foraging benefits arise simply as a by-product of reduced need for vigilance, or as a direct benefit the mixed-species flocking per se. If the benefits are a side product, then ground-feeding species should be unlikely to be found in canopy flocks as the cost of moving in terms of reduced foraging success would be prohibitive. In our study, yellow-rumped thornbills (high stratum foragers) rarely associated with striated thornbills (low stratum foragers). In contrast, the middle stratum foraging buff-rumped thornbills significantly shifted their niche with all their associates. Finally, the ability to shift niches whilst flocking is also limited when other individuals are already exploiting the target niche. The greater diversity of micro-habitats spatially close together (Hino 2002) may partly explain why flock diversity and association strength is often reported as being higher in the canopy than on the ground (Srinivasan et al. 2010). We predict that generalist species should be more frequent participants in MFS than specialist species, as their cost of foraging in a sub-optimal niche will be lower than for specialists.

Social networks provide a useful tool for exploring social interactions in groups and in this paper we have shown its application to exploring mixed-species flocking. This method provides quantitative measures for explaining individual decisions in associations, as well as for quantifying species-level behaviour. By showing considerable individual variation in social behaviour exists, we were able to make several predictions. In particular, we predict that MSF plays an important role in the dispersal ecology of juveniles from cooperative-breeding groups. The next step will be to derive a general framework for classifying individuals, rather than species, into flocking roles (as reviewed in Farley et al. 2008; Harrison and Whitehouse 2011) according to their social participation. Finally, it is becoming clear that MFSs are mutualistic interactions between heterospecific individuals, and future research should attempt to measure the impact of social decisions on individual fitness.

Ethical notes

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CHAPTER 4

Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges

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Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges

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ABSTRACT

Grouping is a very common outcome of selection that operates on individual animals. Largely considered to be driven by immediate benefits, such as avoiding predators, animal groups often consist of individuals that are phenotypically more similar than expected from the population distribution. This suggests that the distribution and fitness of phenotypes may be shaped by multiple levels of selection operating along different axes of behaviour. Thus, quantifying assortative mixing, or the measure of association between similar individuals in social networks, should be a key component of the biologist's toolbox. Yet, assortment is rarely tested in animal social networks. This may be driven by a lack of tools for robust estimation of assortment, given the reliance of current methods on binary networks. In this paper, I extend existing approaches that calculate the assortativity coefficient of both nominal classes and continuous traits to incorporate weighted associations. I have made these available through a new *R* package *assortnet*. I use simulated networks to show that weighted assortment coefficients are more robust than those calculated on binary network to added noise that could arise from random interactions or sampling errors. Finally, I demonstrate how these methods differ by applying them to two existing

social networks estimated from wild populations, exploring assortment by species, sex, and network degree. Given the parallel theoretical developments of the importance of local social structure on population processes, and increasing data on social networks being collected in free-living populations, understanding phenotypic assortment could yield significant insight on social evolution.

INTRODUCTION

Group-living is frequently considered to be an adaptive strategy primarily driven by ecological factors (Krause & Ruxton 2002). However, the fitness benefits accrued by individual participants may not just vary with group size, but also as a function of its phenotypic composition. For example, the predator confusion effect relies upon individuals being physically identical to other members of their group (Landeau & Terborgh 1986); that is they gain fitness benefits through being phenotypically assorted by size, shape and colour. Alternatively, individuals may reduce resource competition by associating with others that are specialised on different niches, which may lead to disassortment by species as seen in mixed-species foraging groups (Buskirk 1976). In this way, repeated non-random interactions between individuals of similar or different phenotypes (or genotypes) can have profound evolutionary implications (West-Eberhard 1979; Wolf et al. 1999).

Social network analysis is a quantitative approach that captures the emergent population-level properties of repeated interactions between individuals (Croft et al. 2008; Krause et al. 2007; Whitehead 1997, 2008). Numerous reviews have suggested that this method will provide an accessible way of estimating the evolutionary consequences of social processes (Croft et al. 2008; Farine et al. 2012; Krause et al. 2007; Wey et al. 2008). Yet, one of the simplest and most consequential social network measures, assortative mixing (Newman 2002a), has been relatively unexplored in animal behaviour, particularly outside of fishes (see Croft et al. 2012; Croft et al. 2009). This is surprising given that it is generally accepted that local social structure within populations can influence individual fitness (for example through indirect fitness, Hamilton 1964).

Assortment can arise either through active or passive processes. Active assortment typically arises from attraction of individuals to others that are similar. For example fish will often form shoals of similarly-sized fish both of single and multiple species (Hoare et al. 2000a; Hoare et al. 2000b; Krause et al. 2000), potentially for predator confusion (Krause & Ruxton 2002). Active attraction of behavioural phenotypes, such as degree assortment (strong connections between similarly gregarious individuals), is thought to be critical in mediating processes on networks such as the spread of disease (Ashby & Gupta 2013) or the evolution of cooperation (Pusch et al. 2008). Active avoidance may also occur, resulting in disassortment between interacting individuals. This is likely to be common in systems where, for example different classes, such as males and females preferentially associate together, as in Tasmanian devils (*Sarcophilus harrisii*) (Hamede et al. 2009). In contrast to active attraction, assortment can arise from passive processes such as differences in habitat use strategies. For example in some taxa it is common that individuals at different life stages occupy different niches, resulting in greater spatial overlap (therefore social association) between similar conspecifics (Holyoak et al. 2008).

A common method to measure assortment is the assortativity coefficient (Newman 2002a, 2003). This provides an index to measure whether associations are typically between phenotypically similar or dissimilar individuals. Although Newman's assortativity coefficient has been used in a number of studies (Aplin et al. 2013; Green et al. 2009; Hamede et al. 2009; Leu et al. 2010; Lusseau & Newman 2004; Lusseau et al. 2006; Manno 2008; Mourier et al. 2012; Wiszniewski et al. 2010; Wolf et al. 2007), its current restriction to binary networks may have hampered wider uptake in animal studies. This is potentially because association data in animal social networks is more frequently inferred (A was seen with B) than known (A directly interacted with B) as is more typical in human networks (Croft et al. 2011; Franks et al. 2010). As a result, this increases the relative influence of sampling error, or noise, in the data. Thus, binary network-based assortment measures could be under-estimating assortment in animal studies. For example, imagine a network where individuals found in stable groups of 6 always have the same 5 associates (they do not have an edge to themselves), and all have the same phenotype. If one sample randomly captures two groups together (either through observer error or otherwise), then each individual in these two groups will have 5 edges connected to associates of the same phenotype, and 6 connected to associates with a different phenotype. If both groups are sampled 50 times, then a weighted network will capture the fact that the proportion of edge weights to the non-similar phenotypes will be very low. In contrast, a binary network does not make this distinction. Consequently, rare chance events can have significantly greater influence on the perceived social structure in a binary network by being given the same weight as all other observed edges.

One approach that has been suggested for overcoming the limitations of binary networks, such as in the example described above, is to construct these after first thresholding (removing or setting to zero) edges above or below a certain value (James et al. 2009; Lusseau et al. 2008). In general, biologists typically repeatedly sample populations in order to infer the social network (Franks et al. 2010; Lusseau et al. 2008), hence thresholding is one way of maintaining some of the information contained in the edge weights which would otherwise be thrown away (Croft et al. 2011; Lusseau et al. 2008). The process to then convert networks to binary is generally by directly replacing non-zero edge values with one. For example, Newman's original assortativity coefficient is estimated based on the number of edges that occur between different classes or phenotypes. By counting edges of each type (where each edge adds 1 to the count), this process is functionally equivalent to having all edge weights converted to equal one.

In order to assess the biological importance of a network measure, it is important to specify a relevant null model (Gotelli & Graves 1996). Yet, it remains unclear what constitutes an appropriate method for building null models to assess the significance of the assortativity coefficient in an observed network. In most studies using Newman's assortativity coefficient, authors have reported the standard error calculated from jackknife simulations. However, Croft et al. (2011) highlighted the need for care to be taken when testing significance. They, and other authors (Bejder et al. 1998; Whitehead 1999; Whitehead et al. 2005), suggest that null models for social network should account for potential sampling biases and non-independence in the data. In the case of assortment, this suggests that it may be inappropriate to assume that the null expectation is a coefficient index of 0 if the sampling method could have introduced some biases. Here there are two generally accepted alternatives that can be used. The first approach for resolving this is a node-based permutation, where the association matrix is repeatedly randomised by shuffling the rows and columns whilst keeping the node labels fixed (for example in Aplin et al. 2013). The second method shuffles the data stream in order to control for individual gregariousness and group size distribution. Both these methods have been extensively described in the context of testing hypotheses for social networks (Bejder et al. 1998; Croft et al. 2011; Manly 1997; Whitehead 2008; Whitehead et al. 2005). However, they have rarely been compared using empirical data in the context of assortativity.

In this paper, I have the following aims: (i) to present a method to incorporate weighted network edges into the Newman (2003) assortativity coefficient. Although previously derived for continuous measures (Leung & Chau 2007), I extend the approach by also deriving the weighted-edge coefficient for nominal node values. To my knowledge, this method has never been used in animal social networks, so I developed an *R* (R Development Core Team 2013) package *assortnet* in order to promote its wider use. (ii) I then quantify the relative performance of the different approaches of calculating assortativity by assessing the robustness of using weighted, thresholded, and binary networks to sampling error. Using simulations, I show that indices incorporating weighted edges are significantly more robust to sampling noise than those using binary edges. (iii) Using networks from two recently published studies (Farine et al. 2012; Farine & Milburn 2013), I then investigate assortment according to different phenotypic traits and demonstrate how weighted and binary measures differ. Given the potential for random interactions to strongly influence binary network structure, I predicted that a weighted assortment measure is likely to provide a more robust estimate of assortment when compared to a binary assortment measure applied to the same network. (iv) Finally, I compare the three common approaches for testing significance in the assortment measure to determine if there are incompatibilities between these approaches.

METHODS

Incorporating edge-weight into assortment measures

Newman (2003) defined the assortativity coefficient for nominal classes of individuals as:

$$r_d = \frac{\sum_i e_{ii} - \sum_i a_i b_i}{1 - \sum_i a_i b_i} \quad (1)$$

where e represents a proportion of a particular type of edge in the overall network. e_{ii} is the count of the set of edges E_{ii} that occur within nodes of type i divided by the total number of edges M, such that $e_{ii} = M^{-1} \| E_{ii} \|$. The sum of e_{ii}

over all values of *i* ($\sum_i e_{ii}$) gives the total proportion of all the network edges that are within-class (assorted). $a_i = \sum_j e_{ij}$ is then the proportion of all edges that start at *i* (finishing at all possible types of node *j*), and $b_j = \sum_i e_{ij}$ is the proportion of all edges that end at *j* (starting at all possible types of node *i*). These values range between 0 and 1 and represent the proportions of each type of starting and finishing edge in the network, such that $\sum_{ij} e_{ij} = 1$ and $\sum_{ij} e_{ji} = 1$. If the network is fully assorted, then $\sum_i e_{ii} = 1$ and $\sum_i a_i b_i = 0$. This equation generates an assortativity value of r_d that ranges from 1 (fully assorted) to $0 > r_d \geq -1$, where the maximum negative value of a full-disassorted network tends towards zero as the number of classes increases (r_d = -1 for two fully-disassorted classes, -0.5 for three, -0.25 for four). The value for the different definitions of *r* that follow all have the same range. Although most applications of social networks in animals use undirected networks, here I present the assortativity coefficients for directed networks as these are the internal implementations in the *assortnet* package and are the most generalised form. In the case of undirected networks, the proportion of edges starting at *i* and arriving at *j* are reciprocal ($\sum_i e_{ij} = \sum_j e_{ij}$).

Calculating a weighted assortativity coefficient can be achieved by replacing the count of edges in Newman's discrete coefficient (shown as equation 1) with their weights as a proportion of the total weight of the graph. Here, each the proportion of edges that occur between nodes of class *i* ($e_{ii} = M^{-1}\|E_{ii}\|$) is replaced by a proportion of total edge weights that occur between these ($e_{ii}^{w} = W^{-1}\sum_i V_{ii}$). Here, W is the sum of all weights in the network and $\sum_i V_{ii}$ is the sum of the edge weights for the set of edges V_{ii} that connect nodes of type i, which ranges from zero to one. If all edge weights are equal to 1, then $W = M$ and $\sum_i V_{ii} = \|E_{ii}\|$ which replicates Newman's binary coefficient. These measures form the weighted binary assortativity coefficient r_d^w by substituting edge weights into equation 1:

$$r_d^w = \frac{\sum_i e_{ii}^w - \sum_i a_i^w b_i^w}{1 - \sum_i a_i^w b_i^w} \quad (2)$$

where e_{ii}^w is the proportion of the total network edge weights that occur within nodes of type i, $a_i^w = \sum_j e_{ij}^w$ is the proportion of the total edge weight that starts at nodes of type i, and $b_j^w = \sum_i e_{ij}^w$ is the proportion of the total edge weight that arrives at nodes of type j. In a fully-assorted network, $\sum_i e_{ii}^w = 1$ and $\sum_i a_i^w b_i^w = 0$.

For continuous measures of phenotypes, such as size or network degree, Newman (2003) proposed using the Pearson correlation coefficient:

$$r_c = \frac{\sum_{xy} xy(e_{xy} - a_x b_y)}{\sigma_a \sigma_b} \quad (3)$$

where a_x and b_y are the fraction of edges that start and end at nodes with values x and y, and σ_a and σ_b are the standard deviations of a_x and b_y. Equation 3 can be re-written in a form that is useful for calculating the assortativity coefficient in social networks (as given in Newman 2003):

$$r_c = \frac{\sum_i (j_i k_i) - M^{-1} \sum_i j_i \sum_{i'} k_{i'}}{\sqrt{\left[\sum_i j_i^2 - M^{-1} \left(\sum_i j_i\right)^2\right]\left[\sum_i k_i^2 - M^{-1} \left(\sum_i k_i\right)^2\right]}} \quad (4)$$

where j_i and k_i are the phenotypic values (such as degree or size) for the incoming and outgoing nodes connected to each observed edge i in the network, and M is the total number of edges.

To derive a weighted version of the continuous assortativity coefficient, Leung and Chau (2007) propose using the same process as I gave in the nominal coefficient above. For example, the average value of the phenotypes of individual n's associates (given by $k_{ni} = \frac{1}{m_n} \sum_{i \epsilon \Gamma(n)} k_i$, where m_n is the degree of n) can be replaced by the weighted average of its neighbouring nodes (given by $k_{ni} = \frac{1}{w_n} \sum_{i \epsilon \Gamma(n)} \omega_{ni} k_i$, where ω_{ni} is edge weight between the focal individual n and individual i, and w_n is the sum of weights of all edges $\Gamma(n)$ that are connected to n). Using this same process, the interaction between phenotypes in equation 4 can be scaled by the weight of the edge connecting them, giving:

$$r_c^w = \frac{\sum_i (\omega_i j_i k_i) - W^{-1} \sum_i (\omega_i j_i) \sum_{i'} \left(\omega_{i'} k_{i'}\right)}{\sqrt{\left[\sum_i \left(\omega_i j_i^2\right) - W^{-1} \sum_i (\omega_i j_i)^2\right]\left[\sum_i \left(\omega_i k_i^2\right) - W^{-1} \sum_i (\omega_i k_i)^2\right]}} \quad (5)$$

where j_i and k_i are the phenotype of nodes that edge i leads into and out of respectively, ω_i is the weight of edge i, and W is the sum of all edge weights. Equation 5 functionally equivalent to equation 15 in Leung and Chau (2007) but given in a more readable format. As with the nominal assortativity coefficient, assortment in a network where all edges have a weight of $\omega_i = 1$ will give the same result as Newman's binary measure for continuous traits (and W is equal to the count of edges M).

I have implemented these methods in the *R* package *assortnet* that contains the functions *assortment.discrete* and *assortment.continuous*. Both take the same five arguments: (1) the network as an association matrix, (2) the phenotype values of each node, (3) a flag to define if weighted edges should be used or to automatically make the network edges binary (the latter giving the same results as the original definitions of the assortativity coefficients r_d and r_c), (4) a flag to calculate the standard error of the assortativity coefficient using a jackknife simulation (Efron & Tibshirani 1994), and (5) a grouping size for the jackknife simulations. This grouping size parameter M removes n edges (as mutually-exclusive groups such that each edge is contained in just one group) at once in order to speed up simulations for very large networks (Efron & Tibshirani 1994). Ideally, M should not be less than one hundredth of the number of edges. This package is available from my website (https://sites.google.com/site/drfarine/r-packages/assortnet), and can directly interface directly with other network libraries in *R*.

Assessing robustness

In order to compare the robustness of the binary, thresholded binary, and weighted assortativity coefficients to random interactions, I created a simple simulation that cumulatively introduced random edges into networks of 10, 50 and 100 individuals (nodes). In each simulation, I created a base network that was fully assorted (r = 1) by allocating edges to individuals of the same class or with the same phenotype with values randomly drawn from a Poisson distribution with a mean of 0.3 (range 0 to 0.8). The mean is equivalent to two individuals being each observed 10 times and each dyad associating on average 4.5 times if using the simple ratio index. It is worth noting here that the assortativity coefficient is not influenced by global network structure. At each simulation step, one dyad consisting of any two individuals was randomly selected and the edge value increased by a value between 0.01 and 0.1 drawn from a uniform distribution. After each step, I recalculated the assortativity coefficient, setting the function flag to calculate either the weighted or binary assortativity index, and using a threshold of 0.2 (or twice the maximum random value) for the thresholded network. Because the same networks were used for calculating all three assortment measures, the results of these simulations are directly comparable.

Simulations were then repeated 100 times for each network size with 2 different nominal classes, and 10 different values of a continuous phenotype. Simulations ran 200, 1200 and 4900 times for 10, 50, 100 nodes respectively. This represents an additional 100%, 50% and 20% of the missing initial observations. For example 10 nodes of 2 types started with 20 edges present, and 20 edges missing (between non-associated types), each of which could have been observed 10 times. This process resulted in an addition of approximately 100%, 50% and 20% of the original weight being added to the network in total, but now distributed randomly across all edges. In the supplementary materials, I show that these results are consistent for both a greater number of nominal classes and a greater number of different phenotypic values.

Assortment in animal networks

I calculated both the weighted and binary assortativity coefficients for networks from two previously published studies in order to explore assortative mixing by degree, sex, species, and foraging location in cooperatively-breeding thornbills (*Acanthiza spp.*, see Table 1) and tits (family *Paridae*, see Table S1). Firstly, I repeated the species assortment calculation from Farine and Milburn (2013) using weighted edges, calculated assortment by foraging location (in this case strata, or height from the ground) to test if the methods could detect the spatial assortment by foraging preferences reported in the study, and tested for any sex assortment within the most common species (buff-rumped thornbill, *Acanthiza reguloides*). Second, I tested for species and sex-level assortment in mixed-species social network published by Farine et al. (2012) that is contained within the *R* package *asnipe* (Farine 2013). Given theory suggesting that degree assortment is important for flow dynamics (Ashby & Gupta 2013; Newman 2003), I also calculate assortative mixing by degree in these two networks. Although I have no biological justification for introducing a threshold (see Discussion), I provide a comparison of the performance of thresholded networks with the binary and weighted assortativity coefficients in a supplementary table. Here, I thresholded the binary network at the mean non-zero edge weight (Croft et al. 2008) prior to re-calculating the binary assortativity coefficient.

Significance testing

I used two permutation methods for calculating the significance of the observed assortment value. Permutation tests create a posterior distribution against which a measure can be assessed by randomising the original data. This process is important as the observations of interacting individuals are typically not independent from each other, therefore violating the assumptions in most parametric statistical tests (Bejder et al. 1998). The first method involves randomising the relationships between the nodes and the phenotypic characteristic. I compared the observed assortment value with 1000 networks where the phenotypic value of the nodes were randomised while maintaining the edge structure of the network. Significance using the node permutation method (P_n) was calculated as the proportion of randomised values that were larger than the observed in the case of assortment and more negative than the observed in the case of disassortment. The second permutation method randomises the observations of individuals between groups in the original data stream. Each step in the randomisation selects two individuals from different groups and swaps their observations, thereby keeping constant the number of observations for each individual and the distribution of group sizes (Manly 1997). Following suggestions by several authors (Sundaresan et al. 2009; Whitehead 1999, 2008; Whitehead et al. 2005), I restricted these swaps to pairs of individuals from groups that were observed in the same location on the same day. This is a conservative null model because it includes any social behaviour implied by the choice of a given location on a given date is controlled for. Significance using the data stream method (P_d) was also calculated by comparing the observed value to the distribution of randomised association coefficients. In all cases, I also reported the standard error of the assortativity coefficient calculated using the jackknife method as described by Newman (2003).

RESULTS

Simulating noise in assorted networks

Weighted edges significantly reduced the impact of random associations on a perfectly assorted network when compared to either a binary or a thresholded binary network (Figure 1, Supplementary figures S1-S3). In most cases, the assortativity coefficient using a binary network dropped below 0.5 very rapidly, even when few additional edges were added (for example Figure S3a drops below 0.5 at approximately 0.15, which represents an increase in density from 0.6 to 0.8 in Figure S4a). This suggests that a large amount of information and robustness was lost when edge weights are discarded (Croft et al. 2008). Thresholded binary networks generally provided an improvement on a non-thresholded network. However these improvements are only valid under the assumption that there should be a strong dichotomy in the edge weights of within- and between-class nodes (that is, where the real network is in a state that is close to the left-hand side of the plots in Figure 1). In contrast, the weighted network coefficient performed robustly even when noise was added to mixed networks showing some assortment (for example when the real network is somewhere in the middle of each plot).

Assortment in mixed-species flocks of thornbills

Farine and Milburn (2013) observed 4098 co-occurrences between 63 colour-marked individuals. These individuals were made up of seven species participating in mixed-species flocks in Australia (see Table 1). Using these co-occurrences, they calculated the association between individuals with the simple ratio index. This describes the proportion of times the individuals were seen together as a function of their combined number of observations (Whitehead 2008).

As part of that study, the authors reported a non-significant value of assortment by species, suggesting random mixing (r_d = 0.013±0.016). However, examining the mixing matrix (Table 1) shows that approximately 20% of all edges occurred between buff-rumped thornbills, and the node-based and data-stream permutations both suggested that assortment was greater than expected in randomised networks using the binary coefficient (P_n < 0.001, P_d < 0.001). The assortativity coefficient calculated using weighted edges more appropriately reflects this (r_d^w = 0.122±0.018), and both permutation tests using the weighted coefficient are highly significant (P_n < 0.001, P_d < 0.001). The mixing matrix by edge weight (Table 2) is significantly correlated to the mixing matrix from the binary method (mantel test: Z=0.065, P < 0.01), which suggests that the weighted edge method was better at extracting the true value in this population.

I extended the results from Farine and Milburn (2013) to examine assortment by sex in the most common species from that study, the cooperatively-breeding buff-rumped thornbill. Both the binary and weighted methods estimated a slight trend for disassortment by sex, where males and females associate more strongly than within-sex ties (r_d = -0.088±0.038; r_d^w = -0.082±0.049). The tendency towards disassortment is perhaps not unexpected in cooperatively-breeding groups if groups frequently consist of two males and only one female. This is because triads have a unique property of having more between-class edges (two M-F edges) compared to within-class edges (one M-M edge). Both permutation tests were significant for the binary coefficient (P_n = 0.012, P_d = 0.029) and whereas using the weighted-edge coefficient suggested no significant disassortment (P_n = 0.324, P_d = 0.084).

One application of the assortativity coefficient is to determine if individuals are assorted due to geographic or habitat-use overlap. The study by Farine and Milburn (2013) recorded the location in habitat when recording co-occurrences, and found that there was significant non-randomness in the location where associations took place. Thus, a useful test of the assortativity coefficient is whether it can detect spatial patterns of assortment without information about the location of interactions. I assigned a values ranging from 1 (low) to 3 (high) to each of the three thornbill species based on their preferred foraging height when not associating in mixed-species flocks as reported in Figure 5 of Farine and Milburn (2013). I found strong support for assortment according to preferred foraging locations, both in the binary (r_c = 0.113±0.016; P_n < 0.001, P_d < 0.001) and the weighted-edge coefficient (r_c^w = 0.296±0.018; P_n < 0.001, P_d < 0.001). Thus, the assortativity coefficient successfully identified that individuals were more strongly connected to others with foraging preference that were more similar than expected by chance. Further, the weighted-edge measure was much larger and provided much stronger (threefold) support for this result.

Finally, I tested for assortment by degree in the mixed-species network of thornbills and associated species. Leung and Chau (2007) suggest that this important network property may be most prone to biases introduced by measuring binary rather than weighted assortativity, and I found strong disparity between the binary and weighted measures. The binary assortativity coefficient suggested that this network tended towards disassortment by degree (r_c = -0.051±0.022; P_n = 0.610, P_d = 0.010). In contrast, the weighted-edge coefficient found significant assortment (r_c^w = 0.256±0.067; P_n = 0.007, P_d = 0.000). Leung and Chau (2007) propose that this difference could arise due to highest probability of observing new edges being between high degree nodes and low degree nodes, and the resulting difference in the influence of this edge in weighted (where it will have a small value) and binary networks.

Assortment in mixed-species flocks of tits

Farine et al. (2012) described a social network consisting of four tit species (great tit *Parus major*, blue tit *Cyanistes caeruleus*, marsh tit *Poecile palustris*, coal tit *Periparus ater*) and Eurasian nuthatches (*Sitta europaea*). Individuals in this population were fitted with passive integrated transponder (PIT) tags, and associations inferred by their co-occurrences when detected at automated feeding stations. They detected 234295 visits by 272 individuals over four weeks, and used the simple ratio index to define the association matrix in this network.

Analysing the assortment by species in the tit network found differences between the weighted and binary measures. The binary assortativity coefficient suggested a very mixed network (r_d = -0.003±0.002), and permutation tests suggested that this effect was either not different from random, or significantly more disassorted than expected according to the node-based test (P_n < 0.001, P_d = 0.657). However, as with the thornbill network, the distribution of edges fell heavily within species (Table A1). Over 40% of all edges occurring within species, which is much higher than expected given the ratio of intraspecific to interspecific edge types. As a result, the weighted-edge assortativity coefficient (Table A2), showed weak but significant assortment by species (r_d^w = 0.034±0.003), supported by both permutation tests (P_n < 0.001, P_d = 0.007). This suggests that the weighted edge method was more robust in detecting these patterns.

All species in this study consisted of birds that breed in socially monogamous pairs, and unsurprisingly there was strong evidence for disassortment by sex within species (Table 3), though this appeared to be influenced by the ecology of each species. Blue and great tits form a large component of these mixed-species flocks and are considered to have a more fission-fusion social dynamics. These two species showed much weaker effects, with blue tits having no significant disassortment by sex. In contrast, the three species that maintain more stable pair bonds over winter (coal tit, *Periparus ater*; marsh tit, *Poecile palustris*;

Nuthatch, *Sitta europaea*), all had very strong mixing between sexes. In the case of coal tits and nuthatches, their edges were entirely constrained to dyads of different sexes.

Given the importance of resource discovery for winter survival (Farine & Lang 2013), individuals in mixed species flocks should maximise their associations to individuals with a high degree that would promote rapid diffusion of information (Aplin et al. 2012; Farine & Lang 2013). Highly connected or central nodes are thought to play a disproportionate effect on socially-mediated transmission, at least in humans (Lloyd & May 2001; Newman 2002b), and previous work in this population has shown that central individual had a higher probability of discovering novel foraging patches (Aplin et al. 2012). Here, both the binary (r_c = 0.108±0.005; P_n < 0.001, P_d = 0.001) and weighted-edge (r_c^w = 0.298±0.005; P_n < 0.001, P_d = 0.001) coefficients suggest that tits show positive assortment by network degree. Although in this case the binary coefficient reported significant assortment (unlike in the thornbills), the weighted-edge coefficient was three times larger, suggesting that this pattern of association may be more difficult to detect using binary networks.

DISCUSSION

Incorporating weighted measures of dyadic associations resulted in much more robust estimates of assortment. This approach is equivalent to changing the assortativity coefficient from being a measure of the number edges that occur between different phenotypes in the network, to being a measure that describes the proportion of interactions that occur between these phenotypes. As I demonstrated through the use of simulations, this has the effect of reducing the impact of sampling errors, random interactions, or weak associations when estimating assortment.

In the analysis of phenotypic assortment in networks of wild birds, I have shown examples where a binary assortativity coefficient has failed to detect a pattern that was previously known to occur. By analysing the foraging height of different species in the network, Farine and Milburn (2013) found that species with closer foraging niches were more likely to be observed associating. This was confirmed using the weighted assortativity coefficient on the same network. However, the binary coefficient not only failed to detect the observed pattern, but suggested these species may be disassorted by niche. In this case, using binary assortment could have radically changed our biological interpretations of social structure. For example Lusseau and Newman (2004) concluded that dolphin social networks differ from those in humans as they did not find assortative mixing by degree. This, in turn, can lead to very different conclusions about selective pressures operating in animal populations.

A difference in the results of binary and weighted coefficient results could suggest that active rather than passive mechanisms are driving assortment in these networks. If individuals are assorted according to niche differentiation (passive), then there may be less opportunities for random or casual associations between different phenotypes, and the binary and weighted assortativity coefficients should closely match. In contrast, active associations may lead to a greater potential for mixing. For example, when two flocks temporarily forage nearby as with the thornbill example from above (Farine & Milburn 2013). In these species, flocks would occasionally contain all three species when groups converged upon an area, and hence edges were formed between high-level foraging striated thornbills and ground-foraging yellow-rumped thornbills.

One recurring challenge for analysing animal social networks has been assessing the significance of observed trends (Croft et al. 2011). Typically, this arises from a lack of a defined null, which describes the expected pattern under a model of random association, for the population under study. The assortativity coefficient partially circumvents this problem as it provides a null model of random mixing ($r = 0$). However, the relationship between this null model and randomisations have not been tested previously. In this study, I reported both the data stream and node permutation approaches to estimating significances alongside the standard error. In almost every case, there was agreement between node permutations and data stream permutations. Permutation tests also agreed with the standard error; a standard error of approximately half the observed value concurred with marginal significance from permutation tests. The only exception occurred when the assortativity coefficient was close to 0, in which case the biological relevance of the randomisations should be interpreted with caution. Together, these findings, albeit from a limited range of scenarios, suggest that any of the three methods are sufficient if they give strong support for rejecting the null hypothesis.

Although this paper describes a method for estimating the assortativity coefficient using weighted networks, two previous approaches have been used to circumvent the issues of binary networks in measuring assortment. The first compared the distribution of edges in the observed network after filtering out weak or strong edges with networks derived from permutations of the original data (Croft et al. 2012; Croft et al. 2005; Croft et al. 2009). If a greater proportion of edges of large weight between particular types of nodes were present in the observed compared to the random networks, then the network was considered to be assorted.

In order to assess the relative robustness of using a threshold, I calculated the assortativity coefficient after thresholding each network (Table A3). I found that although thresholding generally gave intermediate results between the other two methods, it may also be inconsistent with binary and weighted measures. For example, both binary and weighted networks reported strong assortment by degree in tits and nuthatches, whereas the threshold measure gave inconclusive results. This highlights one issue with thresholding in assortment, that the sum of weak edges may contribute to overall assortment. This could be important in studies that focus on phenotypic, rather than individual, interactions. By obscuring biologically-relevant variation in network ties, thresholding can also cause substantial changes in the structure of the network (Butts 2009). In the assortment example given by Croft et al. (2011), the authors found that thresholding a network could generate both type I and type II errors as a result of this. Finally, given that different threshold values can generate different results (Butts 2009; Langer et al. 2013), one severe limitation of the method is that the value can easily be manipulated in order to obtain the most optimal p-value (Langer et al. 2013).

An alternative method for measuring assortment in social networks uses Mantel tests to compare the independent similarity matrix (phenotypic characteristic) with the observed edge weights in the observed association matrix (Wey et al. 2008; Wiszniewski et al. 2010). Although this approach could potentially be combined with Quadratic Assignment Procedures (QAP, Krackhardt 1988), it has a more limiting framework on which to build null models as there is no established method for performing data stream randomisations with QAP. In contrast to these methods, the assortativity coefficient has been fully derived (from the Pearson correlation coefficient), and provides a measure that is comparable between systems. Importantly, the assortativity coefficient may be one of the few network measures to date that can be used in synthesis or comparative studies.

In this study, I have shown that measuring the assortativity coefficient in social networks is a powerful approach for describing the social structure of populations. But are there any contexts in which a binary measure might be preferred over a weighted one? Croft et al. (2011) suggest that weighted networks are the gold standard for analysis, and the results from this study suggest that the weighted assortativity coefficient is the most robust. However, many questions are focused on events that might occur from single contacts, particular those related to transmission and other association-based processes. In these cases, it may be important to consider what social process(es) the network is describing and how these relate to the question. In general social networks represent the probabilities of dyadic associations; i.e. what is the chance of a dyad being observed co-occurring? Further, animal networks are rarely continuously sampled in time. This can lead to some uncertainty that dyads with no edge are true zeros (Croft et al. 2011), or that weak edges are unimportant (Butts 2009), thereby limiting the usefulness of a binary and thresholded networks respectively. Thus, the weighted assortativity coefficient will usually be more appropriate unless the network has low uncertainty. However as I have shown above, using a combination of the two measures may be an informative way to isolate different mechanisms that could lead to assortment.

In conclusion, I have provided a new tool for calculating assortativity in social networks using weighted edges that has been implemented in an *R* package. I have also shown that this method is significantly more robust than the existing approaches using binary networks. Broader exploration of assortative mixing in social networks may be a useful approach for quantifying interactions between phenotypes. This may in turn provide an important component for estimating the strength and direction of selection arising from the social environment.

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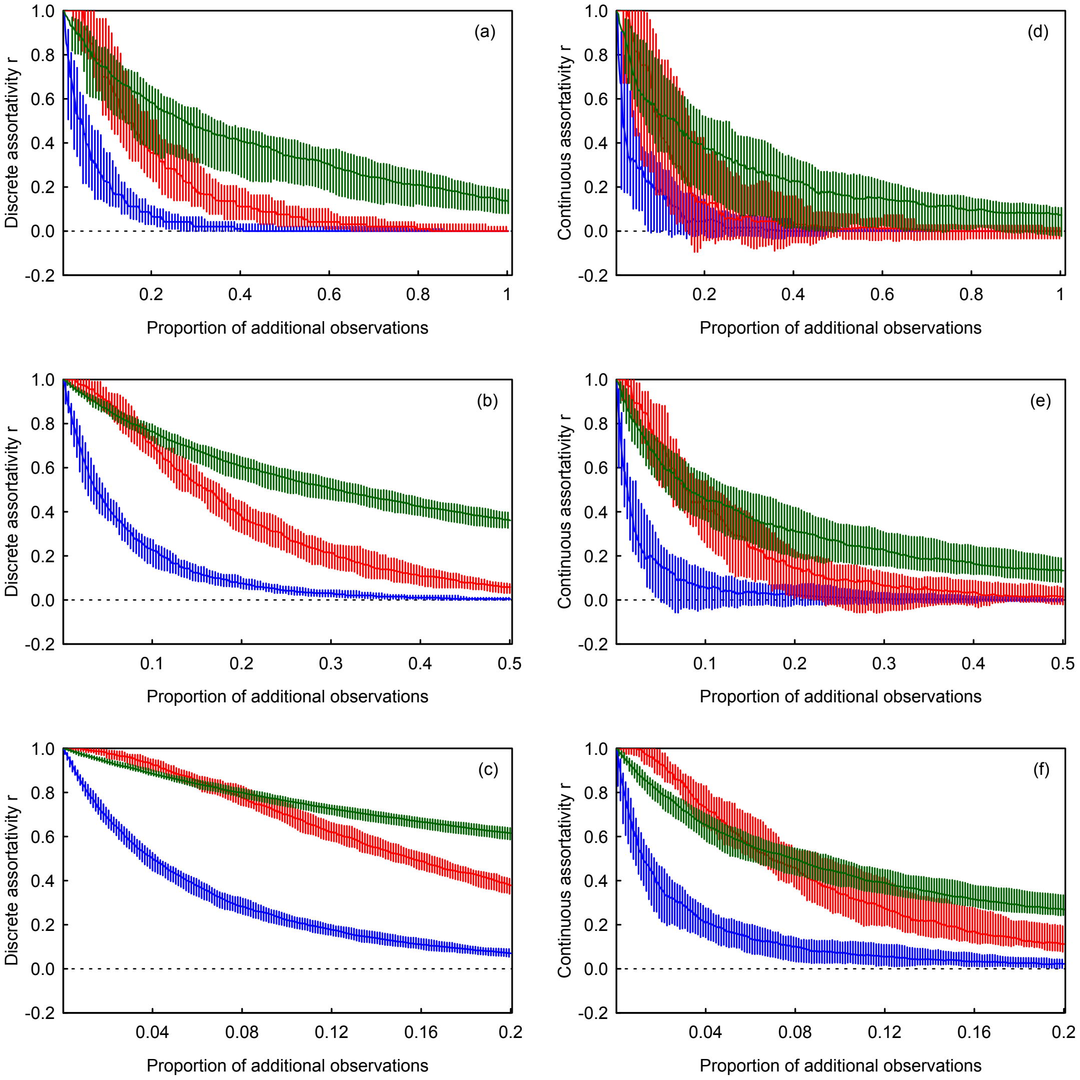
FIGURE

Figure 1. Effect of increasing random associations between (a-c) two discrete categories or classes of individuals, and (d-f) individuals with different 10 possible phenotypic values along a continuum. Figures S1-S3 show the relationships above have very little spread when more classes are added. Each simulation had 10, 50 or 100 individuals, and was run 100 times. Simulations commutatively introduced 200, 1200 and 4900 interactions between random dyads that represented an additional 100%, 50%, and 20% observations in the data. The assortativity coefficient was recalculated after each additional observation (starting at r = 1, or fully assorted). The network in each step was then analysed using binary (blue lines), thresholded binary (set at 0.2, red lines) or weighted (green lines) assortiativity coefficients. The 95% confidence intervals from the simulations are shown by the vertical lines. The network is fully connected when the binary assortment r = 0 (blue line), and the relationship between the number of added observations and network edge density (connectedness) is shown in Figure S4.


(a)
(b)
(c)
(d)
(e)
(f)
Discrete assortativity r
Continuous assortativity r
Proportion of additional observations
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
0.2
0.4
0.6
0.8
1
0.1
0.2
0.3
0.4
0.5
0.04
0.08
0.12
0.16
0.2

TABLES

Table 1. Mixing matrix for binary assortment by species in thornbills and associates.

	SCRO	STTB	BRTB	YRTB	SPWA	WTTC	WEHE	a_i
SCRO	0.001	-	-	-	-	-	-	0.044
STTB	0.009	0.046	-	-	-	-	-	0.182
BRTB	0.018	0.084	0.195	-	-	-	-	0.449
YRTB	0.011	0.025	0.100	0.05	-	-	-	0.212
SPWA	0.003	0.011	0.031	0.017	0.005	-	-	0.069
WTTC	0.001	0.003	0.008	0.004	0.000	0.000	-	0.017
WEHE	0.002	0.005	0.013	0.005	0.002	0.000	0.000	0.027
b_i	0.044	0.182	0.449	0.212	0.069	0.017	0.027	1.000

Mixing matrix for assortment in seven species from Farine and Milburn (2013) showing the distribution of edges between each species using the binary network. Values in cells represent the proportion of edges that correspond to edges between different types of nodes; a_i are the row sums, b_i the column sums (table is symmetric but only half of values are shown). Species abbreviations are: SCRO: scarlet robin (*Petroica boodang*); STTB: striated thornbill (*Acanthiza lineata*); BRTB: buff-rumped thornbill (*Acanthiza reguloides*); YRTB: yellow-rumped thornbill (*Acanthiza chrysorrhoa*); SPWA: speckled warbler (*Pyrrholaemus sagittatus*); WTTC: white-throated treecreeper (*Cormobates leucophaea*); and WEHE: white-eared honeyeater (*Lichenostomus leucotis*).

Table 2. Mixing matrix for weighted assortment by species in thornbills and associates.

	SCRO	STTB	BRTB	YRTB	SPWA	WTTC	WEHE	a_i^w
SCRO	0.005	-	-	-	-	-	-	0.058
STTB	0.006	0.058	-	-	-	-	-	0.157
BRTB	0.023	0.064	0.204	-	-	-	-	0.432
YRTB	0.018	0.015	0.093	0.097	-	-	-	0.250
SPWA	0.003	0.006	0.028	0.020	0.005	-	-	0.063
WTTC	0.001	0.002	0.008	0.004	0.000	0.000	-	0.016
WEHE	0.001	0.006	0.012	0.003	0.001	0.001	0.000	0.024
b_i^w	0.058	0.157	0.432	0.25	0.063	0.016	0.024	1.000

Mixing matrix for assortment in seven species from Farine and Milburn (2013) showing the distribution of edge weights (% of total weight) between each species using from the weighted network (species are per Table 1). The table is symmetric, therefore only half the values are shown.

Table 3. Binary and weighted assortment by sex in tits and nuthatches.

	r_d	SE	P_n	P_d	r_d^w	SE	P_n	P_d
Blue tit	**-0.039**	0.010	**0.047**	**0.001**	-0.033	0.014	0.298	0.245
Great tit	-0.013	0.010	0.550	0.254	**-0.053**	0.014	**0.041**	**0.010**
Coal tit	**-1.000**	0.707	**0.000**	**0.000**	**-1.000**	0.707	**0.000**	**0.000**
Marsh tit	**-0.194**	0.047	0.070	**0.014**	**-0.489**	0.053	**0.001**	**0.045**
Nuthatch	**-1.000**	0.707	**0.000**	**0.000**	**-1.000**	0.707	**0.000**	**1.000**

Binary (r_d) and weighted (r_d^w) assortativity coefficients within sex within species of species in Farine et al. (2012). Standard error (SE) and significance from node (P_n) and data stream (P_d) are given for each coefficient. Values in bold indicate significance.

SUPPLEMENTARY FIGURES

Figure S1: The effect of increasing random associations between (a-c) 2 to 10 different nominal classes, and (d-f) 10 to 30 different continuous phenotypic values, when using the binary assortativity coefficient. The methods are identical to the blue line in Figure 1 (representing 2 nominal classes and 10 continuous values). The values for Figure 1 are the top-most line, with increasing number of classes/values shifting the line downwards.

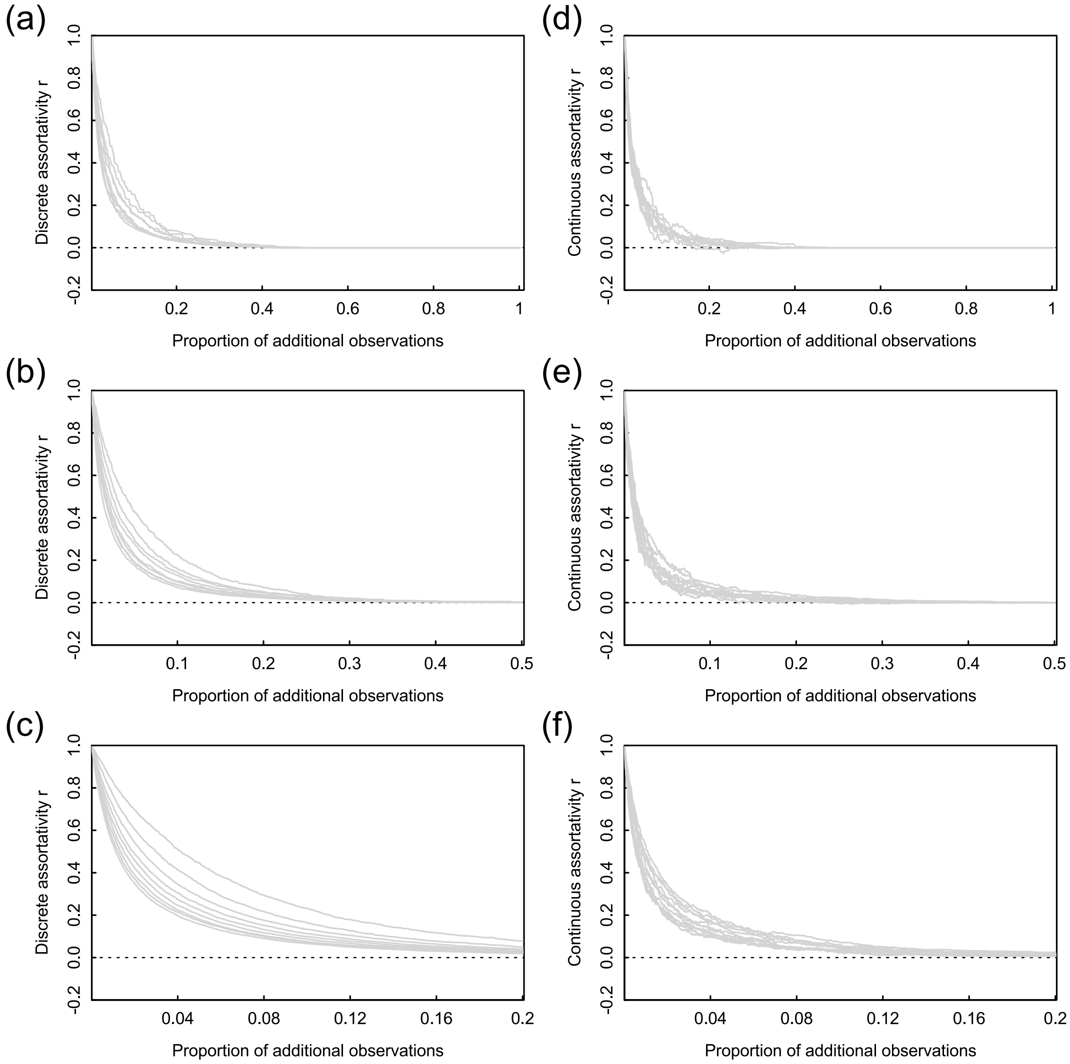


Figure S2: The effect of increasing random associations between (a-c) 2 to 10 different nominal classes, and (d-f) 10 to 30 different continuous phenotypic values, when using the thresholded binary assortativity coefficient. The methods are identical to the red line in Figure 1 (representing 2 nominal classes and 10 continuous values). The values for Figure 1 are the top-most line, with increasing number of classes/values shifting the line downwards.

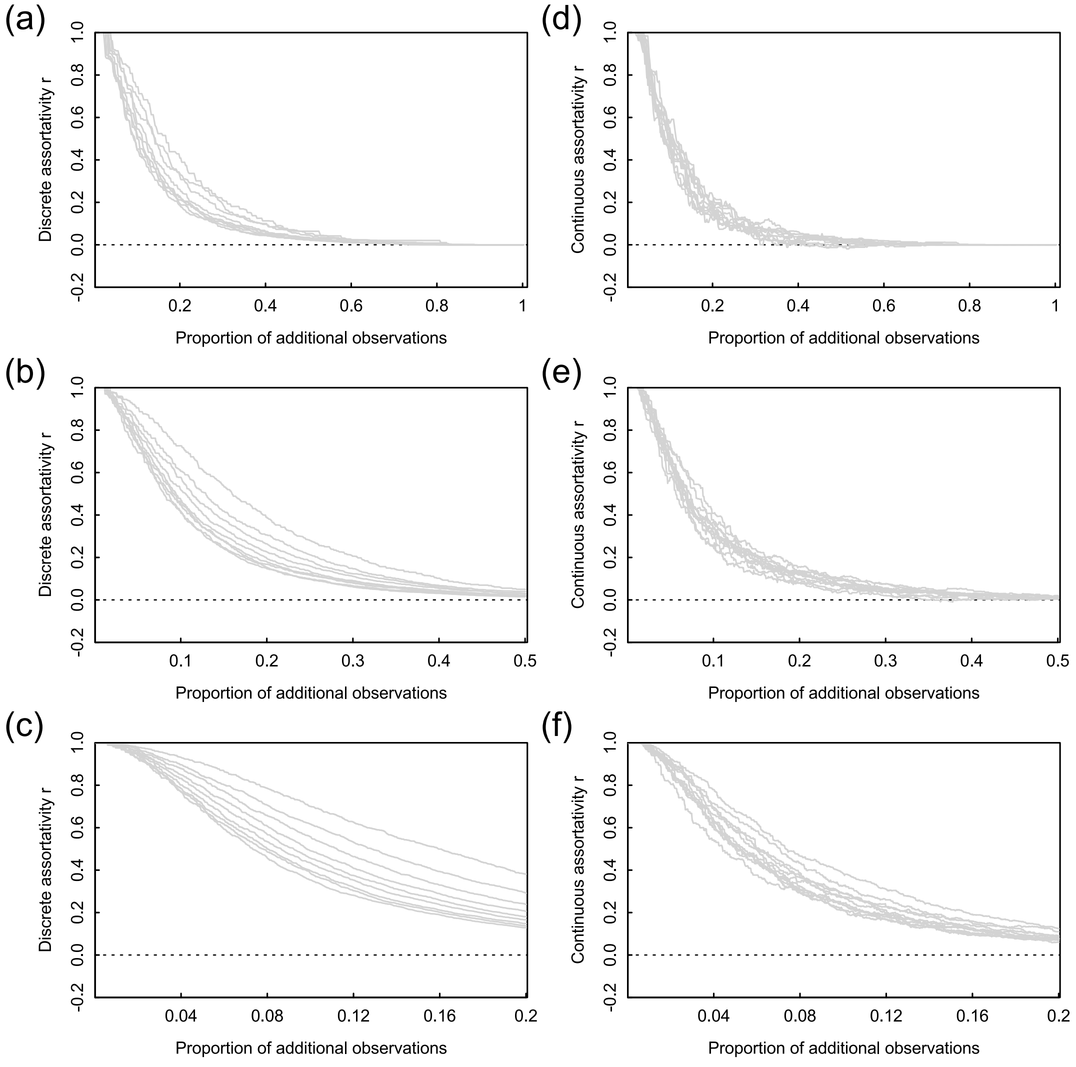


Figure S3: The effect of increasing random associations between (a-c) 2 to 10 different nominal classes, and (d-f) 10 to 30 different continuous phenotypic values, when using the weighted assortativity coefficient. The methods are identical to the green line in Figure 1 (representing 2 nominal classes and 10 continuous values). The values for Figure 1 are the top-most line, with increasing number of classes/values shifting the line downwards.

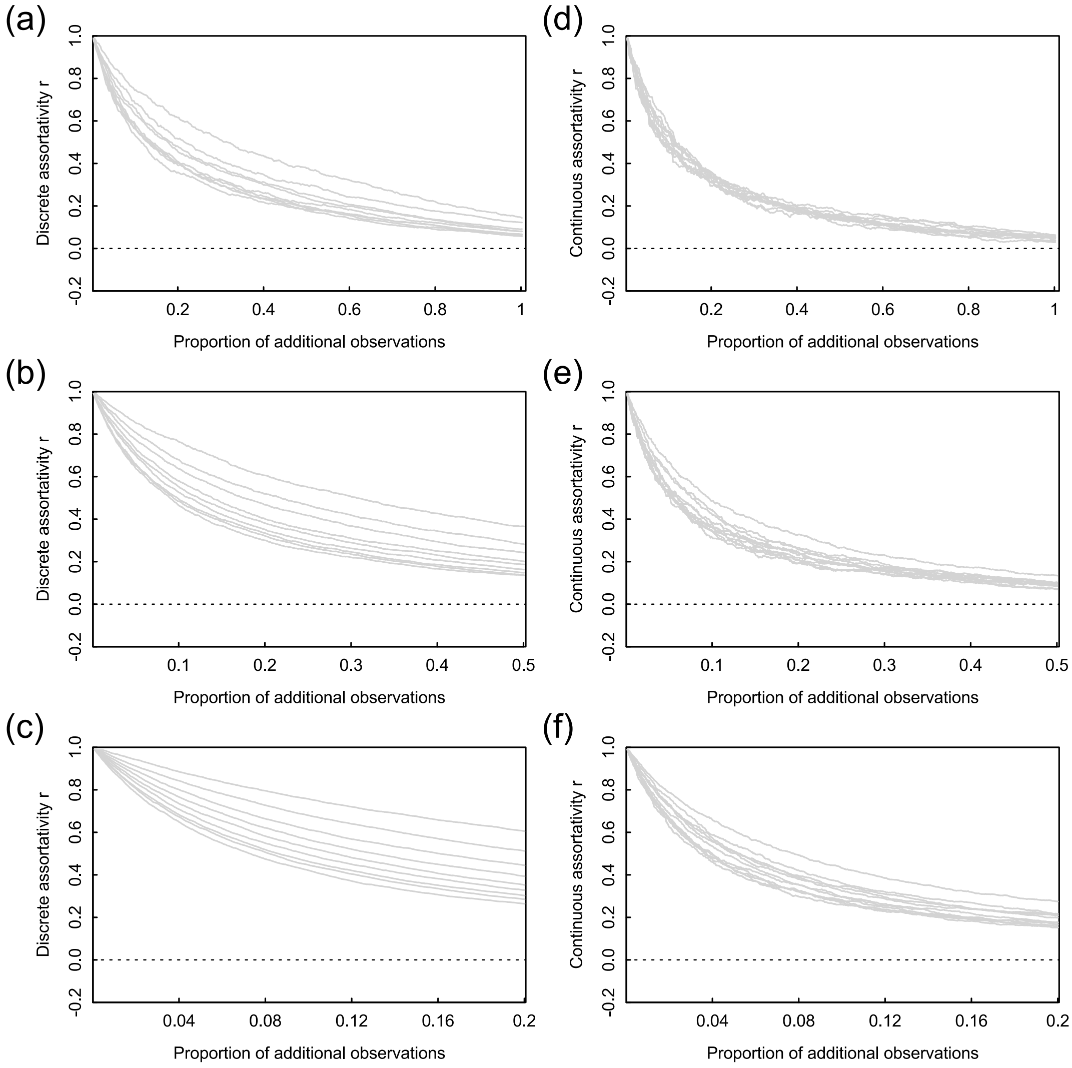
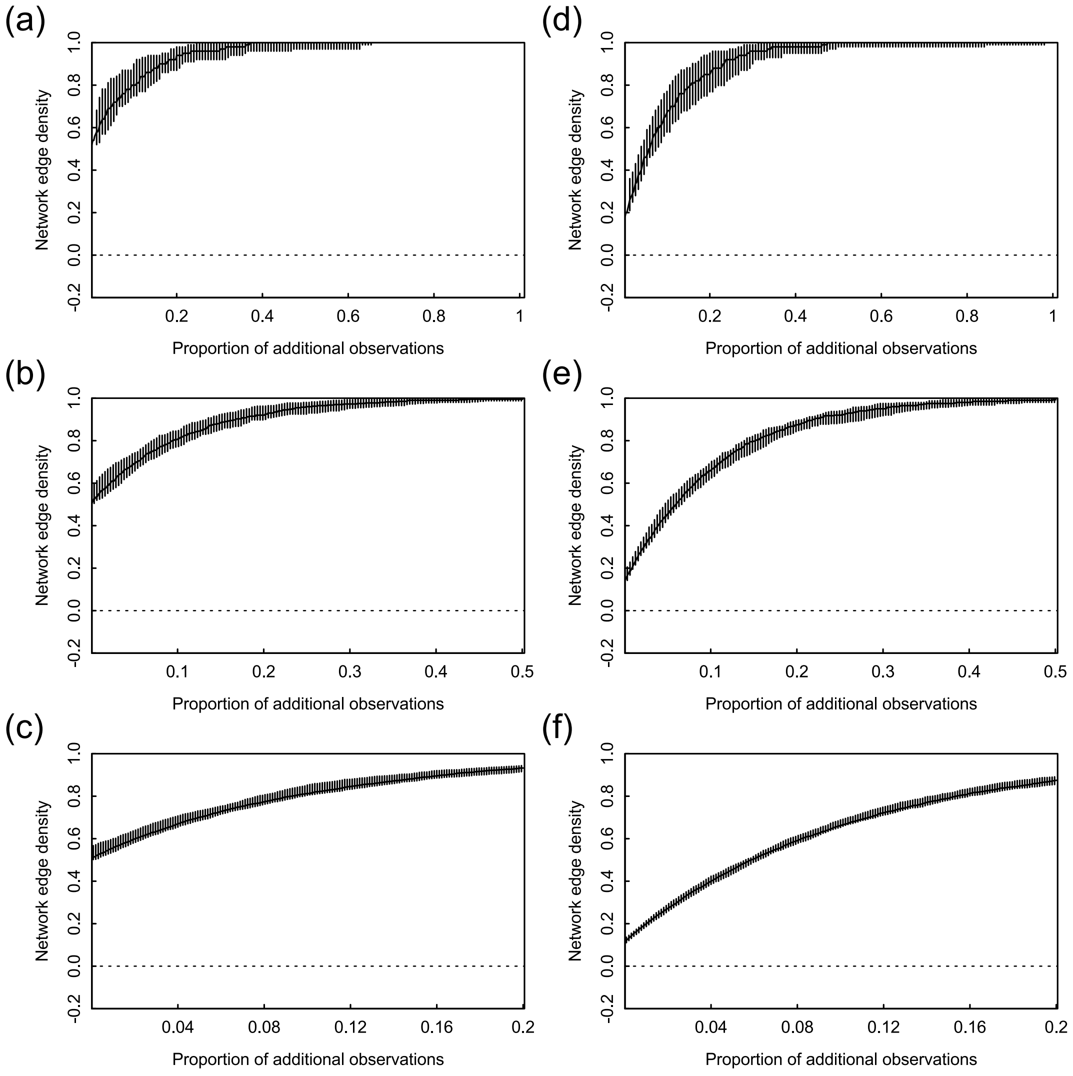


Figure S4: The relationship between added observations and network density (existing number of edges divided by potential number of edges) for (a-c) discrete simulations of 10, 50 and 100 individuals, and (d-f) continuous trait value simulations for 10, 50 and 100 individuals. Each panel provides background information on the simulation process used the matching panels from Figures 1 and S1-S3, such that panel (a) in this figure provides the network density relationship for panel (a) in Figures 1 and S1-S3. Width of the response in each panel shows the 95% spread from the 100 simulations in each associated panel in Figures 1 and S1-S3.



SUPPLEMENTARY TABLES

Table A1. Mixing matrix for binary assortment by species in tits and nuthatches.

	BLUTI	MARTI	GRETI	COATI	NUTHA	a_i
BLUTI	0.214	-	-	-	-	0.465
MARTI	0.032	0.005	-	-	-	0.069
GRETI	0.197	0.027	0.175	-	-	0.418
COATI	0.016	0.003	0.013	0.001	-	0.034
NUTHA	0.006	0.001	0.006	0.001	0.001	0.013
b_i	0.465	0.069	0.418	0.034	0.013	1.000

Mixing matrix for assortment in five species from Farine et al. (2012) showing the distribution of edges between each species using the binary network. Values in cells represent the proportion of edges that correspond to edges between different types of nodes; a_i are the row sums, b_i the column sums (table is symmetric but only half of values are shown). Species abbreviations are: BLUTI: blue tit (*Cyanistes caeruleus*); MARTI: marsh tit (*Poecile palustris*); GRETI: great tit (*Parus major*); COATI: coal tit (*Periparus ater*); and NUTHA: Eurasian nuthatch (*Sitta europaea*).

Table A2. Mixing matrix for weighted assortment by species in tits and nuthatches.

	BLUTI	MARTI	GRETI	COATI	NUTHA	a_i
BLUTI	0.208	-	-	-	-	0.451
MARTI	0.033	0.010	-	-	-	0.075
GRETI	0.183	0.025	0.180	-	-	0.410
COATI	0.019	0.005	0.015	0.003	-	0.047
NUTHA	0.009	0.002	0.007	0.001	0.001	0.019
b_i	0.451	0.075	0.410	0.047	0.019	1.000

Mixing matrix for assortment in five species from Farine et al. (2012) showing the distribution of edges between each species using the weighted network. Table structure and species abbreviations are as per Table A1.

Table A3. Comparison of binary, weighted, and thresholded binary assortativity coefficient results for the analyses on the thornbill and the tit studies.

	Phenotype	Binary	Weighted	Thresholded	P_n	P_d
Thornbills	Species	**R_d = 0.013±0.016**	**R^w_d = 0.122±0.018**	**R_T = 0.072±0.117**	< 0.001	< 0.001
	Sex	**R_d = -0.088±0.038**	R^w_d = -0.082±0.049	R_T = -0.019±0.037	0.587	0.690
	Stratum	**R_c = 0.113±0.016**	**R^w_c = 0.296±0.018**	**R_T = 0.262±0.020**	< 0.001	< 0.001
	Degree	R_c = -0.051±0.016	**R^w_c = 0.256±0.018**	R_T = 0.286±0.020	< 0.001	0.088
Tits and nuthatches	Species	R_d = -0.003±0.002	**R^w_d = 0.034±0.003**	R_T = 0.008±0.002	< 0.001	0.090
	Sex: blue tit	**R_d = -0.039±0.010**	R^w_d = 0.033±0.014	R_T = 0. 027±0.010	0.045	0.313
	Sex: great tit	R_d = -0.013±0.010	**R^w_d = 0.053±0.014**	R_T = 0. 027±0.010	0.543	0.599
	Sex: coal tit	**R_d = -1.000±0.707**	**R^w_d = -1.000±0.707**	**R_T = -1.000±0.707**	< 0.001	< 0.001
	Sex: marsh tit	**R_d = -0.194±0.047**	**R^w_d = -0.489±0.053**	**R_T = -0.378±0.050**	0.101	< 0.001
	Sex: nuthatch	**R_d = -1.000±0.707**	**R^w_d = -1.000±0.707**	**R_T = -1.000±0.707**	< 0.001	< 0.001
	Degree	**R_c = 0.108±0.005**	**R^w_c = 0.296±0.005**	R_T = 0.302±0.004	< 0.001	0.115

Results from assortativity coefficients applied to the tresholded binary networks (r_T) compared to binary (r_d) and weighted (r_d^w) assortativity measures for different phenotypic traits in thornbills and tit networks. Bold values indicate significant effects (P values of binary and weighted methods are shown in the text), and significance estimated from node (P_n) and data stream (P_d) randomisations are given for the thresholded network measures. Networks were thresholded at the median non-zero edge weight (0.09 in the thornbill network, 0.05 in the tit network) before being converted into binary format.

CHAPTER 5

A fission-fusion bird population shows phenotypic assortment in both spatial and social structure

A fission-fusion bird population shows phenotypic assortment in both spatial and social structure

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ABSTRACT

An individual's social environment can profoundly influence their relative behavioural, physiological, or environmental conditions, and subsequently directly impact their fitness. While many species may live a solitary lifestyle or have social associations dictated by family unit, a large number of species exhibit flexible and adaptable social systems via fission-fusion dynamics. Fission-fusion groups are typified by a rapid turn-over in group membership, suggesting that grouping decisions arise from individuals maximising direct fitness. Yet selection is generally considered to operate on the variance in phenotypes, rather than individual identities, in animal populations. Thus, if individuals preferentially associate with like or different phenotypes, this may influence how some components of selection operate upon them. Using a large-scale deployment of automated tracking of individually-marked great tits (*Parus major*), we describe the patterns of membership from over 70 000 observed groups, and how group membership drives assortment in the social network. We found that, despite very low group stability, there were strong patterns of group structure according to sex, dominance class and immigrant status. For example, groups had a more even sex ratio than expected by chance, and exhibited consistent age structure. We tease apart the relative contributions of space use and social choices by comparing observed groups to null models.

INTRODUCTION

Group dynamics are an important part of an individual's social landscape. Group size can impact predation risk through dilution (Krause & Ruxton 2002), selfish herd dynamics (Hamilton 1971), or predator confusion effects (Landeau & Terborgh 1986). Social interactions between individuals can also be important for gathering information about the environment (Dall et al. 2005; Danchin et al. 2004; Doligez et al. 2002; Valone 2007), such as for finding food (Aplin et al. 2012). Group-living often is typified by a trade-off between these benefits and costs incurred through competition (Krause & Ruxton 2002). However, costs and benefits of being in groups may vary according to to the environment (Ruxton et al. 2005), individual phenotypic characters (such as by dominance or sex Schurch et al. 2010) or by the existing composition of the group (similarity or difference in phenotype, for example the oddity-effect; Landeau & Terborgh 1986). If the benefits of being in a group vary with the phenotype of its members, we should then expect regular patterns of associations to emerge between phenotypes in a way that maximises the individual fitness of participants (such as kin structure in cooperatively breeders; Hatchwell 2009). How these patterns emerge in populations, whether from social (attraction or avoidance) or spatial (acceptance or exclusion) effects, remains largely unexplored.

Fission-fusion social dynamics are common across taxonomic groups. These are typified by groups that have short-term structural stability and high turn-over in membership. Some classic examples of animals that exhibit this social dynamic include primates (Fukuda 1989; Le Hellaye et al. 2010; Symington 1990; Winkler 2000), bats (Kerth et al. 2006; Popa-Lisseanu et al. 2008), elephants (Archie et al. 2006; Wittemyer et al. 2005), red deer (Albon et al. 1992), as well as birds (Aplin et al. 2013a; Farine et al. 2012). This dynamic is thought to enable linkages across all levels of these populations, from pair-wise to landscape community interactions (Couzin 2006). Such behaviour could be adaptive if simple pair-wise interactions facilitate the emergence of complex patterns at the population scale (Chapman et al. 1995; Lehmann & Boesch 2004). For example, larger groups may be better at tracking environmental gradients (Berdahl et al. 2013), thus, as the environmental signal deteriorates, shifting individual preferences towards a more gregarious joining policy can lead to group sizes best suited for current conditions (Ruxton et al. 2005). In particular, fission-fusion dynamics are thought to facilitate behavioural plasticity, which could play a critical role in successful individual responses to environmental variability (Sueur et al. 2011).

Individuals may also be able to influence particular selection pressures by choosing their social environment (West-Eberhard 1979). For example, males with poor sexual ornamentation could associate with other poor quality males, enabling them to increase their relative quality, and subsequently benefitting their fitness (Oh & Badyaev 2010). Given that fission-fusion dynamics vary the membership of individuals across groups, the opportunities for these individuals to find an optimal social niche may be markedly higher in these systems than in species with more stable social systems. In this case, although groups may have largely random members, the interactions that occur between phenotypes may themselves be non-random (Wolf et al. 1999). Thus, unlike mechanisms relying on repeated interactions between individuals, such as cooperation (Axelrod & Hamilton 1981), selection could influence individual fitness, regardless of the identity of participants in the groups.

In order to determine at what scale structured interactions between phenotypes (such as assortment or disassortment) could be operating, we recorded the composition of naturally occurring flocks of birds in a winter woodland population. Using a large dataset collected through extensive sampling of individuals fitted with passive integrated transponder (PIT) tags, we determine i) how stable groups remain over time, ii) how groups varied in size according to population density or time of year, iii) whether group composition reflected the local availability of individuals, and finally iv) whether social or spatial variations in the distribution of phenotypes lead to phenotypic assortment over the length of a winter. In doing so, we investigate the role of social dynamics in the evolutionary process.

METHODS

The study took place at Wytham Woods, Oxford (51° 46′N, 1°20′W). The breeding great tits (*Parus major*) in this 385ha woodland are the focus of a long-term study, with over 1000 nest boxes monitored annually. Since 2007, all breeding adults and chicks were caught and fitted with passive integrated transponder (PIT) tags, in addition to the standard British Trust for Ornithology metal ring. Morphometric measurements, including age and sex were recorded for every bird. This has been supplemented by intensive autumn and regular winter catching in order to ring and tag immigrant birds, as part of a study into their social ecology (see Aplin et al. 2012; Farine & Lang 2013). While pairs of great tits maintain breeding territories during the spring, these dissolve post-breeding and the population structure turns into loose fission-fusion groups of predominantly unrelated individuals that roam in search of ephemeral and patchy food sources.

Field observations

We deployed 65 automated feeding stations in a stratified grid from the 3rd of December 2011 to the 26th of February 2012. Each feeding station was fitted with two radio frequency identification (RFID) antennae (one on each access hole) and filled with sunflower seeds. These were automatically opened two days per week, providing synchronous snapshots of the association patterns in the population. Feeders were filled with sunflower seed in order to minimise queuing (and therefore competition) as individuals picked up a seed and processed these in a nearby tree. These feeders also maintained a constant reward, therefore removing any effects of patch depletion or developing differences between nearby feeding stations. Feeders scanned for PIT tags every 1/3rd of a second from pre-dawn until after dusk. In all, we collected 26 days of data collection over 13 sampling periods.

Inferring group membership

Feeding stations provided a highly resolved spatiotemporal data stream of individual visits. As individuals fed in groups, or flocks, the pattern of visit typically contained bursts of high activity, separated by periods of low activity. Given the stochastic nature of this system (groups may feed for different lengths of time), we inferred group membership using a specially developed machine learning algorithm based on Gaussian mixture models (Psorakis et al. 2012). This avoids the need to impose arbitrary temporal boundaries on groups. Instead, it infers the best-fitting window for each group based on the patterns observed over the entire data set. By fitting a Gaussian distribution over closely-spaced visits, visits can then be assigned to burst, or group, for which they have the highest probability of belonging to. This method returns a matrix of groups and the individual's membership to these groups.

Stability

We used a measure of temporal group stability that is similar to the lagged rate of association proposed by Farine (2013). This measure represents the proportion of individuals that are consistent across two groups containing a focal individual X and separated by a time period τ, given by:

$$S(\tau, X) = \frac{1}{G_\tau} \sum_{j,k|(t_k - t_j) = \tau} \frac{G_{j,k}(X)}{G_{j,!k}(X) + G_{k,!j}(X) + G_{j,k}(X)}$$

where $G_j(X)$ is the number of occurrences of groups containing focal individual X and split by τ, $G_{j,k}(X)$ is the number of non-focal individuals occurring in two groups, both containing individual X, and separated by $\tau = t_k - t_j$. $G_{j,!k}(X)$ is the number of individuals occurring only in group j, and $G_{k,!j}(X)$ is the number of individuals occurring only in group k. A value of $S(\tau,X) = 0.33$ is equivalent to half of the group between two evenly-sized groups changing in a time period τ. We limited this calculation to groups that contained at least one common member in order to ensure that there was a common link between groups. In order to estimate how the observed stability differed from random, we calculated $S(\tau,X)$ for groups in a spatiotemporally restricted null model (see below).

Group composition

When investigating how group composition changed over different group sizes, it was necessary to pool certain groups together when calculating test statistics (e.g. 'mean sex assortativity'), due to low sample sizes for larger groups. Therefore, group sizes larger than 13 were binned into 'group size classes' (e.g. 14-15) that contained at least 5% of the total group memberships (Figures 3,4,5 & 6).

Within-group content

We explored how the demographic content of the groups varied with regard to group size for three different characteristics (sex, age, or residency status), all of which have just two classes (male or female; juvenile or adult; immigrant or locally born, respectively). Juveniles are defined as birds that were born in the breeding season immediately prior to the winter (in this case in spring 2011). The demographic of groups were calculated as the proportion of individuals from each classes occurred in each separate group, pooling these data as the mean for each group size. We then compared these means to groups in permuted data (described below).

Furthermore, we also examined whether group size was associated with the body size of individuals within them. As a multivariate measure of size for individuals, PC1 of a PCA using wing and tarsus length (available for 84% of individuals) was used. As males were significantly larger in both measures (t-test; wing: $t = 28.8174$, $df = 931$, $p<0.001$, tarsus: $t = 13.6286$, $df = 885$, $p<0.001$), this measure was generated separately within each sex, and standardized with a mean of 0 with a variance of 1. PC1 correlated strongly with both size measures in both sexes (Pearson correlation coefficient; male wing=99.8%, male tarsus = 32.3%, female wing = 99.8%, female tarsus = 28.8%). We then calculated the mean size of individuals within each age and sex class for each individual group, and again compared the mean of these values of each different group size to the permuted data.

Within-group assortativity

After determining the content of groups in regard to the different demographic characteristics (above), within-group assortativity for each demographic characteristic was examined separately. We calculated the binomial probability that, given the group size and the total number of unique individuals in each class over all groups of that group size, the observed number of individuals in these classes would have occurred by chance. For example, if amongst all the individuals who participated in groups of size two we had an equal number of males and females, a group containing two males (or two females) would be assigned 0.25, whilst a group containing one male and one female would have a value of 0.5. It is always the case that higher values (i.e. closer to 0.5) represent more disassortativity. Following this, an overall mean was calculated for these values for each group size and again compared to the permuted data to test for significance.

We also considered whether groups show assortativity by size, both overall and within the different demographic classes. This was determined by calculating the mean size for each group (and the mean size of the different classes of individuals within the group to make 'within class' comparisons). Then, for each group size, we obtained a kurtosis score for the distribution of these mean sizes (see Aplin et al. 2013a), where high kurtosis scores indicate a peaked distribution (i.e. assortativity) whilst low scores indicate a flat distribution (i.e. disassortativity).

Null models

We used randomisation techniques in order to create two null models. The first assumed random interactions between individuals but a fixed observation stream, which we call phenotypic randomisations. In this method, we created 1000 random network by shuffling the node labels associated with each individual's phenotype. The second maintained spatiotemporal distributions of phenotypes, and we call it the spatiotemporally controlled randomisations. These two randomisations used two general methods of data randomisations. Phenotypic randomisations consisted of randomly re-allocating the phenotype of individuals, maintaining the same observation patterns and the same distribution of phenotypes. Spatiotemporally controlled randomisations used Bejder's restricted permutation test following the methods originally described by Bejder et al. (1998) with subsequent improvements by numerous authors (see Whitehead 2008 pp: 125-127). This null model randomly swaps the observations of two individuals observed in different groups, with swaps being restricted to control for space and time. Each step in the permutation performs one of these swaps, creating an increasingly random data set. In our case, we restricted swaps to occur only between groups that were observed at the same location (same feeder), and on the same day. The resulting output is a data stream where the size (and time and location data) of each group remains constant along with the number of observations for each individual, but the detailed patterns of group membership are changed. This therefore tests whether structure exists within each location given the variation in the number of observations for each individual.

These two null models allowed us to partially differentiate between patterns arising from spatial and social effects (Croft et al. 2008). If the patterns between the two randomisations differ, this suggests that phenotypes are not evenly distributed in space. This is because spatial variation in the number of individuals of each phenotype is maintained static in the spatiotemporally controlled randomisations, but not in the phenotypic randomisations. If the observed data then match the spatiotemporal but not the phenotypic randomisations, then any assortment in this phenotype is attributable to spatial effects. If the data differs from both, then we attribute assortment to be due to social effects given that phenotypes are randomly distributed in space.

We repeated the phenotypic randomisation 1000 times. We ran 1 000 000 iterations of the spatiotemporal randomisations as only a single observation is swapped on each iteration (whereas phenotypic randomisations shuffle all nodes, see Whitehead 2008 pp. 130). Where possible, we compared our data to the distribution of the spatiotemporal randomisations (taken after every 1000th iterations), but where this was not possible (for example for the group stability measure that is highly computationally intensive) we used only the final randomised association matrix after the 1 000 000th iteration.

Social network analysis

We used the R (R Development Core Team 2013) package *asnipe* (Farine 2013) to calculate the simple-ratio association index between all interacting dyads. This index scales edge weights between 0 (never observed together) and 1 (always observed together). We then calculated the assortativity index (Newman 2003), which is derived from the Pearson correlation coefficient for weighted-edge networks in the *R* package *assortnet* (Farine 2013b in review).

RESULTS

We detected a total of 1053 individual great tits, consisting of 274 adult females, 252 adult males, 234 juvenile females, 229 juvenile males, and 64 unsexed individuals that were never caught post-fledging (Table S1) and not included in subsequent analyses. Of the 13 sampling periods, most individuals were detected on a large majority of the sampling periods (mean = 9.4, median = 11). Overall, we logged 3 347 038 detections of individuals over the 13 sampling periods, forming 73 737 unique groups with a mean of 4.7 individuals per group (median = 4).

Stability of groups

We found that groups had a significantly higher stability in the first 10 minutes of the observed data when compared to the same data after one million randomisations (Figure 1a). As the inter-group time interval increases, the difference between the observed stability and the stability of random groups approached zero. Group composition was therefore highly fluid across surprisingly short periods of time. Stability also varied according to group size, with small and large groups being more stable than expected (Figure 1b).

Group size distributions

We found a strong divergence away from a 1:1 relationship between the number of individuals present on a given day and the group sizes observed (Figure 2a).

Logistic models of the mean and maximum observed groups sizes had significantly greater support than linear models applied to the same data (Table 1). This suggests that the relationship between population size and group size saturated, in this case at a maximum of 24 and 8 individuals per group respectively (Figure 2a-b, horizontal dashed lines). Further, the relationship between group size and population size appeared to remain stable over the winter (generalized linear mixed model controlling for population size and location as a random effect shows a very weak slope despite a low *P*-value: t=-1.85, B±SE=-0.012±0.006, *P*=0.06; Figure 2c).

Group composition

Non-random distribution of individuals according to their phenotypes was found among groups, and this differed with group size. Non-random group composition can be driven by spatial distribution of phenotypes (inferred here from the observed data differing significantly from the 'phenotypic randomisation' null model) or socially driven i.e. active decisions by individuals regarding group membership (inferred here from the observed data differing significantly from the 'spatiotemporal controlled' null model), or both. Indeed, we found evidence for all three situations in regards to the considered demographic characteristics.

Although groups of all sizes contained the expected proportions of adult females and juvenile males (Figure S2), we found that large groups contained more juvenile females yet fewer adult males than expected by the phenotypic randomisation model (Figure 3). These comparisons were carried out simultaneously over multiple bins, and although standard bonferroni corrections are not appropriate here due to the non-independence of the data, we found that, for the largest group sizes, the observed proportion of juvenile females and adult males fell outside of the entire range of the data generated from phenotypic randomisation. As the spatiotemporal null model matched the observed data (Figure 3), this suggests a spatially driven pattern, whereby areas containing large groups also contain higher proportions of juvenile females in comparison to adult males.

A similar pattern was also found for the proportion of juveniles that were immigrants in small groups (below 8), which was significantly lower than the phenotypic randomisation null model but predicted well by spatiotemporally controlled permutations (Figure 4), suggesting a non-uniform distribution of juvenile immigrants across the study area. Indeed, the number of individuals present in locations where resident birds were detected was on average lower than the number of individuals present at sites where immigrants were present (t test: t=-3.57, df=411, P=0.0004). However, no such pattern of non-random group content based on residency status was observed amongst adult birds (Figure S3).

As well as the proportion of individuals of different phenotypes included in groups, we also found non-random levels of assortativity in regards to different demographic characteristics. Groups were found to be more dissassortative in regards to sex (i.e. sex ratio closer to equal) than expected by both null models, which also fall within each other's range, thus suggesting a primarily socially driven pattern (Figure 5a). In contrast, groups tended to show assortativity by age, as groups were more likely to contain either adults or juveniles than expected, and again appeared largely driven by social factors rather than variation due to spatiotemporal differences (Figure 5b).

The mean size of individuals within groups did not differ from either the spatial or population-wide distributions of phenotypes (Figure S4). This was true within all demographic classes of individuals, apart from a slight trend for larger juveniles than expected by the node permutation model in mid-size groups (Figure S4). We also found no major patterns of phenotypic assortment in groups according to individual size amongst any of the different demographic classes ($p>0.05$ Figure S5), suggesting that these did not differ dramatically from either the spatial or population-wide distributions of phenotypes.

Assortment in the social network

The social network contained a single fully connected component, with a link density of 0.08 (8% of possible dyadic edges are present). These edges were significantly disassorted by sex (assortativity coefficient r = -0.034 ± 0.0009), which indicates that mixed-sex dyads had a higher probability of both occurring and reoccurring. Age (in years) was significant assorted (r = 0.047 ± 0.0014), suggesting that individuals, particularly juveniles, had a stronger tendency of repeatedly associating during the winter. Finally, we found significant overall assortment by immigration status (r = 0.037 ± 0.0019), that was mostly driven by assortment in adults ($r = 0.11 \pm 0.0034$). Thus, the long-term pattern clearly reflects the short-term social decisions made by individuals.

DISCUSSION

We have shown that although groups were highly unstable in membership over short periods of time, interactions between different phenotypes in the population were not themselves random. In some cases, the patterns of group membership arose from variation in the distribution of phenotypes across space. In others, our results suggest that they arose through association preferences by individuals, potentially based on both their own phenotypes but also the existing composition of the group. For example, adult males (which are often more dominant; Sandell & Smith 1991) tended to avoid large groups, whereas juvenile females (generally subdominant phenotypes; Aplin et al. 2013b) were found in larger groups more often than expected.

These findings have important and far-reaching implications: i) individuals may have different social strategies as a function of their phenotypes; and ii) differences in short-term strategies can maintain long-term variation in interaction rates between phenotypes as measured in our winter-long social network. As a consequence fission-fusion dynamics may influence the pressures of selection operating upon different phenotypes. For example, in species such as great tits, where residency is an important predictor of dominance (Sandell & Smith 1991), associating with other immigrants may help reduce the overall competition a newly arrived individual experiences. This effect of mediating selection pressure by choosing with whom to associate (beyond the simple changes in group size; Chapman et al. 1995) may play an important role shaping the evolution of this social system.

Although phenotypic assortment may be relatively common in nature, few studies have, to our knowledge, linked short-term fission-fusion dynamics to long-term patterns of association in a large-scale social network (but see Kerth et al. 2006). In fish, several studies have found that groups will assort by size (reviewed in Hoare et al. 2000a), often in preference to species identity (Hoare et al. 2000b; Ward et al. 2002). Also, assortment group composition appears to play a particularly important role in avoiding predation, either through individuals minimising their risk relative to the group (Mathis & Chivers 2003) or in order to maintain synchrony (Aivaz & Ruckstuhl 2011). Body size assortment can also emerge simply through spatial variation in the distribution of phenotypes, for example when fish of different age classes (and therefore different sizes) inhabit different niches (Krause et al. 1996).

We found that groups were often more mixed by sex than expected from chance across a wide range of group sizes. This was almost certainly a result of social decisions, leading to significant disassortment over the entire study period. In socially monogamous birds, this is perhaps not unexpected. For example, (Wilkinson 1982) found that groups of bullfinches (*Pyrrhula pyrrhula*) were more mixed by sex than expected by chance. In contrast, brown-headed cowbirds (*Molothrus ater*), showed the strongest links between females within the fission-fusion social dynamics of that species, despite being brood parasites and having been raised in the nests of other species (Kohn et al. 2011). The authors conclude that assortment may play an important role in developing skills needed for breeding in that species (Kohn et al. 2011).

Individuals in our study were also assorted with regard to their status as immigrant or locally-born birds. This appeared to be driven by spatial sorting rather than social decisions in the flocks. Recent work in this population suggests that by associating with other recently arrived individuals, late arrivals could reduce the selection operating on their dispersal phenotype (Farine et al in prep). In parids, there is a strong interaction between residence and dominance, with birds that hold or have previously held a territory having relatively higher dominance than non-residents (Lahti et al. 1996; Sandell & Smith 1991). This may lead to spatial partitioning if resident birds exclude immigrants from core or high-quality zones, and these immigrants associate in marginal or bordering areas. This effect may even include resident juveniles being dominant over recently arrived adults (Sandell & Smith 1991). Alternatively, immigrant birds may have greater similarities in their activity levels; for example immigrants are typically more 'bold' along a spectrum of slow explorer to fast explorer (Dingemanse et al. 2003), and consequently have been found to be more closely associated in this population (Aplin et al in press).

Groups in this population appeared to be strongly influenced by a multitude of interactions. Although these groups were very unstable in time, they maintained consistent relationships between and within particular phenotypes, and maintained strikingly consistent group sizes regardless of season. Importantly, patterns of structure in group membership led to long-term assortment in the social network, that were driven by both social or spatial mechanisms. Our findings suggest that the social decisions made by individuals on a day-to-day basis may have an important role in shaping the strength or direction of selection operating on different phenotypes, even in fission-fusion societies.

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FIGURES

Figure 1. Groups show higher stability than expected from random, both in terms of (a) the (log) time-gap between groups and (b) the size of the initial group. Groups were most stable in the period of 1 to 10 minutes, after which they appeared to have little difference in stability from random groups (see Figure S1 for independent curves). Small and large groups were the most stable relative to chance. Solid lines show the ratio of the observed stability to the stability calculated from randomised data.

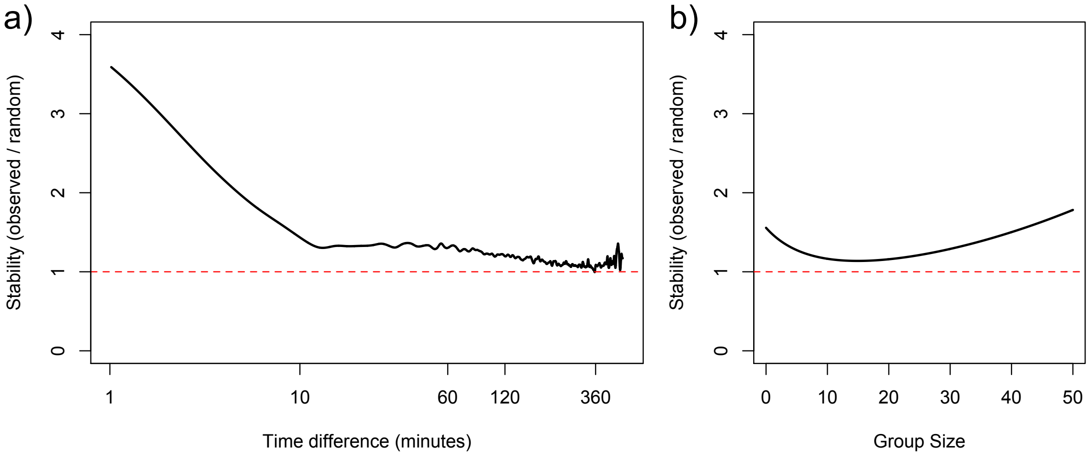


Figure 2. Group size was proportionately smaller as local population size increased. For each location, we calculated the number of individuals recorded at the site in each sampling period. We found that both (a) maximum group size and (b) average group size saturated with increasing population size. (c) We found no effect of season on this relationship, where time of year represents the period ranging from the 3rd of December 2011 to the 26th February 2013.

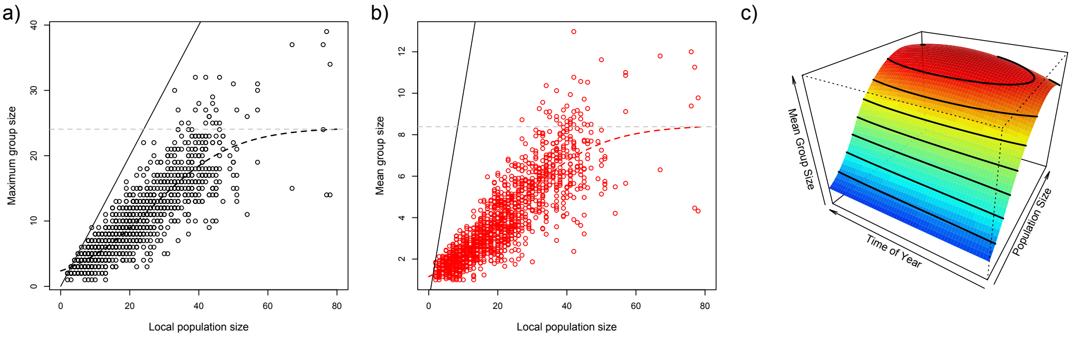
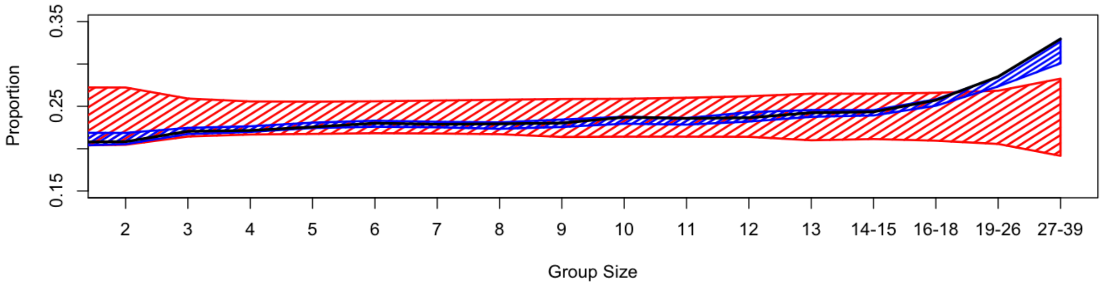
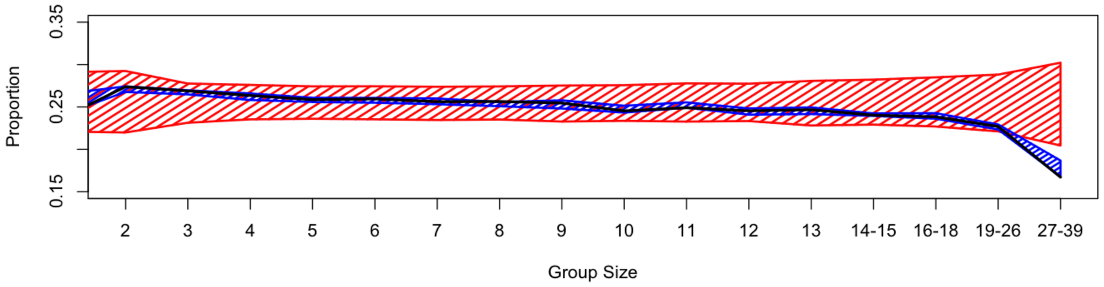


Figure 3. In this and following plots, the black lines show the observed data, the blue polygons show the 95% range of permutation data from the 'spatiotemporal controlled null model', and the red polygons show the 95% range of permutation data generated from the 'phenotypic randomisation null model'). In groups of over 18 individuals, the observed data differs from the phenotypic randomisation null model by having a) higher proportions of juvenile females & b) lower proportions of adult males.



a) Juvenile Females



b) Adult Males

Figure 4. The proportion of juveniles that are immigrants in groups of less than 8 is lower than expected by the phenotypic randomisation null model, but not the spatiotemporally controlled model.

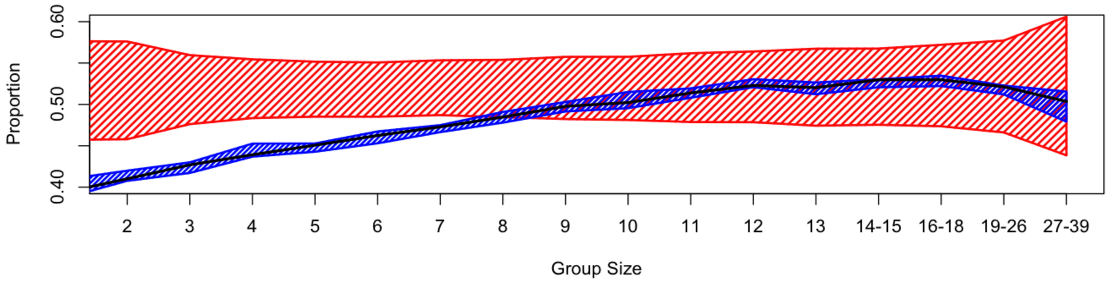
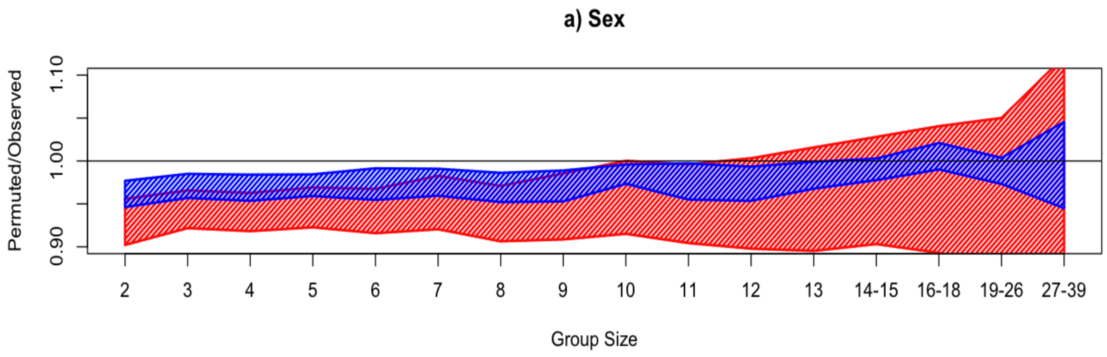


Figure 5. Groups were significantly (a) more dissassorted by sex but (b) more assorted by age class than expected from the randomised datasets. The sex ratio of groups up to a size of 10 is significantly closer to 0.5 than both the spatiotemporally restricted and the phenotypic randomisations. These groups also tend to contain more individuals that are either adults or juveniles than expected. Plots show the ratio of the 95% confidence intervals of the randomisations and the observed data. Areas where the polygon overlap 1 are non-significant (the permutation is equal to the observed value). Plots are presented this way due to the difficultly of directly interpreting binomial probabilities, and the biological insignificance of the exponential decay as group size increases (see Figure S6).


a) Sex

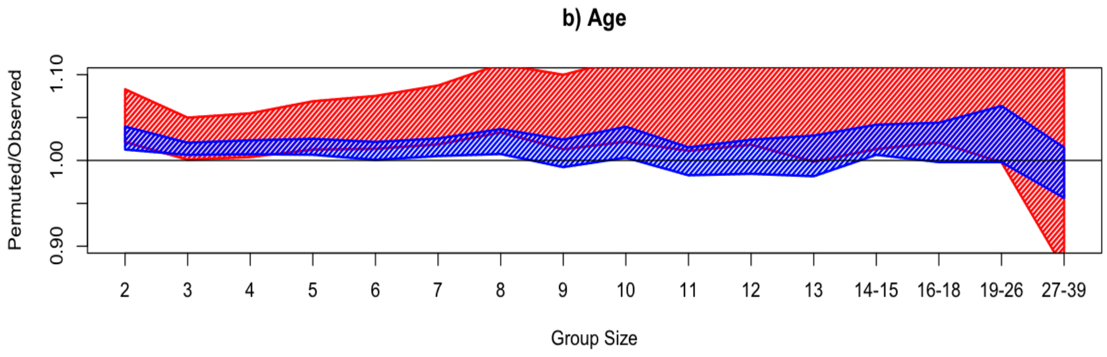

b) Age

Table 1. Summary of AIC support for linear and logistic regressions of the relationship between group size and local population size.

Model	*AIC*
Max group size ~ Population	7052
Max group size ~ logis(Population)	7014
Mean group size ~ Population	4196
Mean group size ~ logis(Population)	4091

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SUPPLEMENTARY FIGURES

Figure S1. Group stability shown for the observed data (top black line) and randomised (bottom grey line) data after 1 000 000 iterations, shown with 95% confidence intervals calculated using jackknife.

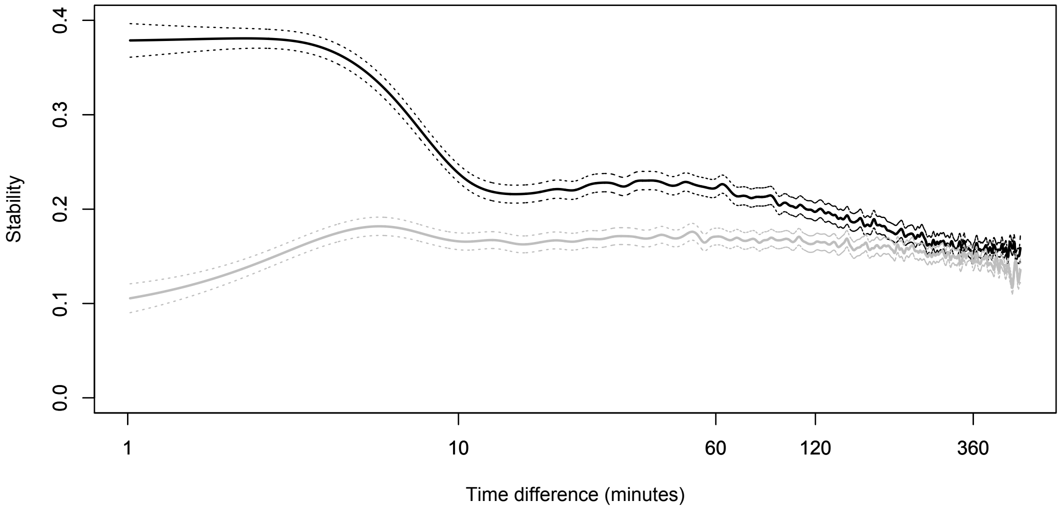


Figure S2. The proportion of a) Juvenile males & b) Adult females in the observed data match that expected from both the phenotypic randomisation null models and the spatiotemporal model.

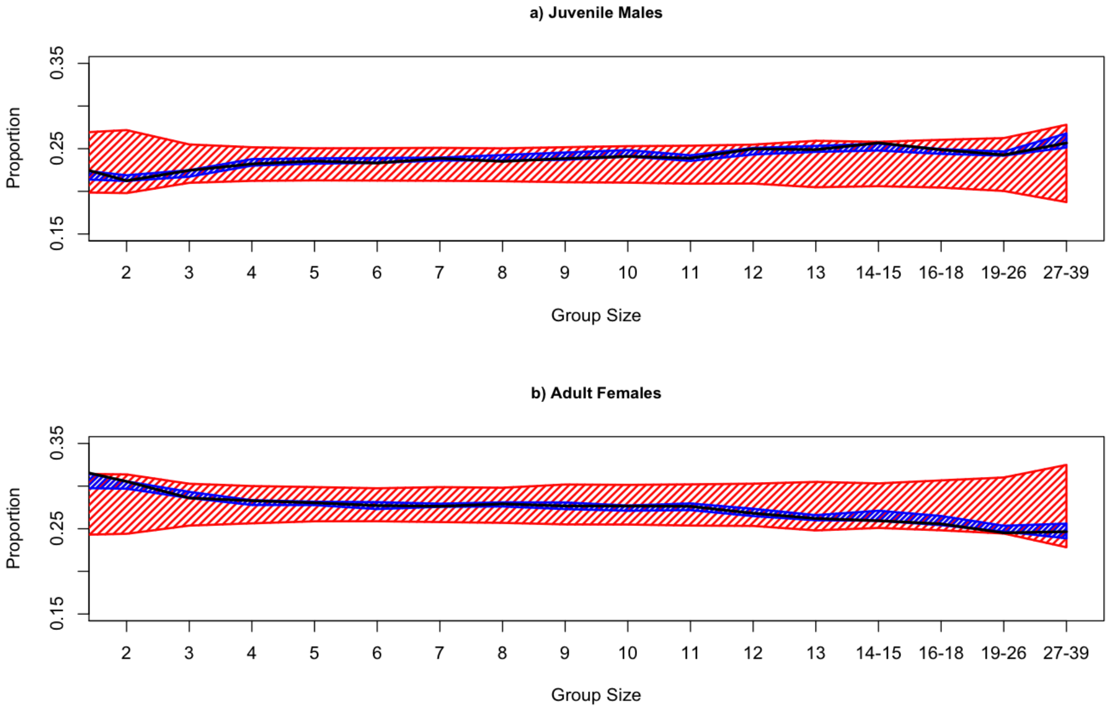


Figure S3. The proportion of adults that are immigrants in all groups matches that expected by both null models.

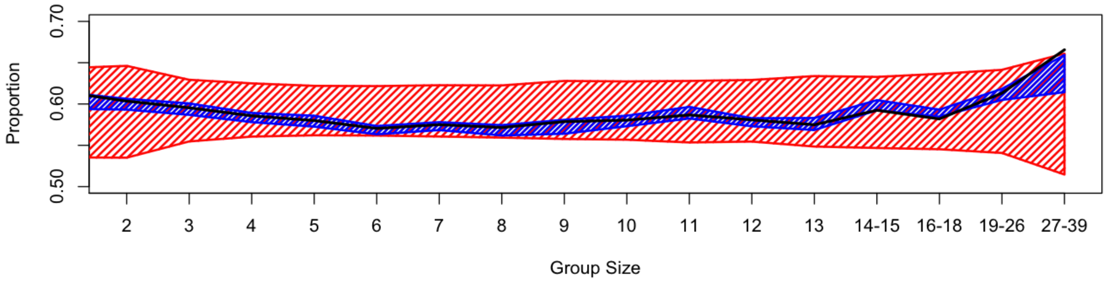


Figure S4. The mean size (PCA1 – see Methods) of individuals within a group for the four classes; JM=Juvenile Male, AF=Adult Female, JF=Juvenile Female, AM=Adult Male. In all cases, the observed data matches the null models, apart from JM, where mid-sized groups (6-12 individuals) contains individual's larger than that expected by the phenotypic randomisation model.

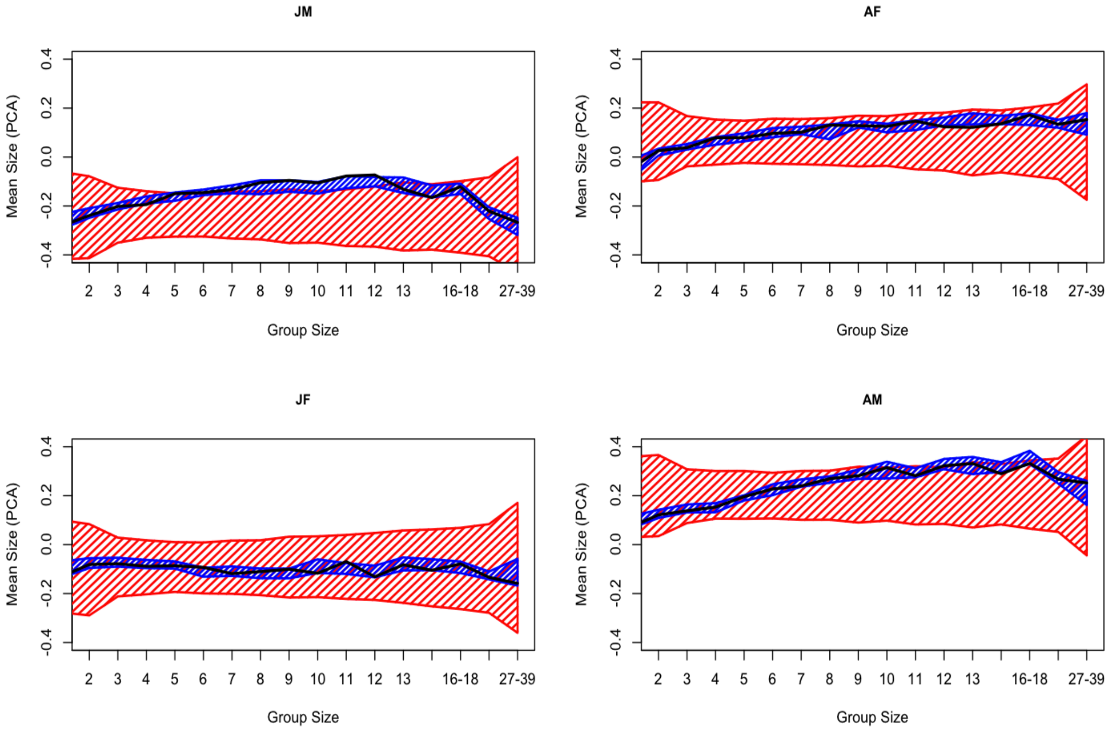


Figure S5. Assortativity for residency status. Over all group sizes, the observed data is very similar to the spatiotemporally controlled null model. However, the observed residency assortativity for groups between 4-9 individuals appeared higher than that expected by the phenotypic randomisation model.

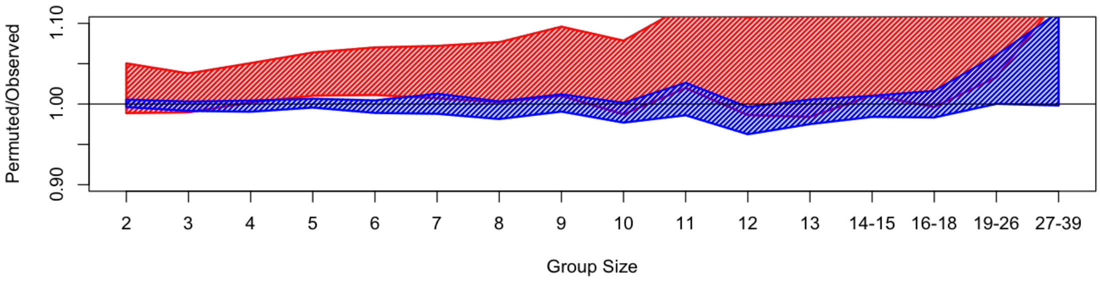
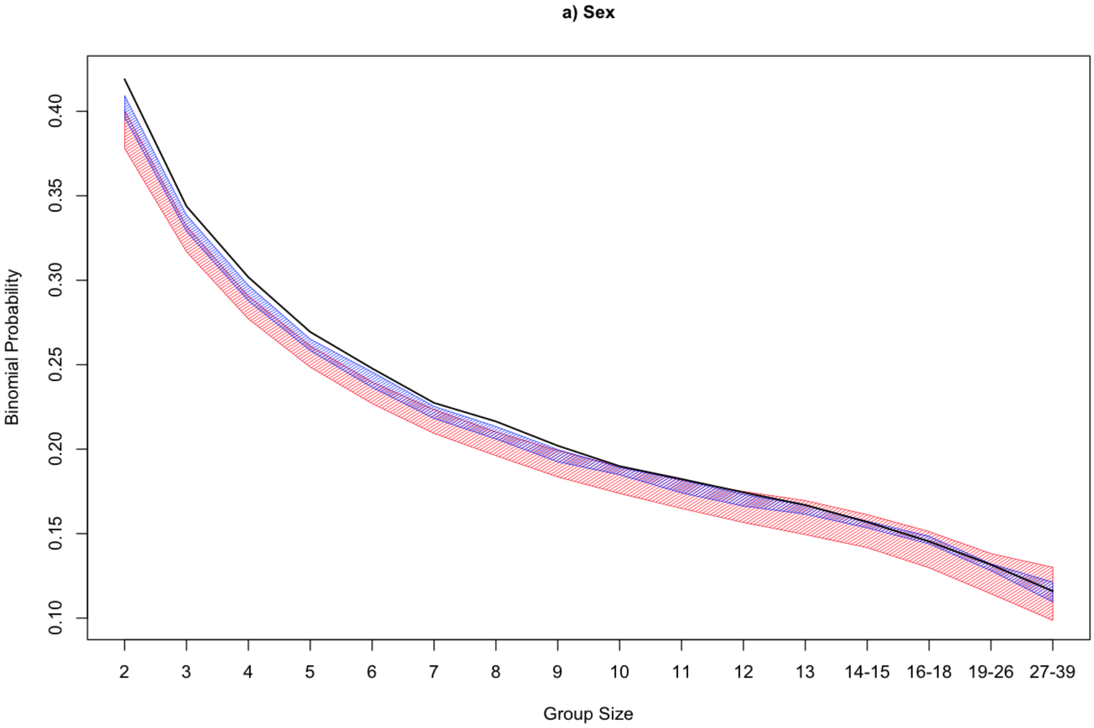
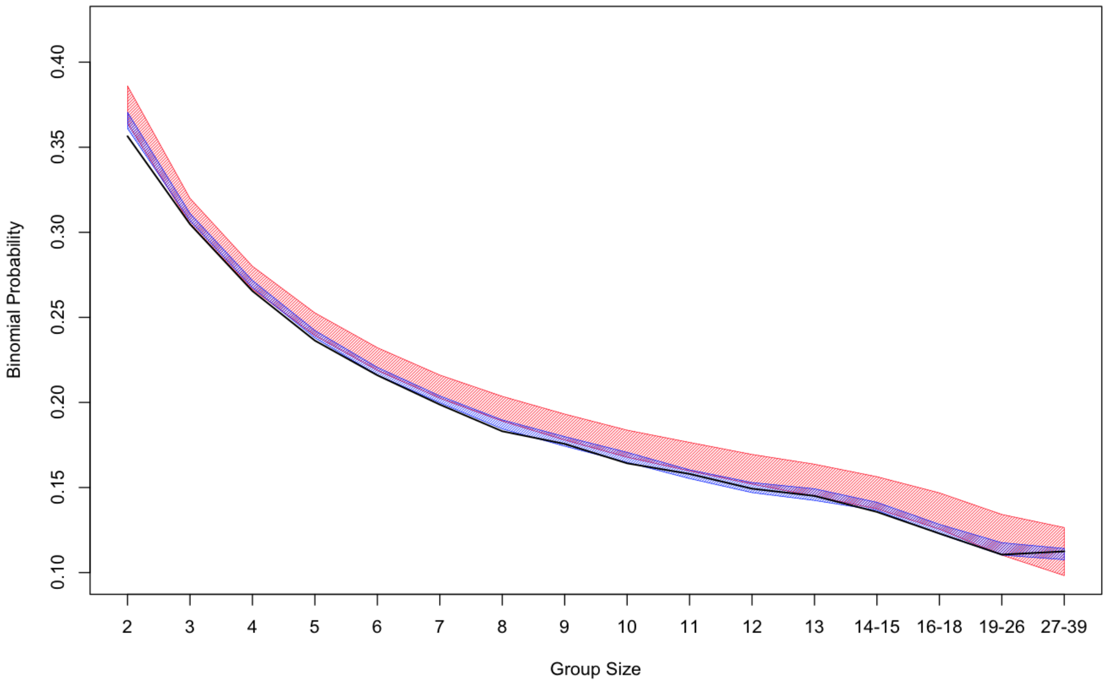


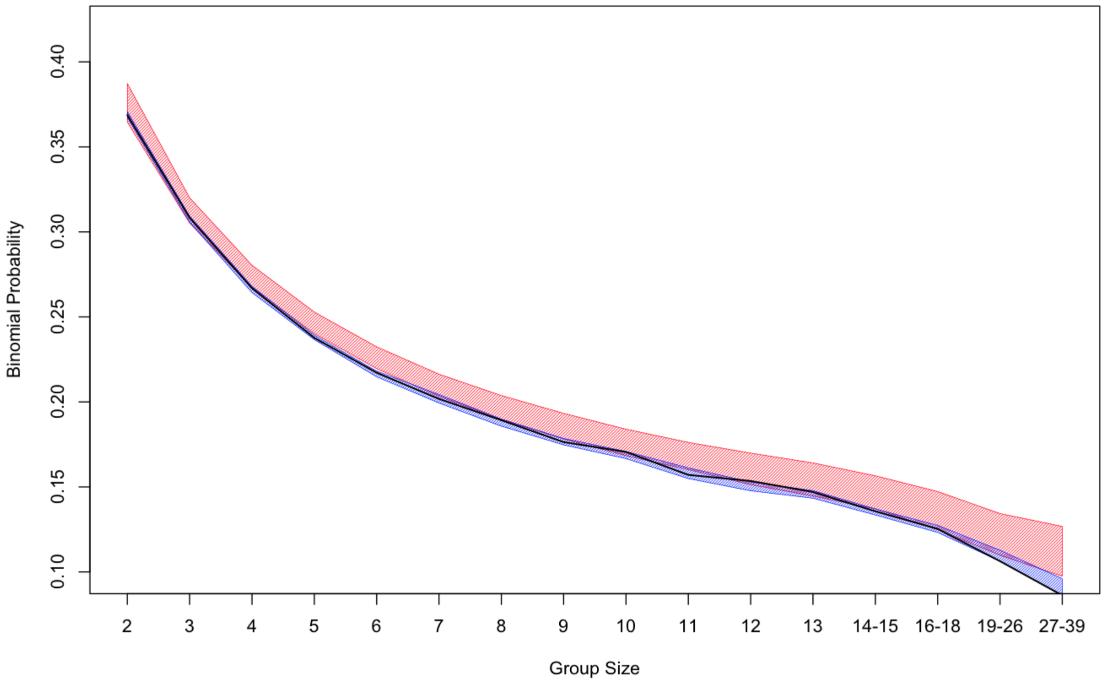
Figure S6. Observed, spatiotemporal controlled null model, and phenotypically random null model binomial probabilities (i.e. Assortativity index) for a) Sex, b) Age and c) Residency Status, over the different group sizes. This data is presented in the manuscript as Permuted/Observed values, due to the biological insignificance of the exponential decay of the binomial probability with group size, and the difficultly of easily interpreting such data.



b) Age



c) Residency



CHAPTER 6

Selection for territory acquisition is mediated by the social network in a wild songbird

Selection for territory acquisition is mediated by the social network in a wild songbird

Damien R. Farine & Ben C. Sheldon

ABSTRACT

Social behaviour may be a key cause of selection that operates on animals. If the interactions between the phenotypes of individuals in animal groups are not random with respect to the local population, then social interactions can influence the direction and strength of selection that operates on phenotypes. Social network analysis is a method that quantifies the structure of social interactions between individuals, and hence is ideally suited to capture non-random interactions between phenotypes. The structure of phenotypic interactions can be measured using assortative mixing: the correlation between an individual's phenotype and that of its associates. Yet, there has been little evidence linking patterns of association with differential selection based upon interacting phenotypes. In this paper, we use a recently described method for calculating assortativity on weighted networks, which is the correlation between an individual's phenotype and that of its associates. We integrate this measure into an existing framework for measuring the magnitude of social selection operating on phenotypes. Using data from winter social networks and breeding territory acquisition from a wild bird population, we find that despite significant selection for early dispersal, overall selection on territory acquisition is

mediated by social structure via interactions between the phenotypes of social associates. Given parallel theoretical developments of the importance of local network structure on population processes, and the rapidly increasing data on social networks being collected in free-living populations, the integration of these concepts could yield significant insights into social evolution, and the role of social selection in evolution.

INTRODUCTION

One of the fundamental motivations in the study of evolution in natural populations is to understand the relationship between phenotypic trait distributions and fitness, quantified as selection (Endler 1986; Kingsolver et al. 2001; Wade & Kalisz 1990). The environment is a key determinant of an individual's fitness, and indeed understanding the causes of variation in selection is fundamentally an ecological challenge (MacColl 2011; Moore et al. 1997; Wade & Kalisz 1990). In many species that exhibit social behaviour, the environmental causes of selection can include selection mediated by the interaction between an individual's phenotype and the phenotype of their associates (McGlothlin et al. 2010; West-Eberhard 1979; Wolf et al. 1999). Thus, a trait that co-varies with the social phenotype of the individual will itself be under social selection (Formica et al. 2011; Wolf et al. 1999). In this way, social interactions can shape evolution by generating variance in individual fitness when the distribution of phenotypes in social groups is non-randomly drawn from the wider population. This suggests that phenotypic assortment – the grouping of like individuals – should be a critical parameter under investigation in social species.

Previous studies aiming to understand the evolutionary consequences of social behaviour in animals have generally focused on the importance of individual roles in determining fitness (Szekely et al. 2010; Westneat & Fox 2010) or the selection on phenotypes imposed by environmental niche space (MacColl 2011). However, it may be difficult to determine whether selection acts directly on the match of phenotypes to their environment, or is influenced by the relative state of phenotypes compared to competitors or social partners. For example Price et al.'s classic study of drought-induced natural selection on beak size in *Geospiza fortis* (Price et al. 1984) would seem a prime candidate for selection imposed directly by the environment. However, as Grant and Grant (2006) subsequently showed, the presence of a larger competitor species changed the direction of selection on bill size in a subsequent drought suggesting that interactions with other individuals may have played an important role in determining selection on individual phenotypes. Thus, in some cases, the form of selection on phenotypes is likely to depend on relative measures, which may be determined by local effects (e.g. who an individual interacts with). An example of a localised measure is social dominance, where benefits may relate to rank rather than absolute dominance. In some situations, it may pay for individuals to associate with the same phenotype, for example in the case of predator confusion (Landeau & Terborgh 1986).

Wolf et al. (1999) proposed that the total effect of selection could be partitioned between the selection gradient operating on the individual's phenotype (or focal phenotype) and selection arising from phenotypic assortment (social selection).

They extended the measure of selection gradient proposed by (Lande & Arnold 1983) using partial regression of the relative individual and social trait contributions to the observed fitness:

$$s = P\beta_N + C^I\beta_s$$

where s is the total effect of selection, P is the phenotypic variance-covariance matrix, β_N is the natural selection gradient, C^I is the covariance matrix of interacting phenotypes , and β_s is the social selection gradient. This formulation suggests that social and natural selection gradients can operate simultaneously on individuals, and also that individuals may be able to modify the strength of natural selection through their choice of social niche.

In order to estimate the relative gradients of natural and social selection, we need to accurately measure the phenotypic covariance between interacting phenotypes. Social network analysis is a quantitative approach that is typically used to capture the emergent population-level properties of repeated interactions between individuals (Croft et al. 2008; Krause et al. 2007; Whitehead 1997, 2008); it has been suggested as an accessible way of estimating the evolutionary consequences of social processes (Croft et al. 2008; Farine et al. 2012; Krause et al. 2007; Wey et al. 2008). As a way of measuring differences in social behaviour, social network position has been shown to influence benefits in the short-term, such as finding food (Aplin et al. 2012), and in the medium to long-term for gaining mating opportunities (McDonald 2007; Oh & Badyaev 2010). However, all these studies have depended on network measures based on the global structure of the social network for the observed population; selection can often operate at much finer scales (Svensson & Sinervo 2004). One network statistic that has received much less attention, but which seems ideally suited to quantifying non-random phenotypic interactions is assortative mixing (Farine 2013; Newman 2002). Assortative mixing describes the correlation between the phenotypes of individuals and their associates, or the covariance of interacting phenotypes, that operates at a local scale.

In this study, we investigate the effect of dispersal phenotype on territory acquisition in a wild bird population. In many species, individuals disperse from their native territories shortly after reaching independence, and often have a prolonged period before having the opportunity to breed themselves. By settling in a location early in this phase, individuals may gain advantages over competitors by acquiring more information or familiarity about their environment (Clobert et al. 2009; Forero et al. 2002; Nocera & Betts 2010; Nocera et al. 2006), gaining social dominance (Koivula et al. 1993), or accessing the best breeding sites (Lens & Dhondt 1994). However, this advantage may be dependent on the individual's arrival relative to the arrivals by others. We use a large-scale study combining winter social networks and subsequent observations of breeding behaviour to test whether the acquisition of a breeding territory is mediated by the dispersal phenotype of the individual or its phenotype relative to its associates. We expected that birds that settled early would have a higher chance of gaining a breeding territory, benefiting from residence-related dominance (Sandell & Smith 1991), but that late-arriving birds might be able to reduce the fitness consequences of late arrival if they associated with even later arrivals.

METHODS

Study system and estimation of fitness

The study was conducted on the population of great tits (*Parus major*) at Wytham Woods, Oxford (51°46'N, 01°20'W), starting in May 2011 and running until July 2013. Wytham woods is a 385ha area of broadleaf deciduous woodland, and is surrounded by farmland. As part of long-term monitoring of this population, all breeding attempts in an array of over 1000 nest boxes are recorded (Charmantier et al. 2008). Pairs of great tits defend territories over the breeding season, during which the majority of breeding adult birds were caught. These were fitted with uniquely coded metal rings supplied by the BTO and a passive integrated transponder (PIT) tag, enabling automated detection by radio frequency identification (RFID) antennae. Every surviving nestling was also fitted with both a metal ring and a PIT-tag at 15 days old. In order to capture, ring and tag birds that immigrated into Wytham Woods, extensive mist-netting was conducted during the autumns of 2011 and 2012. Birds were also regularly mist-netted in villages and farms immediately surrounding Wytham Woods. In order to assess the robustness of the results we carried out analyses using, first, all birds (i.e. both those tagged as breeding birds and nestlings) and then second, for the restricted subset of birds that already were tagged when the winter observations began, and which could thus be observed from the first weekend's data collection. Because the network of feeding stations was evenly spaced, and the observation effort was high, we assumed that any tagged bird that had not yet been observed in the wood was not resident.

Fitness was estimated in terms of individual success in hatching chicks in the spring immediately after the winter data collection period. Individuals detected at a nest box were given a value of 1 for that year, and 0 if they were never detected. In order to maximise the chance of detecting breeding attempts in 2012 and 2013, every known great tit nest was fitted a PIT-tag detecting faceplate when chicks were 5 days old. The faceplate on nest boxes are detachable, and were temporarily replaced with a customised faceplate with a built-in RFID antenna (Dorset ID) for up to one hour. The identification of parents already fitted with a PIT tag (approximately 90% of all adults Aplin et al. 2013) was determined as they entered the nest box in order to feed or brood chicks.

Residency time

The territorial behaviour of great tits dissolves after post-breeding, and the population exhibits fission-fusion dynamics (Aplin et al. 2013; Farine et al. 2012). In order to estimate the arrival time of individuals into Wytham Woods, and to identify their social affiliates, individuals were detected in a stratified grid of 65 automated feeding stations fitted with RFID antenna and filled with sunflower seed. Social data was collected for 13 weeks from the start of December 2011 to the end of February 2012, and for 14 weeks from December

2012 to February 2013. Each week, feeding stations were programmed to automatically open for the same two days per week, thereby providing a snapshot of the population structure.

From these data, we extracted the earliest date that each individual great tit was detected. Birds were then assigned the week number (where a value of 1 was given to birds detected on in the first week) as the delay in dispersal time. Arrival times were then standardised to zero mean and unit variance in order to report standardised values of selection.

Inferring the social network

The associations between individuals were inferred from their co-occurrence at the automated feeding stations. We used a recently developed method implementing Gaussian mixture models (Psorakis et al. 2012) that detects non-random bursts of activity, defining each burst as a gathering event. Using a gambit of the group approach (Franks et al. 2010; Whitehead 2008), we calculated dyadic association strength using the simple ratio index (Whitehead 2008). Association strength represents the probability of two individuals being observed to co-occur based on their visits both together and apart, and ranges from 0 (never seen together) and 1 (always seen together). Previous studies have shown that networks estimated via this method are significantly non-random, even when controlling for spatiotemporal effects (Aplin et al. 2013; Farine et al. 2012).

Estimating social selection in social networks

When applied to a single trait, the interactant covariance C^I can be defined as the Pearson product-moment correlation coefficient of a focal individual's phenotype and that of its associates (Formica et al. 2011). In the context of social networks, this is the same measure as the assortativity coefficient for continuous traits (Farine in revision). In this case, P becomes the variance of the phenotype of individuals. If using the weighted assortativity coefficient r_c^w (Farine in revision), then the regression for measuring β_N and β_s should take the form of:

$$w_i = P_i \beta_N + \bar{P}_{i'}^{w} \beta_s$$

where w is the fitness of individual i, P_i is its phenotype, and $\bar{P}_{i'}^{w}$ is the weighted mean phenotype of that individual's associates.

We used a generalized linear model to regress individual's phenotypes and weighted mean of their associate's phenotypes when calculating selection gradients. Given that the fitness measure was binary (0 or 1), we specified a binomial error distribution in the model.

Estimating competition for breeding territories

In order to estimate the role of competition on selection for early arrival, we calculated the ratio of conspecific competitors to available nest boxes in each individual's wintering range. The number of conspecific competitors was calculated based on the proportion of time that individuals spent in each location, summed by location, to generate an estimated total population size at each feeder site. We assigned each great tit nest box (N = 1077) to the nearest feeder site (N = 65), and estimated local competition by dividing the local population size by the number of nest boxes used. For each individual, we then calculated the weighted average competition from their foraging range based on the amount of time they spent at each location.

RESULTS

Social Network

Social interactions across both non-breeding seasons were sparse (network densities were 0.0028 and 0.0030 respectively) but both years were a single fully-connected component. We detected 1053 individual great tits in the 2011/12 winter social network, of which 520 (49.4%) were first-year juveniles. In the 2012/13 social network, we detected 729 individuals, of which 152 (20.9%) were juveniles; the difference in age structure between the two winters results almost wholly from differences in nestling productivity in the preceding breeding seasons, as the number of adult birds (533 and 577) was similar in each year. Juveniles had a significantly higher betweenness in both winters (year 1: juveniles = 2167±259, adults = 745±63; t-test: $t = 5.323$, $df = 580$, $P < 0.001$; year 2: juveniles = 2879±722, adults = 853±62; t-test: $t = 2.795$, $df = 153$, $P = 0.005$; values given as mean±SE), suggesting that juveniles were less sedentary than adult birds.

Individuals were significantly assorted by dispersal phenotype (arrival date) in the social networks from both years. In 2012, the assortativity coefficient r_c^w (± SE) was 0.288±0.003 overall, and 0.359±0.005 in juveniles. In 2013, the assortativity coefficient was slightly lower at 0.188±0.004 overall and 0.214±0.018 in juveniles. In both years, the assortativity coefficient was higher in juveniles than in adults. These patterns were largely driven by differences in spatial distribution of resident and immigrant birds (Figure 1). We found that although areas of high population density were correlated between years (r=0.79, 95% range=0.67-0.86; Figure 2), there was no correlation in the proportion of juveniles that were immigrants or residents (r=0.12, 95% range=-0.12-0.36). This suggests that the local immigration rate was more subject to stochastic effects.

Social selection

Of the 520 juveniles detected in the winter of 2011/12, 179 (34%) were detected as successfully holding a breeding territory and hatching chicks in the following breeding season. We found that there was significant negative selection on individual arrival time, with late arrivals having a lower chance of breeding (Table 1a). However this was counteracted by positive social selection whereby individuals that associated with late-arriving birds had an increased chance of holding a breeding territory (Table 1a). The results were similar in terms of the parameter estimates when restricted to the 283 locally-born juvenile birds that had PIT tags fitted prior to any dispersal movements (Table 1b).

Combining these values with the assortativity coefficient into the equation for estimating total selection on arrival date, we found an overall value of s = -0.444. Here the negative selection on individual arrival time ($P\beta_N$ = -0.776) was counteracted by assortment in arrival times between social partners ($C^I\beta_S$ = 0.332), resulting in a reduced overall strength of selection. Selection was much lower in locally born birds (s = -0.083), due to both a lower strength of selection on individuals ($P\beta_N$ = -0.620) and a greater impact of social selection ($C^I\beta_S$ = 0.537).

Of the 152 juvenile great tits detected in the winter of 2012/13, only 48 (32%) were detected as holding a breeding territory in the spring. We found less support for effect of selection for early arrival time or of social selection on arrival time in this smaller sample (Table 2a). However, the effect size for social selection was similar to the previous year, and suggest a significant effect of social selection in locally-born individuals (Table 2b).

When social and non-social selection were combined, we found weak evidence of selection for early dispersal phenotype on territory acquisition (s = -0.028), but with a similar pattern of selection for early arrival ($P\beta_N$ = -0.220) being counteracted by social assortment by arrival time between social partners ($C^I\beta_S$ = 0.192). In 83 locally-born juveniles, our model estimated a similar component of social selection ($C^I\beta_S$ = 0.505) to the previous year, despite weak selection on individual phenotype ($P\beta_N$ = -0.231). This resulted in positive selection (s = 0.275) driven almost entirely by social effects.

Competition for territory acquisition

Although the parameter estimates for selection on individual phenotype and social selection were qualitatively similar in both years, we found that effects in the second year (2012/13) were less clear-cut. However, in this the second winter and spring many fewer juvenile individuals were present in the population (520 versus 152 juveniles) potentially resulting in a reduction of competition for territories. By estimating local population size across the study area, we found that juvenile birds were competing against significantly more individuals (both adult and juvenile) per great tit nest box in the first year than the second year (mean±SE: year 1 = 1.74±0.05, year 2 = 1.39±0.09; t-test: t = 6.31, df = 1557, P < 0.001). Notably, competition in areas with a large local population (many individuals per nest box) led to an average competition that was much higher than the ratio of birds to nest boxes across the entirety of Wytham Woods (year 1: 1053/1077=0.98, year 2: 729/1077=0.68).

DISCUSSION

We incorporated social network analysis into a multilevel analysis of selection, finding evidence that the social structure of phenotypes in a social network can mediate natural selection. We found that an individual's success in acquiring a territory was predicted not only by its own dispersal phenotype, but also the phenotype of its associates. Individuals whose associates arrived later in the winter had greater chance of settling on a territory in the following spring.

Coupled with significantly high assortment for this trait, the social component of selection largely counteracted the negative selection on individual time of arrival. This clearly demonstrates how local interaction patterns can impact natural selection operating on individual phenotypes.

Our results revealed consistent directions and strengths of social and non-social selection gradients across two years. However, the slope estimate from the regression on the second year of data was not significant. This was likely due to reduced competition for nest boxes in 2013 compared to 2012 (see Figure 1), which was the result of poor breeding conditions in the spring of 2012 and the lowest reproductive success in the history of the Wytham Woods study (Sheldon, B.C. unpublished data). Low breeding success led to a large reduction in the number of juveniles in the second winter, despite having almost the same number of adults present (533 in the first winter, 577 in the second).

In order for social selection to occur, the social environment experienced by different individuals must vary. In a companion study, we found that the social network of great tits in Wytham Woods exhibited significant social structure in a number of phenotypic traits (Farine et al, Chapter 5). For example, social groups were comprised of more even sex ratios than expected by chance. In terms of dispersal phenotype, we found, in that study, significant assortment by immigrant status, where great tits that were born in Wytham Woods being more likely to associate with other resident individuals. Using a range of null models, we were able to disentangle the scale at which individual decision-making led to each component of population structure. Unlike disassortment by sex and assortment by age, we found that assortment by immigration status was driven by differences in spatial range rather than within-location attraction and avoidance. These results could be explained by the findings of the current study. We suggest that, given the importance of prior residency on dominance in this species (Sandell & Smith 1991), newly arrived individuals should respond to competition by settling in areas of relative low population density rather than areas of high-quality habitat. Alternatively, immigrating birds may be using social cues for finding the best habitats by following large groups. This could lead to a trade-off between optimising either short-term benefits from wintering in high-quality habitat, or potential long-term breeding success from reducing competition for territories.

Social selection is likely play a particularly important role in mediating evolutionary dynamics in species that exhibit socio-behavioural flexibility. In fission-fusion societies, such as great tits (Aplin et al. 2013), groups can merge and split to form multi-layered social structures that operate over a range of time scales (Couzin 2006). This flexible social structure is thought to facilitate behavioural plasticity as an adaptive response to changing environmental conditions (Lehmann & Boesch 2004). However, it may also provide individuals with an opportunity to find a good social environment. In house finches (*Carpodacus mexicanus*), poorly ornamented males had a relatively greater probability of pairing with a female if they had greater social connectivity than poorly ornamented males with low social connectivity (Oh & Badyaev 2010). By moving between groups, more social males were able to find an environment that increased their relative attractiveness, thereby reducing the selective load resulting from their own phenotype. However, little is known about how individuals make decisions between options with different social environments. Highly-resolved temporal tracking of dispersing individuals in an intensively monitored population would be one way to establish how individuals trade-off different settlement options.

One challenging concept for social selection is that individuals that gain benefits from their social environment through their social associations typically do so at the expense of their social partners. This is conceptually similar to Hamilton's model of the selfish herd (Hamilton 1971), in which individuals reduce their relative risk of predation by moving to safer parts of the group, subsequently increasing the risk to others (maintaining an average 1/N risk across the herd). For example, Formica et al. (2011) found that in response to selection for large body size, male forked fungus beetles (*Bolitotherus cornutus*) could partially counteract this selection by associating with smaller conspecifics and hence transferring fitness costs to these. A further example in which individuals can benefit from disassortment in a frequency-dependent context is producer-scrounger games (Dubois et al. 2012). However, some cases may also exist where mixed-phenotype groups may generate benefits for all participants. Groups of great tits with different personalities may exhibit short-term emergent properties of collective behaviour that are not found in more uniform groups (Farine et al., in revision). Similarly, in terms of predation, the rapid movement of phenotypically identical individuals can make tracking of prey more difficult for predators, thus impacting the probability of a successful attack (Landeau & Terborgh 1986). These examples highlight how population phenotypic structure in social animals can have a profound impact on selection. Failure to consider this is constitutes a substantial omission in our ability to understand the process of natural selection.

This study provides evidence that selection for a phenotypic trait may be altered by patterns of interaction among individuals. Individuals were more likely to acquire territories if they dispersed early, but late arrivals could increase their likelihood of breeding if they associated with other late arrivals. Importantly, this finding provides a evolutionary mechanism that could underpin patterns of social structure found in previous studies on this population, such as the spatial disaggregation of immigrant birds (Farine et al., in prep). Given the growing number of studies gathering long-term social network data in animal populations (Farine et al. 2012; Rutz et al. 2012; Ryder et al. 2012), the ability to incorporate a network assortativity measure into models of selection will help us to elucidate the contribution of interacting phenotypes in social evolution.

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FIGURES

Figure 1. Proportion of local juvenile population that were immigrant in the first (a) and second (b) winters. Immigrant individuals (born outside of Wytham Woods) were spatially disaggregated from locally-born juveniles (see also Chapter 5), leading to significant social variation in dispersal phenotype across the study area. Immigrants accounted for 45% of all juveniles in both years.

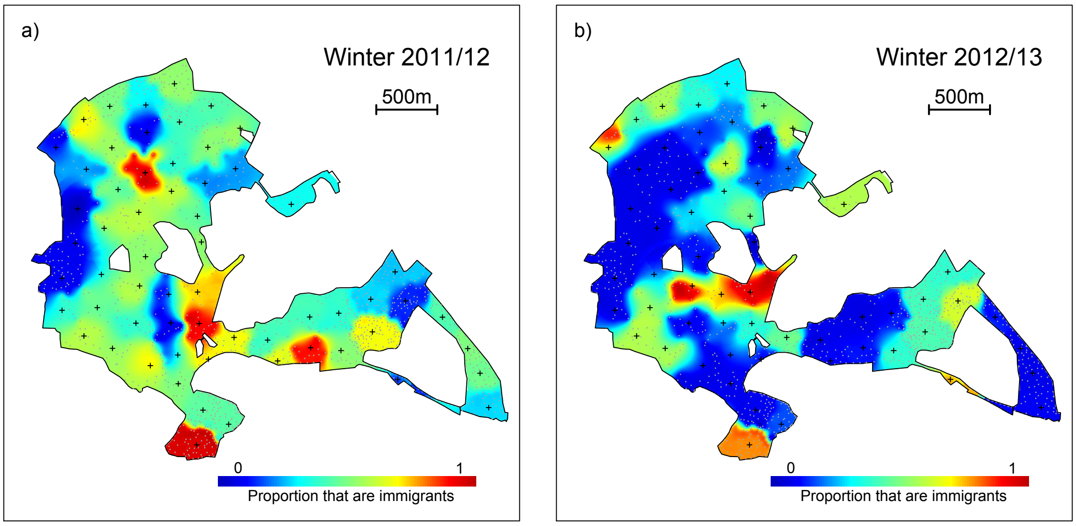
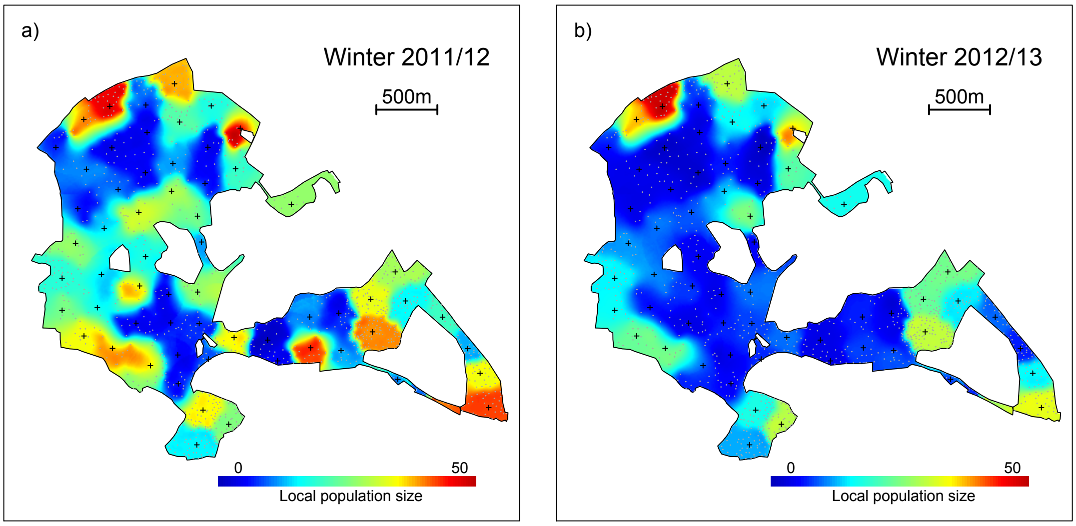


Figure 2. Variation in local population size estimated from each automated feeding station (crosses) in the first (a) and second (b) winters. Great tit nest boxes are represented as grey dots. Population size was much smaller in the second year, resulting in lower competition for nest boxes. Surfaces were interpolated from estimated population size at each feeding station by fitting a spherical kriging model with a range of 200m in R (R Development Core Team 2013).



TABLES

a)

Type of selection	Trait	$\beta^{(standardised)}$	SE	P
Non-social	Arrival date	-0.776	0.148	<0.001
Social	Weighted arrival date of associates	1.152	0.307	<0.001

b)

Type of selection	Trait	$\beta^{(standardised)}$	SE	P
Non-social	Arrival date	-0.620	0.191	0.001
Social	Weighted arrival date of associates	1.508	0.443	<0.001

Table 1. Social and non-social selection gradients of winter dispersal phenotype on spring 2012 territory establishment for all first-year great tits (a) and restricted to locally-born great tits that were fitted with PIT tags as nestlings (b).

a)

Type of selection	Trait	$\beta^{(standardised)}$	SE	P
Non-social	Arrival date	-0.220	0.187	0.240
Social	Weighted arrival date of associates	1.021	0.610	0.094

b)

Type of selection	Trait	$\beta^{(standardised)}$	SE	P
Non-social	Arrival date	-0.231	0.234	0.813
Social	Weighted arrival date of associates	2.363	1.015	0.020

Table 2. Social and non-social selection gradients of winter dispersal phenotype on spring 2013 territory establishment for all first-year great tits (a) and restricted to locally-born great tits that were fitted with PIT tags as nestlings (b).

CHAPTER 7

The early bird gets the worm: foraging strategies of wild songbirds lead to the early discovery of food sources

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Animal behaviour

The early bird gets the worm: foraging strategies of wild songbirds lead to the early discovery of food sources

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Animals need to manage the combined risks of predation and starvation in order to survive. Theoretical and empirical studies have shown that individuals can reduce predation risk by delaying feeding (and hence fat storage) until late afternoon. However, little is known about how individuals manage the opposing pressures of resource uncertainty and predation risks. We suggest that individuals should follow a two-part strategy: prioritizing the discovery of food early in the day and exploiting the best patch late in the day. Using automated data loggers, we tested whether a temporal component exists in the discovery of novel foraging locations by individuals in a mixed-species foraging guild. We found that food deployed in the morning was discovered significantly more often than food deployed in the afternoon. Based on the diurnal activity patterns in this population, overall rates of new arrivals were also significantly higher than expected in the morning and significantly lower than expected in the afternoon. These results align with our predictions of a shift from patch discovery to exploitation over the course of the day.

1. Introduction

Small birds exhibit predictable management of body mass in order to manage overnight survival. Under high perceived predation risk, individuals employ a strategy whereby they trade-off their starvation risk by reducing fat storage to maintain greater flight ability [1,2], delaying weight gain until later in the day [3,4]. During winter months, birds are under increased time and energy constraints resulting from shorter day length and colder temperatures. Therefore, they must ensure that they have access to enough resources to meet a higher rate of energy intake late in the day. Despite considerable work on body-mass strategies, the process relating to the discovery and sampling of resources has received much less attention.

Models dealing with resource uncertainty predict that individuals should increase fat storage linearly during the day [3,5], a strategy that is clearly incompatible with avoiding predation [6]. Existing work highlights the ability of individuals to locate the most profitable food sources using optimal sampling [7]. Thus, by sampling a number of sites earlier in the day, individuals should be able to exploit the most profitable site later in the day as the risk of overnight starvation increases. This would be particularly important for individuals employing a body-mass delay strategy; rather than exploiting known patches in the morning, birds could be searching (either socially or asocially) for new resource locations while they are light or when predation risk is low. Models of caching behaviour suggest high rates of caching in the morning with high retrieval rates late in afternoon [8].

Taken in combination, these models suggest that knowledge of the location of a reliable food source is paramount for individuals to optimally manage the risks of predation and starvation. Yet, models have not incorporated strategies that gather information about food availability as a way of dealing with resource uncertainty.

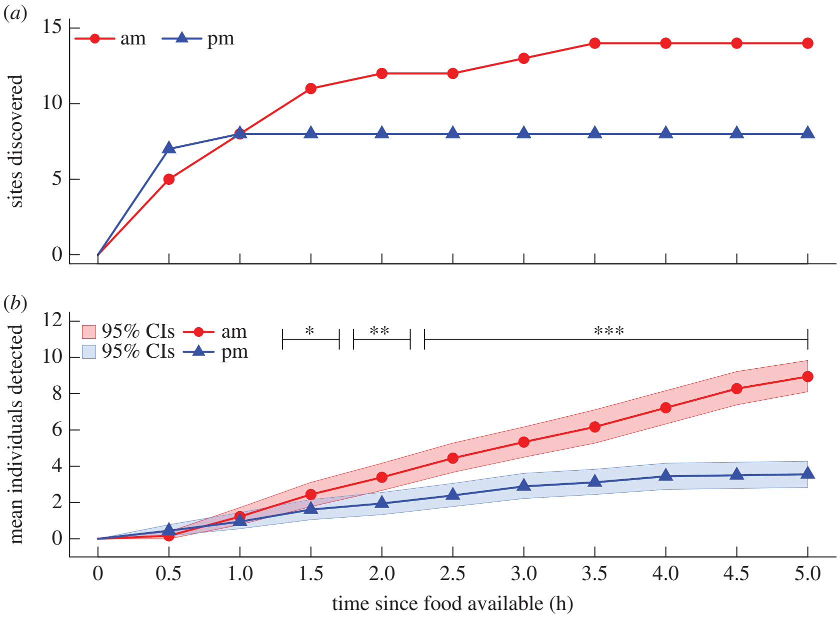

Figure 1. (*a*) The discovery of sites was significantly higher in the morning than the afternoon. Discovery of afternoon sites all occurred in the first hour, suggesting that these treatments commenced at the tail end of the searching period. (*b*) Cumulative number of new individuals arriving over time (shown with 95% CIs, stars represent significance). Asterisks represent significance (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$). (Online version in colour.)

Here, we propose a new hypothesis; individuals should prioritize discovery and assessment of potential resources early in the day, before switching to exploitation as the day progresses.

In this study, we tested for temporal dependence in food discovery behaviours. We predicted that if individuals are shifting strategies from exploration to exploitation, we should observe a non-random pattern of within day-discovery, with higher probabilities of discovering food earlier in the day. Given the presence of multiple species in the population, we then tested for species-level differences, testing the prediction that caching species should be more likely to discover novel food sources earlier given their need to accumulate food earlier than non-cachers [8].

2. Material and methods

(a) Discovery of foraging patches

We ran 36 independent trials at 18 unique sites within Wytham Woods in Oxfordshire, UK (51°46′ N, 1°20′ W) in a fully balanced experimental design. Sites were chosen by randomly selecting coordinates within the boundaries of the woodland ensuring that they were sited at least 150 m apart and 100 m away from any permanent feeding locations. Each day, three feeders (sites) fitted with radio-frequency identification (RFID) antennae were placed at different sites in the morning (from 07.00) and three more at other sites in the afternoon (from 12.00), for 5 h each. Two weeks later, each site was deployed during the other time period. Thus, each of the 18 sites was sampled twice, once in morning and once in the afternoon. Feeders detected individual great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*) and nuthatches (*Sitta europaea*) that had been fitted with PIT-tags either as nestlings or during extensive pre-winter catching as part of on-going research into social behaviour in this population [9,10]. We tested whether sites were more likely to be discovered early in the day by recording the arrival of first individual at each site in each treatment (a ‘discovery’). Subsequent arrivals by new individuals were used to test whether a greater number of individuals arrived in morning treatments, using 1000 randomizations of the data that controlled for social effects (see the electronic supplementary material). We calculated 95% confidence intervals (CIs) using 1000 bootstraps on each treatment.

(b) Population-level patterns

In order to assess the relationship with activity levels in the population, we used data from a permanent grid of 65 feeders fitted with RFID antennae. These feeders are placed approximately 250 m apart and designed to open concurrently 2 days per week (from pre-dawn to post-dusk), providing a snapshot of the population structure and activity pattern. We used data from this grid over the three weeks that discovery feeders were deployed (but opened on different days and kept spatially separated from these sites). In order to avoid effects of changing day lengths when combining data, we scaled the daily foraging data to fit into 20 evenly spaced segments that were approximately half-an-hour long (range 28.8 min to 31.2 min long). Finally, we tested the alternative hypotheses that arrivals to novel feeders were related to activity levels by dividing the probability of arriving at feeders by the independent feeding and movement rates at those times. All statistical analyses were conducted in R [11].

(c) Species effects

In order to assess whether there was a non-random distribution of discoveries according to species, we calculated the odds of each species discovering the novel food site given the frequency of species visiting the feeders in the population. The CIs were estimated using 1000 jackknife simulations of the data where one data point was removed in each simulation. We then tested for a non-random distribution in arrival order of the different species by calculating the mean for each species. We estimated two-tailed significance by running 1000 permutations of the arrival order (randomizing orders between individuals within sites and days) and calculated the number of mean randomized orders that were greater or less than the observed mean order in each species.

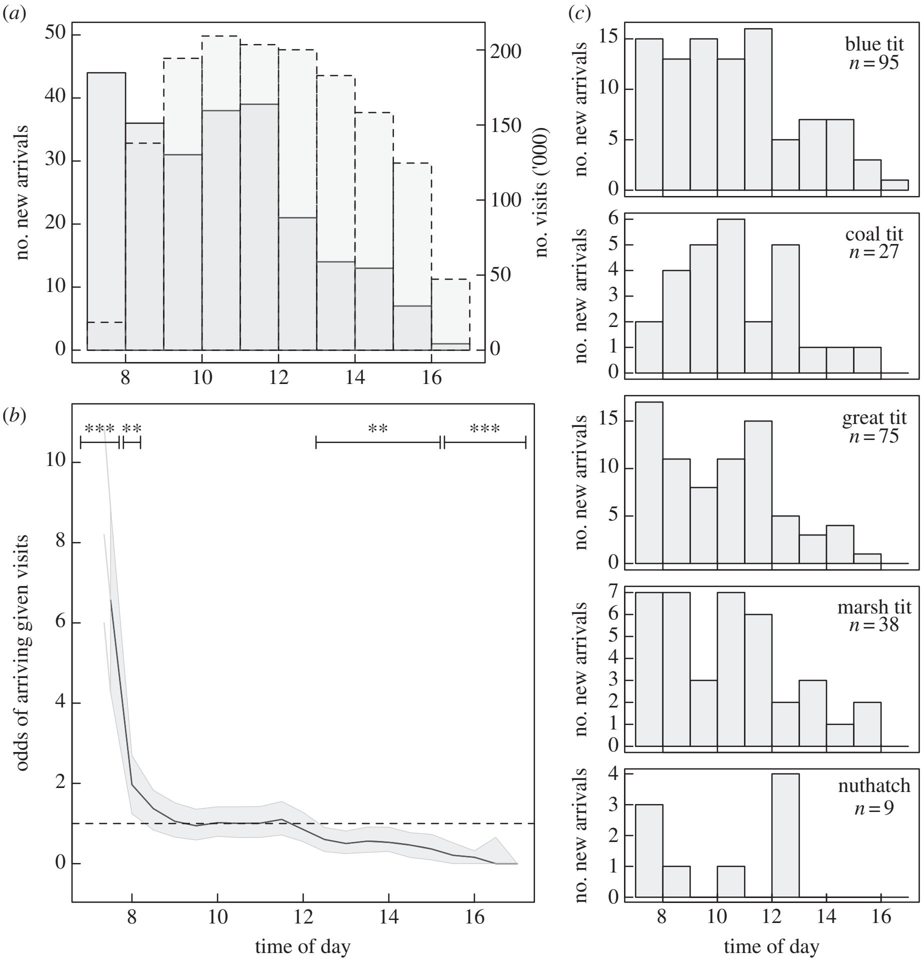

Figure 2. (*a*) Data showing fewer new individuals arriving at sites in afternoon treatments (from 12.00 onwards, solid bars), which differed from the feeding activity (dashed bars). (*b*) The odds of arriving given the feeding activity was greater in the morning and dropped to below expected in the afternoon (dashed line shows expected 1-to-1 ratio, shading are 95% bootstrapped CIs, significance is calculated from the number of bootstraps overlapping 1). Asterisks represent significance (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$). (*c*) The pattern was general across species.

3. Results

(a) Discovery of food patches

There was a clear difference in site discovery events across the day. In total, 22 of the 36 feeders were discovered (14 in the morning and eight in the afternoon treatments; paired *t*-test: $t = 2.92$, d.f. = 17, $p < 0.01$; figure 1*a*). No site, which was discovered in an afternoon treatment, had not discovered in its paired morning treatment. Furthermore, the number of new individuals arriving at sites was significantly higher throughout the morning than the afternoon (180 individual morning discoveries versus 64 in the afternoon; figure 1*b*). This is unlikely to have occurred due to environmental differences between sites as the experimental design was fully balanced with both morning and afternoon treatments conducted at each.

(b) Relationship with activity pattern

We found that morning discoveries occurred significantly more often than expected from the foraging activity (figure 2*a*,*b*). The odds of individuals discovering a resource in the first hour of the day was at least eight times more than expected, whereas from 13.00 onwards the odds dropped below the value expected from foraging activity. Although arrivals by individuals at feeders may be mediated by social mechanisms such as local enhancement [9], group sizes were larger in the afternoon than in the morning (see electronic supplementary material, figure S1) and therefore unlikely to explain the observed pattern.

(c) Species effects

The patterns of new arrivals were similar across all species (linear models: all $p > 0.05$, figure 2*c* and electronic supplementary material, table S1). However, there were proportionally fewer blue and great tits than expected given their relative abundance in the population (odds ± 95%CIs 0.75 ± 0.19 and 0.95 ± 0.30, respectively, expected = 1). By contrast, coal tits, marsh tits and nuthatches all had higher numbers of individuals finding feeders (odds ± 95%CIs 2.22 ± 1.50, 2.42 ± 1.34 and 2.09 ± 2.26, respectively). The same pattern held with the order of arrival after a site had been discovered (expected range is 95% of the posterior distribution). Both blue (mean 12.5, expected 9.6–12.5, $p = 0.05$) and great tits (mean 13.6, expected 9.4–12.8, $p < 0.01$) arrived later than expected. Coal tits (mean 8.6, expected

8.0–14.5, $p = 0.09$), marsh tits (mean 5.6, expected 8.4–13.8, $p < 0.001$) and nuthatches (mean 5.7, expected 5.8–17.8, $p < 0.05$) mostly arrived earlier than expected.

4. Discussion

Using experimental deployment of novel food patches combined with automated detection, we demonstrated that birds exhibit clear differences in foraging strategy over the course of a day. Patterns of discoveries closely matched our predictions with sites having a greater probability of being discovered in the morning than the afternoon. These patterns were not explained by the general feeding activity.

An alternative explanation for the observed daily patterns in patch discovery is that there is a switch between the marginal values of foraging and gaining information in the early morning. Under this hypothesis, individuals need to replenish energy lost overnight, thereby increasing the marginal value of known patches early in the morning. As patches are exploited and the value of acquiring energy decreases, the marginal value of a bird’s current patch decreases; consequently causing all individuals to leave their patches in search for new ones. However, while this would result in a high rate of morning discoveries, it should also be accompanied by a morning peak in between-site movements as individuals refresh their information and relocate to the richest remaining patches. Analysis of movements between known feeding sites by individuals in the permanent grid does not support this hypothesis (see electronic supplementary material, figure S2).

The second part of our hypothesis relates to the exploitation of better patches late in the day. Movements by individuals between known feeders showed a clear burst of relocations approximately 2 h before dusk, followed by a drop in movements (see electronic supplementary material, figure S2) that were not related to the pattern of site discoveries (see electronic supplementary material, figure S3). A recent study on closely related species also found a peak in feeding activity at known food sources approximately 2 h before sunset [12]. These results are inconsistent with our hypothesis; as individuals should preferentially forage immediately before sunset. However, this could emerge from a trade-off with several other competing pressures on survival strategies, including: (i) time spent searching for or guarding roosting sites, and (ii) exclusion from high-quality patches by socially dominant individuals. End-of-day foraging strategies warrant further investigation, and experiments using varying patch qualities is a clear future step.

This study shows clear differences in the behaviour of individuals over the course of a day. We found that individuals partitioned foraging into searching and feeding behaviour, potentially enabling optimal management of the opposing predation and starvation risks. This implies that behavioural plasticity plays an important role in mediating survival in a way that has not previously been considered by existing studies.

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Data accessibility. We provide the data of patch discovery via the Dryad repository (doi:10.5061/dryad.9g6q2) [13].

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Farine and Lang: The early bird gets the worm: foraging strategies of wild songbirds lead to the early discovery of food sources

SUPPLEMENTARY METHODS

Deployment times

Deployments of feeders were designed to fit equally between dawn and dusk. Due to travel times between each deployed feeder, morning sites were deployed between 7am and 8am, with sunrise occurring at 7am at the start of our study. These were then removed between 12pm and 1pm, exactly five hours after being deployed. Afternoon treatments were set out between 12pm and 1pm (after being collected from morning sites), and removed between 5pm and 6pm. Sunset at the start of our study was 5:23pm.

Permutation test

Due to the large number of undiscovered sites, and the potential for social effects in the number of individuals that arrived at a given site, we used a permutation test to examine the difference between morning and afternoon treatments. The same permutation test was conducted on each half-hour segment (from 0 to 5 hours) by comparing observed difference in the mean number of individuals that arrived at morning treatments and afternoon treatments with the posterior distribution of differences. For each permutation, we randomly swapped feeders between morning and afternoon treatments and calculated the resulting difference in the means between these two resulting groups. This process was repeated 1000 times to generate the posterior distribution of randomised differences. The reported P-values are the proportion of times the difference between the am and pm means from a permutation was greater than or equal to the observed difference. Given that discoveries may not have been independent, we randomised all individuals at a feeder in a given half-hour as one observation rather than re-distributing each individual independently.

Group size over the day

In order to test for the potential confounding effect that larger group sizes may result in a greater number of individuals discovering sites in the morning rather than the afternoon, we examined the group size distribution for each half-hour period in the day from the permanent grid of feeders. In order to infer groups in this stream of data, we used Gaussian mixture models [1]. This approach has previously been used for inferring social network structure in this population [2]. It determines regions of temporally dense activity in the visitation profile in order to infer the best-fitting number of clusters or 'gathering events'. It then finds the best-fitting model for each visit cluster based on the power-law distribution of the difference in arrival times between consecutive individuals. Finally, it calculates the membership of individuals in groups based on their visit time. Thus, this machine-learning method automatically estimates the best fitting group co-membership in the population by reducing overall entropy in the system. Groups ranged in duration from 2 to 10 minutes in length, and from 2 to 29 individuals. In order to assess the pattern of group size over the course of the day, we then fit a smooth spline to the group size distribution using the central time of each group.

Underlying movement pattern

Our hypothesis takes two parts: i) that individuals should search more actively for food in the early parts of the day, and then ii) that these individuals should exploit the best food patch at the end of the day. In order to test if this could be happening, we isolated all within-day movements by individuals between known food patches from the permanent grid of feeders, comparing the distribution of these movements over the course of the day to the activity pattern from the overall visits. The hypothesis suggests that movements between these known sites should abruptly end as the birds shift to exploiting the site they decide is best.

SUPPLEMENTARY RESULTS

Discovery by species

Species	*Coefficient*	*SE*	*P*
Blue tit	3.863		
Coal tit	0.099	0.496	0.841
Great tit	-0.463	0.351	0.189
Marsh tit	-0.257	0.437	0.556
Nuthatch	-0.419	0.794	0.598

Table S1. Model of arrival times by species using data from Figure 2c shows that there is no significant difference between species using blue tits as the reference category.

Group size

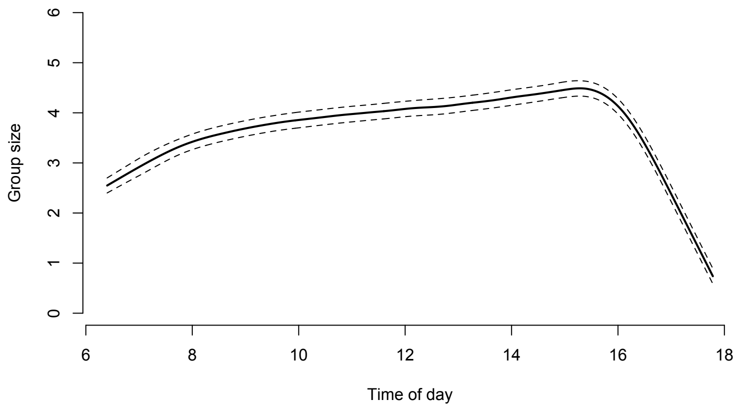

Figure S1. Observations from the permanent grid of 65 feeders suggest increasing group size over the course of the day, until a fission event late in the afternoon. The greater number of discoveries observed in this study were unlikely to have resulted from larger groups early in the day.

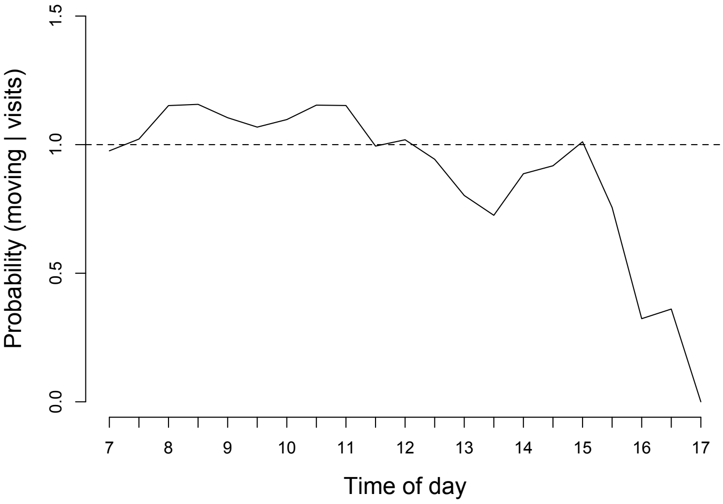

Figure S2. The pattern of movements by individuals between feeders in the permanent grid supports the hypotheses that individuals settled on their optimal food source at the end of the day. There was little deviation of movements between feeders during the first half of the day, suggesting that the searching behaviour exhibited by birds at that time of the day was independent of movements between known food sources. The number of movements in the second-half of the day were lower than expected, with the exception of a peak approximately two hours before dusk that could be due to individuals moving to their preferred food source for exploitation.

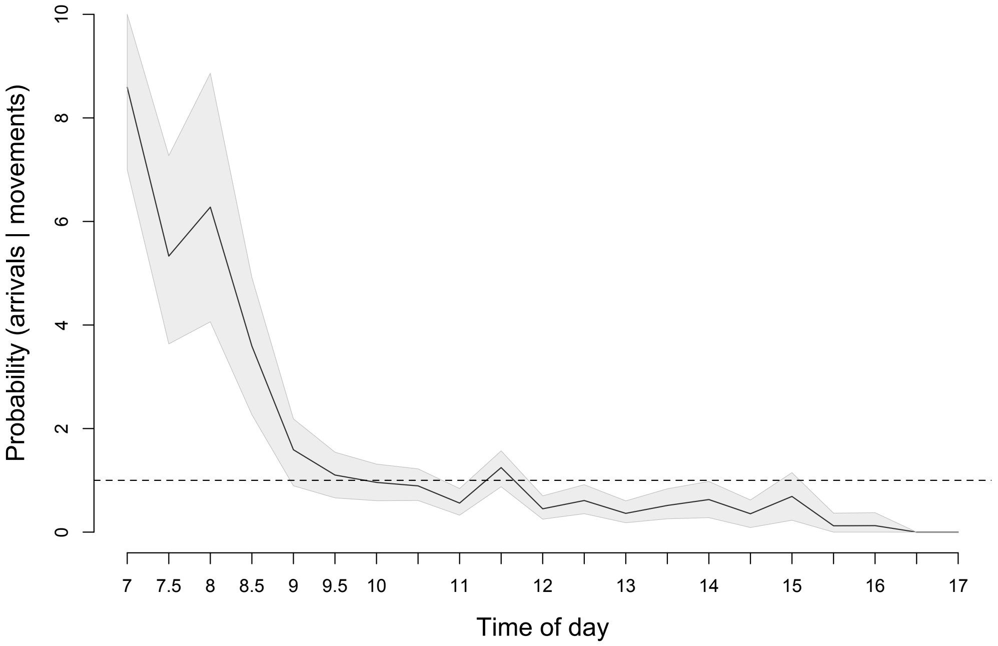

Figure S3. Odds of discovery of an experimental site (data from Figure 2a) given the pattern of movements by individuals between known sites. This shows that the large number of early morning arrivals was not explained by movement rate in the underlying population. Solid line is the ratio of new arrivals (discoveries) at novel food resources and the movement between known sites from the permanent grid of feeders. Grey shading is the 95% confidence range of the odds calculated using bootstraps per Figure 2b.

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CHAPTER 8

Individuals use similar interaction rules for conspecifics and heterospecifics in mixed-species flocks

Individuals use similar interaction rules for conspecifics and heterospecifics in mixed-species flocks

Damien R. Farine, Lucy M. Aplin, Colin J. Garroway, Richard P. Mann,
Ben C. Sheldon

ABSTRACT

Associations in mixed-species foraging groups are common in animals, yet have rarely been explored in the context of collective behaviour. It is thus unknown whether interaction rules with which individuals maintain behavioural synchrony also generalise to heterospecific interactions. We used an automated data collection protocol to analyse the movement decisions of wild birds within mixed-species foraging groups in relation to the proportion of heterospecifics and conspecifics. Replicated food patches were installed in a population of forest passerine birds over two winters, recording 91,576 feeding events by 1904 individuals of five species. We demonstrate highly synchronised feeding behaviour; individuals actively moved from low to high-density parts of the flock. Fitting a model to interaction patterns within the flock suggested that individuals applied similar decision-making rules to both conspecifics and heterospecifics. The rule consisted of movements towards areas with a greater proportion of the flock, irrespective of species. This suggests that heterospecifics provided similar information, such as patch quality or safety from predators, to conspecifics. Our

results demonstrate that social interactions with individuals of other species can be equally as important as those with conspecifics.

INTRODUCTION

Living in groups forms an integral part of the life history of many animals, providing positive benefits to individual participants through reducing predation risk (Cresswell & Quinn 2004; Hamilton 1971; Ioannou et al. 2012; Krause & Ruxton 2002), facilitating information transfer (Couzin 2009) and improving decision-making (Sumpter et al. 2008; Ward et al. 2011; Ward et al. 2012; Ward et al. 2008). However social living may also be costly, as it can increase resource competition (Dhondt 2012; Krause & Ruxton 2002), and exposure to parasites and disease (Krause & Ruxton 2002). One common strategy for reducing competition for shared resources while maintaining anti-predation benefits is to join mixed-species groups (Greenberg 2000; Harrison & Whitehouse 2011; Krause & Ruxton 2002). By associating with ecologically similar, but not identical, species, individuals may potentially be able to continue acquiring relevant benefits such as safety from shared predators (Sridhar et al. 2009) and information about the environment (Seppanen et al. 2007), while reducing niche overlap (Greenberg 2000; Harrison & Whitehouse 2011; Krause & Ruxton 2002). If this hypothesis is true, we predict that given a choice of where to forage within a patch, individuals will move to, and maintain, areas of high density, regardless of species. However, the strength of social attraction may vary, reflecting individual and species differences in the balance of costs and benefits. To test these predictions, we fit a model quantifying social attraction within groups to automated data collected from wild flocks of songbirds. We then test if this simple rule is sufficient to describe these patterns via simulations.

Studies of the social behaviour of monospecific groups have shown that strikingly complex patterns of movement and behaviour can emerge from relatively simple social interactions between individuals (often referred to as collective animal behaviour; (Ballerini et al. 2008; Buhl et al. 2006; Guttal & Couzin 2010; Ioannou et al. 2012; Sumpter 2006, 2010)). These patterns can be reproduced using simple algorithmic rules (Couzin & Krause 2003; Herbert-Read et al. 2011; Katz et al. 2011; Sumpter 2010). The emergence of complex grouping behaviour from simple social rules based upon attraction to, and repulsion from, nearby conspecifics (Arganda et al. 2012; Couzin & Krause 2003; Herbert-Read et al. 2011; Katz et al. 2011; Perez-Escudero & de Polavieja 2011; Perez-Escudero et al. 2013; Sumpter 2010) should apply equally in mixed-species groups, thereby generating heterospecific social behaviour (Buskirk 1976) (such as in mixed-schools of fishes (Hoare et al. 2000), herds of ungulates (Fitzgibbon 1990), or flocks of birds (Farine 2013; Farine et al. 2012; Farine & Milburn 2013)). As Morse (Morse 1970) stated, "[group] formation depends upon positive responses by individuals to members of their own or other species", where the positive response separates mixed-species groups from aggregations due to localised food or water.

A recent study in flying flocks of two species of corvids found that individuals associated and aligned most strongly with conspecifics (Jolles et al. 2013), suggesting a two-level interaction structure might maintain first pair, and then group formation. Importantly, this study highlighted potential heterogeneity in collective behaviour at the species level. However, it could not distinguish individuals, and thus could not identify individual-level decisions, infer interaction rules, or generate predictions about collective decision-making processes.

One approach that has successfully linked individual decision rules to the biology of social groups is the combination of empirical data with mathematical models of decision-making derived from theory (Sumpter et al. 2012). Fitting models to empirical data has been used to determine the rules that maintain synchrony in birds (Ballerini et al. 2008), fish (Herbert-Read et al. 2011; Katz et al. 2011), and invertebrates (Ame et al. 2006). For instance, cockroaches have a tendency to aggregate and fill available capacity in a subset of shelters before utilising empty ones (Ame et al. 2006). Once a predictive model is generated, simulations can be used to make predictions about the adaptive function of these rules. For example, the aggregation rule used by cockroaches produced an emergent pattern that was found to maximise individual fitness when simulated in agent-based models. As a result, this study suggested that temporary areas, or patches, that are safer than those that surround them can emerge as a by-product of the dynamic self-organisation by individuals responding to the distribution of others, even in a uniform landscape (Ame et al. 2006).

We recorded the movement decisions of individually marked birds participating in mixed-species flocks to determine the relative importance of conspecifics and heterospecifics in generating coordinated group behaviour. We investigated (i) whether interaction rules used by individuals varied in response to conspecifics and heterospecifics, (ii) whether the flocking rules we inferred can reproduce the patterns of movement by individuals in mixed-species flocks, and (iii) if interaction rules varied between members of the flock. We observed the movements of birds within flocks formed at four identical feeders in a contiguous habitat patch and fitted a Bayesian decision-making model (Arganda et al. 2012) to quantitatively estimate the attraction of individuals to conspecific and heterospecific flock members. Using an agent-based model, we then simulated flocks of birds using these same rules to identify if it was sufficient to recreate the pattern we observed in wild mixed-species groups. In doing so, this study provides a benchmark for understanding the nature of mixed-species flocks using approaches from computational biology.

METHODS

Study Site and General Protocol

The study took place at Wytham Woods (51° 46′N, 1°20′W), Oxfordshire, United Kingdom. Great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Peocile palustris*), coal tits (*Periparus ater)* and Eurasian nuthatches (*Sitta europaea*) were caught in mist-nets using multi-access feeders regularly during the two winters in which the study took place. In addition, locally-breeding birds and their offspring were caught in their nest-boxes during the spring as part of long-term field studies in this population (Aplin et al. 2012; Farine & Lang 2013). All individuals were fitted with a British Trust for Ornithology (BTO) metal leg-ring and a plastic leg-ring containing a uniquely coded PIT-tag (IB Technology, Aylesbury). We estimate that the proportion of the population fitted with PIT-tags exceeded 90% at the time of the study (Aplin et al. 2013a). All handling and ringing was undertaken under license by the BTO, and approved by the University of Oxford's Local Ethical Review Panel. We conducted five replicates of the study in February 2011, and fifteen replicates between December 2011 and February 2012. Patches were placed throughout the woods, capturing the variation in population densities across different microhabitats. On some occasions, up to three replicates were running simultaneously; however these were spaced at least 1km apart and no individuals were detected at more than one replicate when replicates were simultaneous.

Field Observations

At each replicate, we deployed a square of four identical feeders filled with un-husked sunflower seeds (henceforth a *patch*; Figure 1a). Each feeder contained two access holes, both fitted with an antenna capable of reading the PIT tag fitted to birds as they land on the surface of the antenna (Francis Instruments, Cambridge). We filled feeders with sunflower seed, allowing birds to pick up a seed from the feeder and then perch nearby to remove the husk, thereby minimising interference competition (Aplin et al. 2013b). Further, these feeders provide food at a constant rate thereby removing any effects of perceived resource depletion on foraging decisions (Stephens et al. 2007). Eating seed in this fashion, birds did not form independent groups on each feeder, but maintained more natural flock formation in the nearby trees.

Feeders were placed 50m apart, which is within visual and auditory range of other birds, but avoids the potential for individuals to feed on different feeders from the same perching location. Patches were fully contained within a contiguous habitat type, and some feeders were occasionally moved inwards up to 5m in order to minimize differences in habitat features known to alter feeding behaviour (Dolby & Grubb 2000). Each patch was set out and marked in the days preceding deployment. Feeders were then installed after dark the night before commencing data logging to maximize natural discovery and behaviour at the patch. Patches were checked from day two onwards and removed once the food in any one feeder was fully depleted; if this did not happen the deployment was ended on the fourth day and data from that day were discarded. The antennae recorded the identity of all birds visiting the feeder, scanning for the presence of a tag every 1/16th of a second and logging one record per bird in each 15 second interval.

Data Analysis

Response to flock mates: We combined the records from each of the four feeders into one data-stream and extracted every occurrence of an individual moving between feeders within a patch (Figure 1b). Individuals were defined as having remained within the patch if the gap between successive logged visits was no greater than 240 seconds. This value was based on the estimated inflection of the Poisson distributed movement times (Figure S1), representing the point where the distribution changes from the peak to the tail. Biologically, this point represents where repeated samples taken from the right-hand side of the distribution are more different (inter-visit intervals are more likely to be different) than from the left-hand side (intra-visit intervals are less likely to be different). For each movement event, we recorded which feeders the individual moved from and which it moved to, as well as the distribution of all other individuals in the patch at the time of each event.

In order to determine the attraction or repulsion to others in their flock, we used Bayes' rule to calculate the probability of birds leaving from, or arriving at, feeders conditioned upon the relative proportion of individuals present on each feeder. The distribution of individuals across feeders was taken from detections on each feeder in the 30 seconds prior to departure or arrival (two 15 second time steps from our logging hardware, see Figure 1b). The density-dependent probability of leaving (L) or arriving (A) at a feeder of density ρ was then calculated using (Mann 2011; Perez-Escudero & de Polavieja 2011):

$$P(L \text{ } or \text{ } A \mid \rho) = \frac{P(\rho \mid L \text{ } or \text{ } A) \, P(L \text{ } or \text{ } A)}{P(\rho)}$$

where $P(\rho)$ is the frequency (i.e. distribution) of densities ρ that were observed on all feeders (taken from all visits in the data), and $P(L \text{ } or \text{ } A)$ is the prior probability of leaving or arriving at a given feeder independent of proportion (which we fixed at $P(L \text{ } or \text{ } A) = 1/4$). $P(\rho \mid L \text{ } or \text{ } A)$ is the observed frequency of a density ρ at the feeder where and when individuals were detected to be either leaving or arriving. Finally, the observed probability of leaving and arriving given density was divided by a theoretical asocial prediction (*TASP*) . This calculates the odds-ratio of leaving (the *tendency to leave*) or of arriving (the *tendency to arrive*) at a given density. In the *TASP*, individuals arrived at feeders with a probability inverse to the density ($P(\rho) \propto {}^{1}/_{\rho}$) but left in proportion to the number of at that feeder ($P(\rho) \propto \rho$; as would be expected if randomly selecting individuals rather than feeders).

Modelling heterospecific versus conspecific decision rules: In order to calculate the relative weighting applied to conspecifics and heterospecifics in within-patch foraging decisions we fitted a decision-making model (Arganda et al. 2012) to our observed data using maximum likelihood estimation of the model parameters. The derivation of the model (Arganda et al. 2012) introduces a parameter S equating to an individual's judgement that others make a 'good choice' S times more often than a bad choice (see equation 1). This model was set within the context of information use, which can refer to food quality, information about predation risk (Arganda et al. 2012; Perez-Escudero et al. 2013), or as a result of local enhancement and social learning known to occur in this population (Aplin et al. 2013b). In this study we quantified model parameters primarily to assess the relative contribution of different components within flocks on individual movements. The probability of choosing an option is a flexible response, ranging from near-linear to a sigmoidal response to distribution of individuals across different choices, making this model qualitatively compatible models of predator avoidance in space. For example, in models of the selfish herd, a sigmoidal function best replicated the patterns of groups observed in space (Beecham & Farnsworth 1999; Viscido et al. 2002).

Our prediction for an individual's decision (the probability of going to site X_i based on the behaviour B of previous individuals in choosing that site) is based on the relative distribution of individuals across the patch at that time, given by the equation (Arganda et al. 2012):

$$P(X_i|B) = \frac{1}{1+S^{-\frac{(n_x - k\sum_{i \neq x} n_i)}{N} \times 10}} \quad \text{(eq.1)}$$

Here, n_x defines the number of individuals already on feeder x, and $\sum_{i \neq x} n_i$ is the sum of individuals on each of the other feeders i. N represents the total number of individuals in the patch. Given that $\sum_i P(X_i|B)$ can exceed 1, an additional step of probability matching is used (where the each probability is divided by the sum of probabilities) (Arganda et al. 2012). Group sizes were scaled to 10 in order to maintain a consistent size that S acts upon, as large groups require a smaller S value to drive the same pattern as in a small group. From this equation (see also Figure 2), a value of $S = 1$ suggests no socially mediated response, or an equal probability of picking any site regardless of where individuals are located ($P(X_i)$ = 0.25 for all four feeders at all times after applying probability matching). When $S > 1$, individual decisions are influenced by the distribution of others within the patch (Figure 2). At small values of S (note that 'small' depends on group size as S scales in inverse proportion to mean group size), the probability curve is almost linear with only a small increase in the probability of choosing a busy feeder over empty feeder. At larger values of S, this curve becomes sigmoidal, and the probability of choosing empty feeders approaches 0. The second parameter in this model, k, estimates the influence of individuals at a feeder on the quality estimate of other feeders. High values of k indicate that the relative difference in the proportion of individuals is used (by choosing one option, an individual reduces the quality of all others for the following individual), whereas low values of k suggest that individuals use probability matching based on the absolute number of individuals on each feeder rather than their relative difference (Arganda et al. 2012). Biologically, values of $k < 1$ may represent birds occasionally choosing slightly less populous sites when the number of individuals in the patch is high. k was kept constant at the population level in subsequent species-level analyses.

Simulations: In order to compare observed behaviour with that expected from the model alone, we generated artificial simulated data using the decision probabilities given by this model. At each time step in the simulation, a random bird in a fixed population of $N = 5$ for conspecifics and $N = 10$ for heterospecifics was selected, and either remained at its current feeder or moved to a new feeder with the calculated density-dependent decision probabilities predicted by the model. The simulation was run for 50 000 decisions and between-feeder movements analyzed in the same manner as the experimental data. Confidence intervals calculated from the 95% range of simulation results are shown in Figures S5-S7. All analyses, calculations, and data handling were conducted in the software programme *R* (R Development Core Team 2013).

RESULTS

Response of individuals to flock mates

In total, we recorded 1 904 different tagged individuals (825 blue tits, 813 great tits, 133 marsh tits, 101 coal tits and 32 Eurasian nuthatches). A total of 91 576 feeding visits were recorded by these individuals (34.3% by blue tits, 32.5% by great tits, 16.4% by marsh tits, 11.2% by coal tits, and 6.0% by nuthatches). Plots of the raw data within patches show bursts of synchronised feeding activity within and across species (Figure S2). Using a likelihood ratio test on the distribution of visit interval times within feeders and days for all replicates, we found significantly stronger support for a power-law distribution (a long-tailed distribution representing many small gaps separated by fewer large gaps) of inter-event patch visit times over exponentially distributed (drawn from a uniform data stream) time gaps ($D = 102281$, $df = 1$, $P < 0.0001$). This non-random pattern suggests that birds arrived and departed patches in discrete flocks.

We analysed the feeder choices made by individuals when moving within patches during feeding bursts. In total we detected 2259 feeder swaps (21.6% by blue tits, 20.4% by great tits, 17.9% by coal tits, 31.2% by marsh tits, 8.9% by nuthatches). For both conspecifics and heterospecifics, departure probability was highest for feeders with a low overall proportion of individuals relative to other feeders (Figures 3a & 3c). This relationship was reversed at the arrival feeder: the arrival tendency was highest for feeders with a relatively high proportion of individuals (Figures 3b & 3d). These results suggest that both heterospecific and conspecific components of mixed species flocks contribute to flock-level foraging decisions (Figure S3). When the data were restricted to the first day of each replicate, an identical pattern was observed (Figure S4), confirming that the observed patterns are not the result of changing patch quality over time. Taken altogether, these results suggest that birds were actively reducing their relative distance to others, as predicted by selfish herd theory (Beecham & Farnsworth 1999; Hamilton 1971; Viscido et al. 2002).

A common rule for conspecifics and heterospecifics

The estimated response by individuals to heterospecifics and conspecifics were similar, with S=3.0 for both (95% confidence intervals conspecifics: 1.8-6.6; heterospecifics 2.4-4.0) and k=0.12 (0.04-0.25) for conspecifics and k=0.17 (0.13-0.21) for heterospecifics. The flock-level estimate pooling both con- and heterospecifics (S=7.0, 95%CI=4.8-11.2; k=0.11, 0.09-0.13) was higher than either estimate alone. This is an important finding, suggesting that individuals generally chose the feeder that contained the greatest total number of individuals, despite the fact that it might not have the largest number of either conspecifics or heterospecifics. Simulations of decision-making in flocks using these parameter values replicated the results well (Figure 3a-d, S4-S6), suggesting that the simple rules in the model are sufficient alone to generate the patterns seen in the data.

Within-flock variation in flocking rules

We tested for species-level differences in the use of interaction rules with conspecifics and heterospecifics. As our data was insufficient for calculating individual- or species-level measures, we combined data into species pairs according to dominance (based on Morse 1978). We found that when swapping between feeders, dominant blue tits and great tits had lower values of S with their conspecifics (S=3.4, 95%CI=3.0-3.8; k=0.12) than for heterospecifics (S=4.7, 95%CI=4.0-5.4; k=0.12). In contrast, subdominant coal tits and marsh tits had a higher conspecific (S=2.7, 95%CI=2.4-3.0; k=0.12) than heterospecific (S=2.1, 95%CI=1.8-2.4; k=0.17) social attraction, but lower overall values of S.

DISCUSSION

We used automated monitoring of foraging decisions in a wild bird population to quantify aspects of the decision-making processes of wild birds in mixed-species flocks. We first showed that feeding flocks of birds displayed non-random flocking patterns, regardless of species, similar to many other single species fission-fusion social systems. Within these flocks individual birds actively moved to areas within habitat patches with higher densities of individuals. Our results show that coordinated social foraging behaviour in this species can be predicted by a simple rule of attraction toward groups. Crucially, at a flock level, this rule was applied equally to heterospecifics and conspecifics, which combined to form a stronger attractant than either of the two components of the flock independently. These findings highlight the potential value of applying collective decision-making models to mixed species groups. In addition, our study is one of the few to examine collective behaviour in wild groups, where environments are dynamic and uncertain.

The high values of S inferred from the data suggest a strong response by individuals to both conspecifics and heterospecifics. It implies that the relative probability of moving towards parts of the flock with several individuals present is much higher than the probability of moving towards relative emptiness. This is analogous with a 'locally-crowded horizon' rule used for modeling selfish herds (Viscido et al. 2002). The k parameter, whether individuals use relative or absolute differences, may also be biologically important. Here the value of k was relatively low, which suggests individuals were often moving to feeders of medium density as well as areas of higher density, giving that two sites of medium density have an equal probability of being chosen (Figure 2). This could reflect the variable group sizes we observed and result from effects of competition. When large groups were present, individuals may have favoured movements towards areas of medium density, thereby gaining an balance between anti-predation benefits and competition. Alternatively, it may reflect an overall tendency to avoid low-density sites. The combination of these forces is considered crucial in the formation of the group-size distributions observed in nature (Beecham & Farnsworth 1999); it may be an important process preventing continuous aggregation of individuals into one increasingly large group.

Although the *S* parameter is derived for social information broadly across the flocks, individuals or species could vary in how much attention to they pay to conspecific or heterospecific information. Within species, individuals could vary in the value of social information, results from a recent study suggest that they vary along the shy-bold personality spectrum (Farine et al in revision). More generally, patterns may also exist between species. For example, previous studies suggest that blue and great tits gain most benefits from foraging with subdominant species (Morse 1978; Sasvari & Hegyi 1998), and willow tits (*Poecile montanus*), a close relative of the marsh tit, will recruit heterospecifics to food, potentially acting as leaders (Suzuki 2012). The value of *S* may even be limited in some species as a result of high levels of competition, for example great tits were found to be least attractive to other species in a previous observational study (Morse 1978). Although, in this study, we didn't have enough data to infer species by species interaction rules, we found that the values of *S* for different dominance classes clearly reflected attraction to subdominants, and higher within-species attraction within subdominants. The latter, by behaving less cohesively with heterospecifics, could be acting as leaders by paying more attention to conspecifics. Quantifying interaction rules at a phenotypic level (such as species, dominance, or sex) may be a powerful approach to disentangling asymmetrical cost-benefit trade-offs within flocks.

The model we fitted to the data estimated aggregation strength as a decision-making process by individuals using a general form of social information. This same model was used in an elegant experiment recently performed on fishes by Miller et al (Miller et al. 2013; Perez-Escudero et al. 2013) that suggested riskminimisation and social information mechanisms are interlinked, and that both contribute to individual decisions. Thus, by exploiting social information in its broadest definition (basing decisions on the behaviour of others or being attracted to popular choices), animals could be using a general rule that satisfies combined needs to reduce risk, such as through dilution, and gain information about the environment, such as finding the best sites to forage. Subsequently, herding (*sensu* Hamilton (Hamilton 1971)) may simply be an emergent social property of an individual-level prioritisation of social over personal information (Chamley 2003). Using this rule, if perceived predation risk goes up, individuals simply increase their use of social information, driving the group closer together via social reinforcement (Ame et al. 2006). Varying social information use in response to ecological conditions may represent a simple mechanism underlying fission-fusion dynamics in the study species.

By successfully replicating our data using simulated flocks, we have described a candidate model for exploring the interaction between forces of selection (such as predation or competition) and behavioural rules. Given its simplicity, we predict that this result should be generally applicable across a wide range of animals forming mixed-species aggregations. However wild environments are dynamic and uncertain, with shifting levels of predation and resource availability. It remains to be investigated whether individuals can adjust collective decision-making rules to conspecifics and heterospecifics over changing social and environmental gradients.

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FIGURES

Figure 1. Overview of the experimental design and data collection. (A) Schematic of an experimental habitat patch. Individual *k* leaves feeder F_i with relative density ρ_i and arrives at feeder F_j with relative density ρ_j. Here, $i = 1$ and $j = 3$. Birds are free to arrive and leave the patch at all times. (B) A toy example of the focal individual *k* (in black) and its flock in a patch. *k* is detected feeding on feeder 1 at $t = 1\text{-}2$, during which time the distribution of individuals across feeders F_1-F_4 is 0, 0.25, 0.75, 0 respectively (note that the focal individual is removed from influencing it's own decision), hence $\rho_i = 0$. Individual *k* is then detected at feeder 3 at t = 4, where $\rho_j = 0.75$.

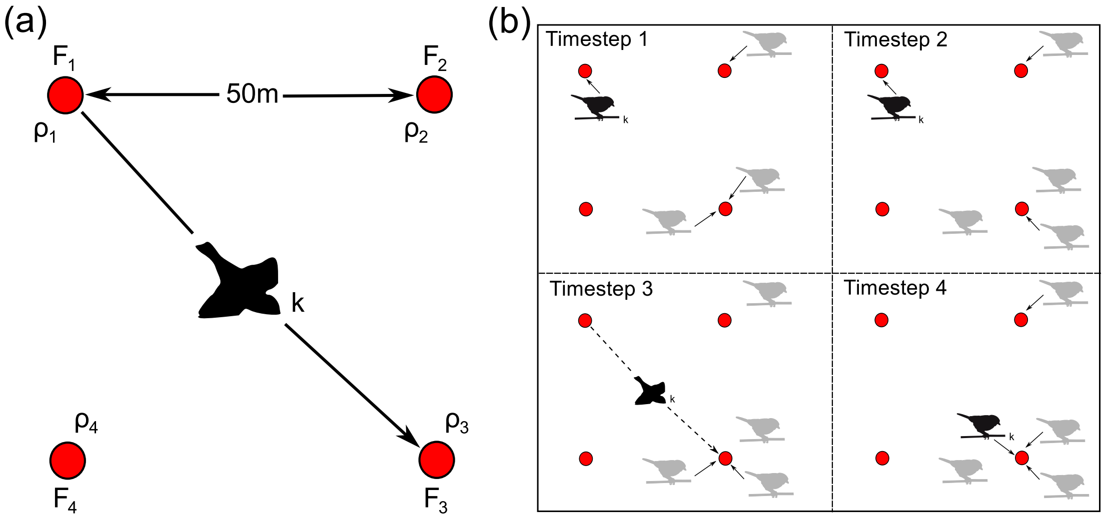


Figure 2. Overview of the relationship between the proportion of individuals on a site and (a) the probability of that site being identified as good, and (b) the probability of choosing that site in a two-site decision. Functions are shown for different values of parameter *S* and *k* in the model by (Arganda et al. 2012). Higher values of *S* (solid lines) form a stronger threshold value, whereas lower values of *S* result in responses similar to linear gradients. Lower values of *k* shift the probability curve left, and hence create larger regions of indifference between two sites (in this case creating an area with an equal probability of choosing either site at proportions from 0.3 to 0.7). One important feature of this model is that the probability of picking a density of 0 is never 0.

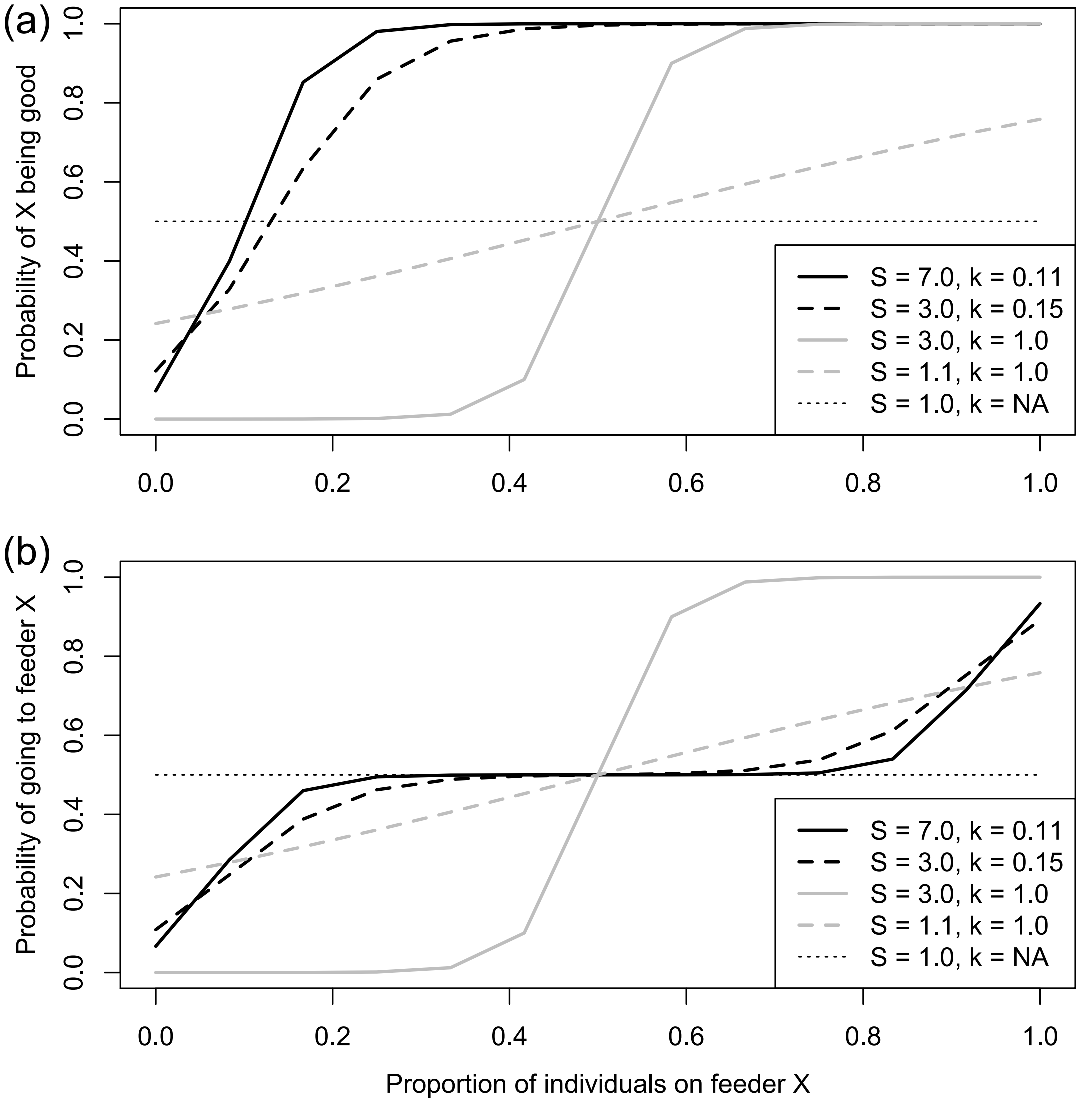
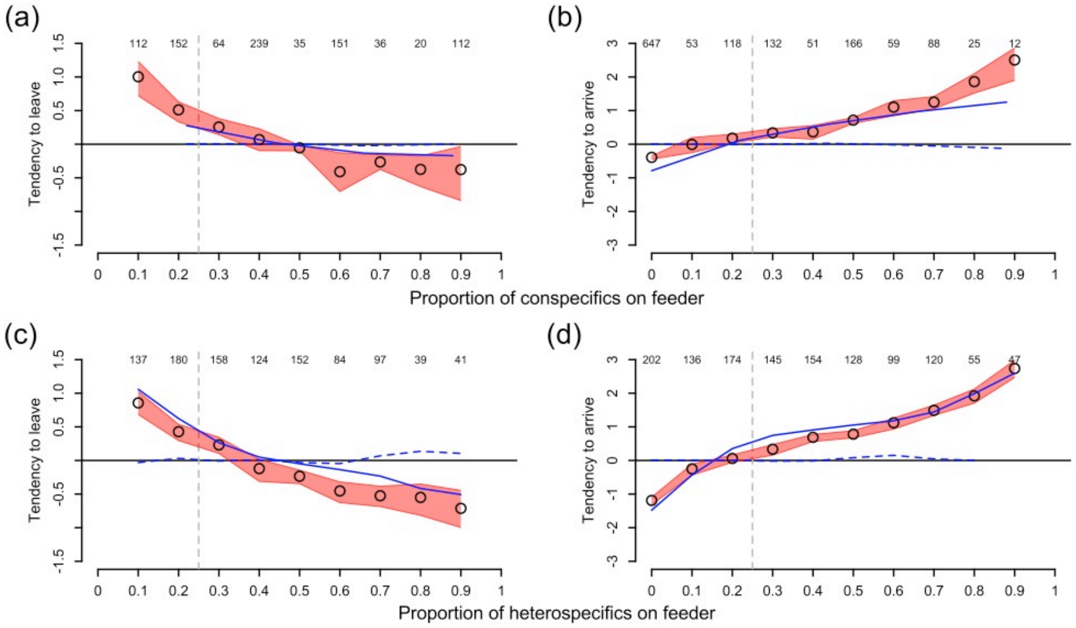


Figure 3. Within-patch movements with respect to distribution of conspecifics (A-B) and heterospecifics (C-D). Y-axes represent measured log ratio of the observed probability (P_{obs}) of a given move, and a theoretical asocially predicted probability (P_{tasp}) of that move given the proportion of individuals at the feeder when leaving (A and C), and arriving (B and D). Relative densities were calculated using the number of conspecifics or heterospecifics present at each feeder and across patch. Open circles represent log of the tendency to leave or arrive (see text for definition). Red envelopes are the maximal variability range from 1000 jackknife estimations with 40% of the original data removed. Solid blue lines represent the data from a stochastic simulation of 50 000 decisions made with (A-B) 5 conspecifics and (C-D) 10 heterospecifics, and the social information parameter S = 3.0. Dashed blue lines are from the same stochastic simulation but with no social information (S = 1). Variability of the simulation data from 1000 such simulations are given in Figures S5-S7. The vertical dashed lines represent mean expected density on each feeder (0.25) in the absence of any collective behaviour; solid horizontal lines indicate density-dependent expectation of the theoretical asocial prediction (log P_{tasp}). Values above each plot give the sample size (*n* departures or arrivals) for each data point below it.


(a)
Tendency to leave
1.5
1.0
0.5
-0.5
-1.5
112
152
64
239
35
151
36
20
112
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
(b)
Tendency to arrive
3
2
1
0
-1
-2
-3
647
53
118
132
51
166
59
88
25
12
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Proportion of conspecifics on feeder
(c)
Tendency to leave
1.5
1.0
0.5
-0.5
-1.5
137
180
158
124
152
84
97
39
41
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
(d)
Tendency to arrive
3
2
1
0
-1
-2
-3
202
136
174
145
154
128
99
120
55
47
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Proportion of heterospecifics on feeder

SUPPLEMENTARY FIGURES

Figure S1: logged frequency of delay times between observations of individuals made at different feeders. Red line (time = 240) represents the value used in the analyses.

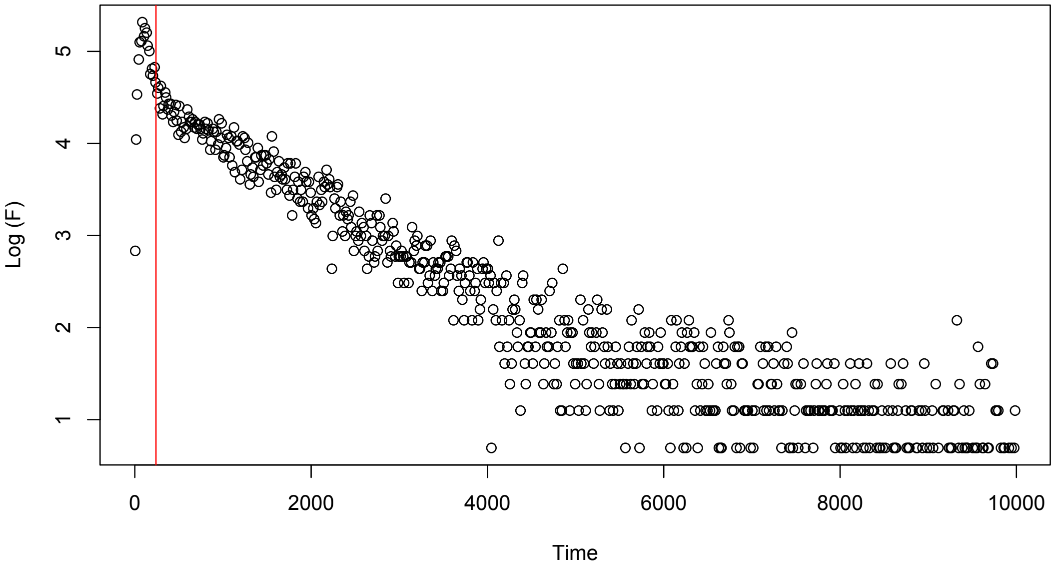


Figure S2: graphical representation of the data for three days (5-7 February 2012) at one replicate of the patch. Each panel is one feeder within a set of four running concurrently. Lines within boxes each represent the feeding activity as the number of visits per 30 seconds by individuals of each species (top to bottom: marsh tit, nuthatch, great tit, blue tit, coal tit). The lines for each species are displaced vertically in units of 10 for clarity.

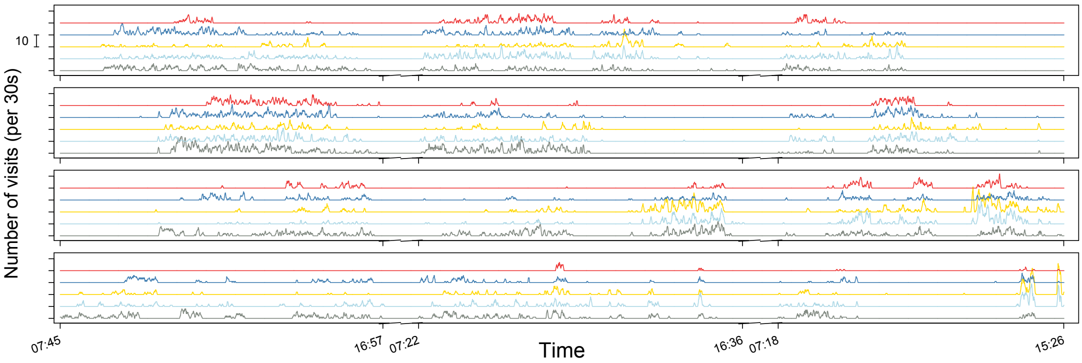


Figure S3: within-patch movements with respect to density, expressed in terms of (a) departures from a feeder, and (b) arrivals at a feeder. All data for all species pooled. Open circles represent the measured log ratio of the observed probability (P_{obs}) of a given move and the theoretical asocially predicted probability (P_{tasp}) of that given move. Red envelope is the maximal variability range for these data inferred from 1000 jackknife estimations of the points with 40% of the original data removed in each that suggest the results are robust to resampling. The blue curve represents the data from a simulation of 50,000 decisions made with (A-B) 5 conspecifics and (C-D) 10 heterospecifics, and the social information parameter set at conspecific and heterospecific values (Figure 3). Dashed blue line from the same simulation with no social information (*S* = 1). Variability of the simulation data from 1000 simulations is given in Figure S7. The vertical dashed line represents the mean expected density on each feeder (0.25) in the absence of any collective behaviour; the solid horizontal line indicates density-dependent expectation (log P_{tasp}). Values along the top give the sample size (*n* departures or arrivals) for each given density.

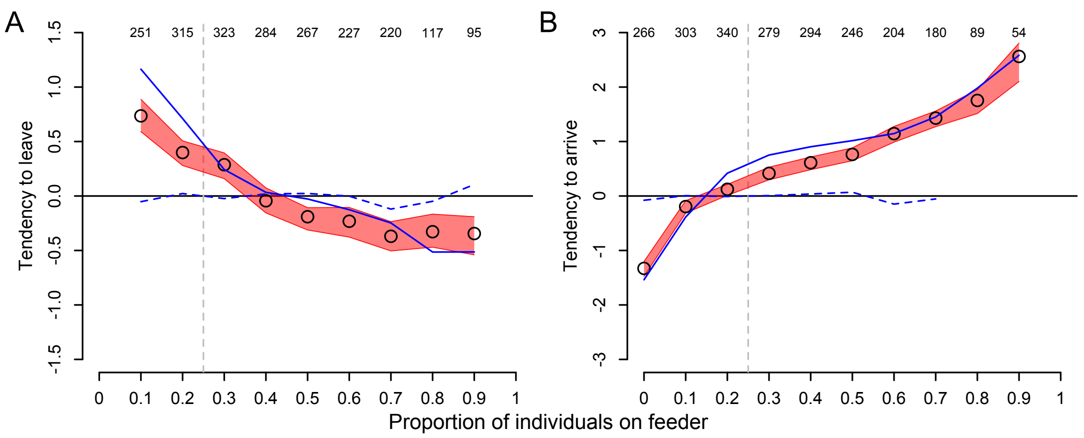


Figure S4: analysis repeated on the data from day 1 alone shows greater error around the same emergent pattern. This suggests that the observed behaviour is not caused by potential variation in the food amounts at different feeders altering their perceivable quality. Simulated data from social (solid blue lines) and asocial (dashed blue lines) are using the same parameters as the full data from Figure 3. The vertical dashed line represents the mean expected density on each feeder (0.25) in the absence of any collective behaviour; the solid horizontal line indicates density-dependent expectation (log P_{tasp}).

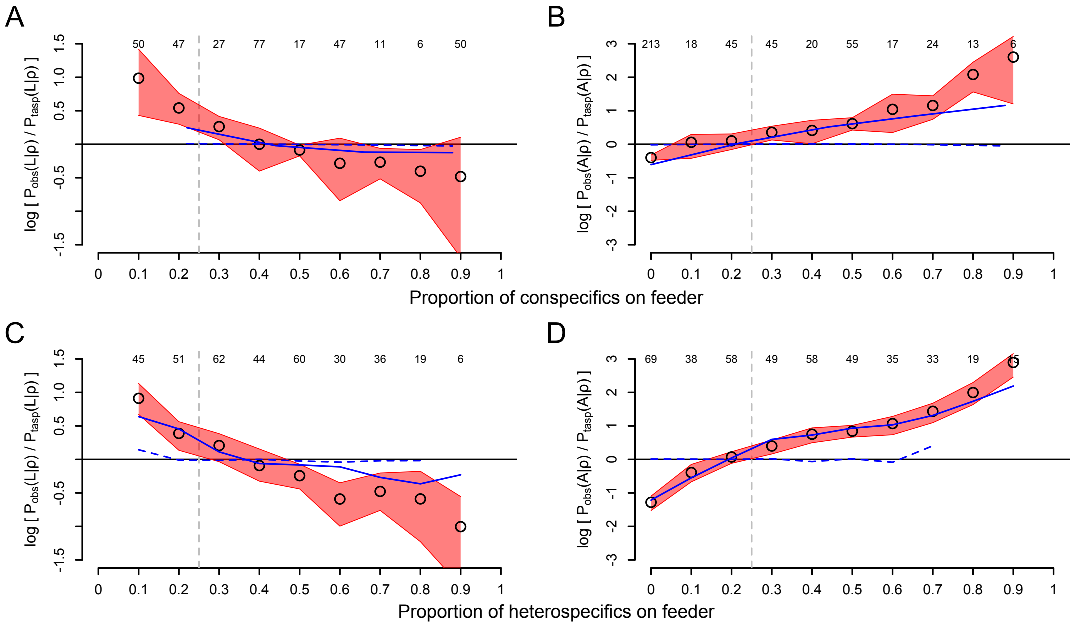


Figure S5: full range of 1,000 simulation results on (a) departures from feeder and (b) arrivals to feeder with parameter S = 3.0 and k = 0.12 (polygon around solid blue line) and S = 1 (polygon around dashed blue line). Each run simulated 5,000 decisions made by individuals in a constant population of 5 individuals. Individuals could only depart from a site of minimum 0.2 (1 individual on a site) as the simulations had a fixed population size. Open circles are the original data from conspecifics and the numbers represent the frequency of the original data points. The vertical dashed line represents the mean expected density on each feeder (0.25) in the absence of any collective behaviour; the solid horizontal line indicates density-dependent expectation (log $\mathrm{P}_{\mathrm{tasp}}$).

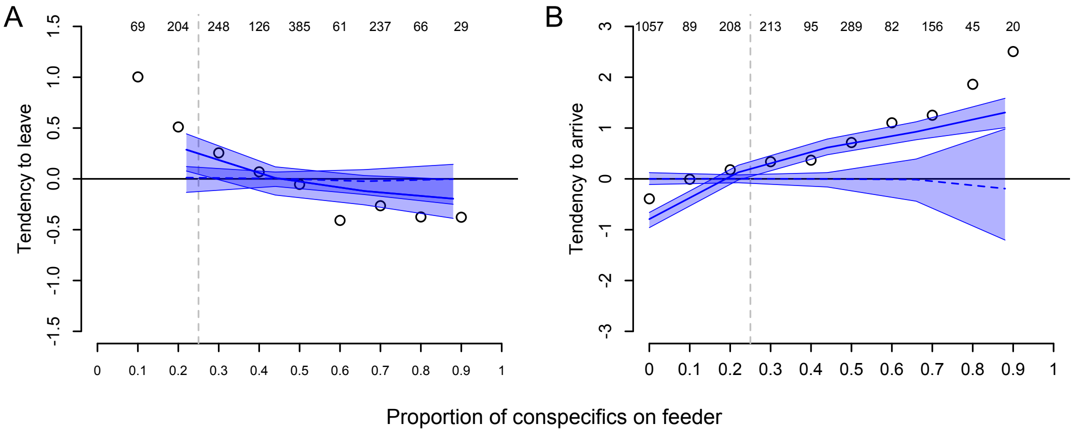


Figure S6: range of simulation results for 1,000 runs on (a) departures from feeder and (b) arrivals to feeder with parameter S = 3.0 and k = 0.17 (polygon around solid blue line) and S = 1 (polygon around dashed blue line). Each run simulated 5,000 decisions made by individuals in a constant population of 10 individuals. Asocial (S = 1) simulations never reached densities as high as social simulations. Open circles are the original data from heterospecifics and the numbers represent the frequency of the original data points. The vertical dashed line represents the mean expected density on each feeder (0.25) in the absence of any collective behaviour; the solid horizontal line indicates density-dependent expectation (log P_{tasp}).

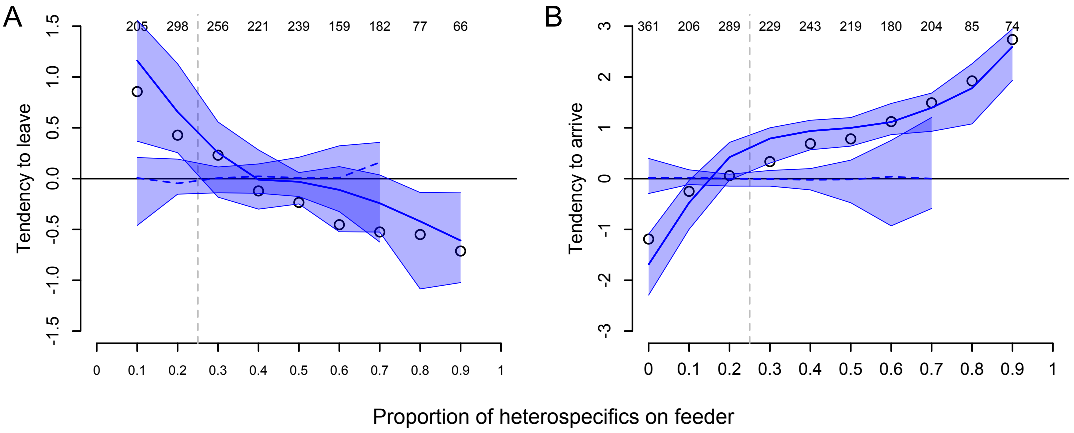
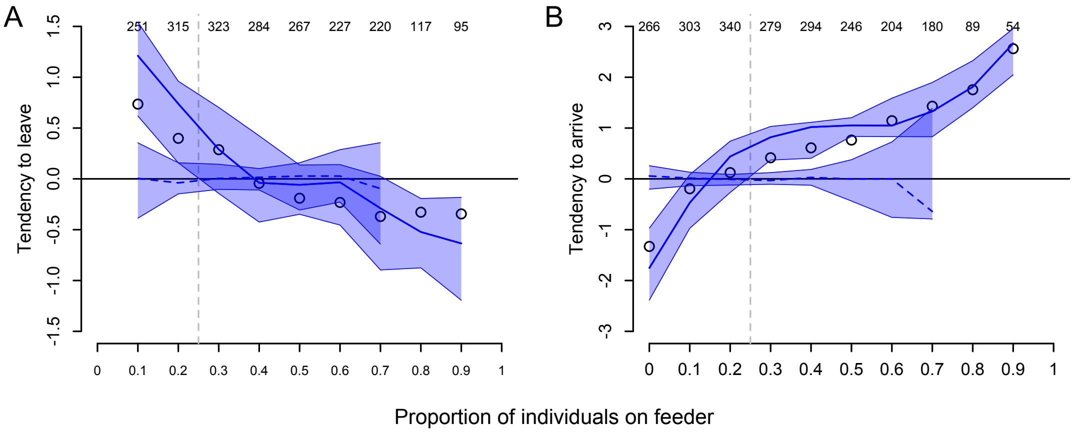


Figure S7: range of simulation results for 1,000 runs of the simulations on (a) departures from feeder and (b) arrivals to feeder with parameters $S = 7.0$ and $k = 0.12$ (polygon around solid blue line) and $S = 1$ (polygon around dashed blue line). Each run simulated 5,000 decisions made by individuals in a constant population of 15 individuals. Asocial ($S = 1$) simulations did not reach as high arrival densities as groups never all fed on the same feeder. Open circles are the original data and the numbers represent the frequency of the original data points. The vertical dashed line represents the mean expected density on each feeder (0.25) in the absence of any collective behaviour; the solid horizontal line indicates density-dependent expectation (log P_{tasp}).



CHAPTER 9

The ecology of collective behaviour: experimental evidence from wild birds shows that competition and predation drive social interaction rules within and across species

The ecology of collective behaviour: experimental evidence from wild birds shows that competition and predation drive social interaction rules within and across species

D.R. Farine & B.C. Sheldon

ABSTRACT

Group-living is generally considered to be an adaptive evolutionary response to selective pressures imposed by the environment, in particular predation and competition. Because groups emerge from decisions by individuals, understanding the individual decision-making processes that underpin group formation is therefore key to understanding the evolution of sociality. Nonetheless, few studies have explicitly quantified the relationship between dynamic social interaction rules and social flexibility in response to variation in the environment. We manipulated competition and perceived predation risk in experimental habitat patches to determine their effects on interaction rules in multi-species flocks of wild songbirds. A novel automated field data collection protocol enabled us to capture 43 718 visits by 464 individuals, and 796 unique movement decision across experimental treatments. Model-fitting suggests that individuals responded to high competition conditions by relaxing the social rule that maintains cohesion, while strengthening it under high predation. We found strong evidence for within-flock heterogeneity in interaction rules; despite the significant reduction in social attraction to conspecifics under high competition,

there was no change in the attraction to heterospecifics, supporting the hypothesis of reduced nice overlap driving heterospecific associations. Our results demonstrate how individuals can adapt to selective pressures by dynamically varying their social interaction rules, potentially providing simple mechanisms for collective behavioural plasticity.

INTRODUCTION

A fundamental question in biology relates to understanding how groups of unrelated individual animals are formed and maintained (Hamilton 1971; Krause & Ruxton 2002, 2010). Groups of animals such as bird flocks, fish schools or swarms of insects frequently exhibit coordinated behaviours that are thought to be an adaptive response to variable selection (Krause & Ruxton 2010; Sumpter 2010). For example, group size appears to be highly flexible in many species (Krause & Ruxton 2002), and in freely associating fish group size has been shown to vary in response to experimentally manipulated environmental conditions (Hoare et al. 2003). Yet, given that such groups are generally made up of individuals attempting to maximise their own individual fitness, we should expect that social structure will emerge as a property of individuals changing "their behavioral response to others dynamically in order to increase their probability of being in groups of a size that approximates their current 'optimal' group size" (Couzin & Krause 2003). This view, that group structure is an emergent property of local interaction rules, as opposed to global group joining or leaving decisions, has remained largely untested.

Coordinated social behaviour provides potential fitness benefits to participants by reducing predation risk (Cresswell & Quinn 2004; Guttal & Couzin 2010; Ioannou et al. 2012; Landeau & Terborgh 1986), facilitating information transfer (Couzin 2009), and leading to better informed decision (Sumpter et al. 2008; Ward et al. 2011; Ward et al. 2012; Ward et al. 2008). For example, individuals can gain anti-predation benefits by positioning themselves closer to conspecifics in order to dilute their risk. Studies on cockroaches (Ame et al. 2006) have shown that gregarious behaviour can emerge as a simple by-product of individuals resting longer under shelters with more cockroaches, eventually resulting in a consensus decision about which shelter the group will use (Ame et al. 2006; Ward et al. 2008). However, social living can also be costly as it increases competition, and disease and parasite transmission (Krause & Ruxton 2002). Thus, the relative trade-off in the costs and benefits of grouping may change in response to variation in environmental conditions, or even with the composition of the group (Couzin & Krause 2003).

If the form and structure of animals groups is an emergent property of individual decision-making rules, we should therefore expect that these rules are dynamically adjusted in response to the cost-benefit trade-off as perceived by the individuals forming the group (Couzin & Krause 2003). For example, swarms of locusts have been shown to emerge as a result of exceeding a threshold density (Buhl et al. 2006) that causes a functional shift in interaction rules into a 'forced march' by individuals avoiding being cannibalised (Bazazi et al. 2008). Casual observations in birds also suggest that flocking parameters, such as the size of the repulsion zone, may dynamically adjust in response to the environment, for example when a predator is spotted (Lukeman et al. 2010). Thus, we suggest that understanding the ecology of collective behaviour, or how social structure is influenced by ecological conditions via changes in interaction rules, is an important research goal that links population-level processes back to individual fitness. For example, associating with ecologically similar, but not identical, species is one strategy that individuals can use to reduce the effects of competition with conspecifics whilst maintaining some of the putative benefits of group-living (Beauchamp 2010; Buskirk 1976; Farine et al. 2012; Farine & Milburn 2013; Morse 1970; Sridhar et al. 2009). Evidence that individuals maintain stronger association rules with heterospecifics than conspecifics under high competition would provide clear evidence that the structural response of groups to the cost-benefit trade-off is an emergent property of adaptable and dynamic interaction rules. Reducing the cost of competition is one of the predominant hypotheses for why animals form mixed-species groups (Buskirk 1976). In contrast, an increase in the attraction parameter with both conspecifics and heterospecifics under high predation risk would support the hypothesis of risk dilution as an additional driver of mixed-species groups.

Studying the ecology of flocking dynamics is now being made possible through recent technological advancements that make it viable to track entire groups or populations of animals in the wild (Krause et al. 2013). Electronic tags now allow groups of individually-marked individuals to be tracked either at high definition or for continuous periods, sometimes for the duration of their lifetimes. In this study we use a large population of free-ranging birds fitted with passive integrated transponder (PIT) tags which enables high resolution tracking of foraging behavioural decisions. This has enabled us to capture information on the emergent social structure of birds at unprecedented scales (Aplin et al. 2013a; Farine & Lang 2013), yielding inference as to how social structure can mediate population processes (Aplin et al. 2012).

We test experimentally i) if individual interaction rules changed under different competition and predation pressures, and ii) how dynamic rules varied in response to heterogeneity in group composition. We modelled the weight that individuals placed on the relative distribution of conspecifics when observed moving within flocks of wild birds. We then experimentally increased interference competition by forcing birds to feed more closely to each other, and increased perceived predation pressure by flying model sparrowhawks over feeders twice per day. Studying multi-species groups allowed us to compare the estimate of social cohesion that individuals maintained with conspecifics and heterospecifics in order determine if individuals responded differently in the presence of within-flock variation in the cost-benefit trade-off.

RESULTS

Response of flocks to competition and predation

We selected six habitat patches in which flocking individuals were given the choice of four identical foraging locations (feeders spaced 50m apart, see methods). This design enabled birds to either aggregate near one feeder (high coordination) or disaggregate (low coordination) within their flocks (Figure 1).

Each patch was subjected to three treatments (competition, control and predation) in a fully balanced experimental design. Across all treatments (18 replicates), we detected 464 individuals (231 blue tits *Cyanistes caeruleus*, 151 great tits *Parus major*, 33 marsh tits *Peocile palustris*, 39 coal tits *Periparus ater*, and 3 nuthatches *Sitta europaea*), making 43 718 individual visits (34.5% blue tits, 33.2% great tits, 13.5% marsh tits, 16.6% coal tits, and 2% nuthatches).

In the first treatment (competition), we increased potential interference competition by filling feeders with peanut granules that forced individuals to remain on the feeder to feed, and blocking one of the two access holes. In the second treatment (control) we replicated previous studies in which birds had access to both feeding holes to pick up a sunflower seed, which is the standard method for collecting data in this population (chapter 8). In the third treatment (predation) we increased apparent predation risk by flying models of sparrowhawk (*Accipiter nisus*), a common predator (Vedder et al. 2013), over standard feeders (two holes with sunflower seed) twice per day (see methods for additional details).

We found that experimental treatments had no effect on the average number of individuals present in patches (Generalized Linear Mixed Model: treatment effect ± 95%CI=0.316±0.578, P=0.30, site explained 79% of the variation). This suggests that flocks largely maintained their natural group sizes based on their foraging environment outside of the patch. Individuals were detected by radio frequency identification (RFID) antennae retrofitted to standard bird feeders, which provided food at a constant rate to avoid effects associated with patch depletion.

Within-flock responses to conspecifics under competition and predation

To quantify the influence of environmental conditions on the interaction rules that maintain cohesion in flocks of conspecifics, we fitted a Bayesian model of collective decision-making (Arganda et al. 2012; Perez-Escudero & de Polavieja 2011; Perez-Escudero et al. 2013) that has become widely used in the field of collective animal behaviour. Previous studies, using our data collection protocols (chapter 8), and across a wider range of taxa (Arganda et al. 2012; Miller et al. 2013), have shown that simulations using the parameters of this model perform remarkably well at replicating empirical data. In the model, foraging individuals make a probabilistic choice in choosing a feeder based on their social weighting S that represents how much they believe that the conspecifics present in the patch have made a 'good choice'. Simplified, the probability of choosing a location (X_i) is proportional to the number of conspecifics that an individual has observed making that decision (B). Figure 2 shows the probability of picking a site based on both high and low values S, where S = 1 represents no social influence, given by the equation:

$$P(X_i|B) = \frac{1}{1 + S^{-\frac{(n_x - k\sum_{i \neq x} n_i)}{N} \times 10}}$$

where n_x defines the number of individuals already on feeder x, and $\sum_{i \neq x} n_i$ is the sum of individuals on each of the other feeders i. N represents the total number of individuals in the patch, and used maintain a consistent group size upon which S acts. The second parameter of the model, k, estimates the use of relative versus absolute differences in the number of individuals on each different options, where low k values result in individuals avoiding low density locations (see Figure 2). Given that $\sum_i P(X_i|B)$ can exceed 1, an additional step of probability matching is used.

Fitting the parameters of this model revealed that individuals used a significantly higher S weighting under high predation, and a significantly lower S weighting under high competition when compared to the control treatment (Figure 3A). We used maximum likelihood estimation to infer the parameters S and k from the within-patch movements by birds relocating between different feeders. The high S value under predation (S=20.9, 95%CI=9.8-45.3) suggests that individuals were more likely to move towards the most populous feeders than under the control treatment (S=2.5, 95%CI=1.9-3.2). In contrast, there was much weaker tendency to move towards conspecifics under high competition (S=1.7, 95%CI=1.5-1.9). That $S > 1$ under competition was not unexpected, given that predation risk was unlikely to be non-zero, and groups still need to maintain some degree of cohesion. However, the equivalent effect of this downshift in S is to increase the probability of moving away from the group. Figure 3B demonstrates the probability curves for conspecific movements under each treatment.

Although we found no significant changes in the k parameter between competition and control treatments (competition: k = 0.18, 95%CI=0.12-0.25; control: k = 0.16, 95%CI=0.11-0.25), the value of k under the predation treatment was estimated to be lower than both of these (k = 0.07, 95%CI=0.02-0.12). This low value of could arise if birds that were predominantly seeking to reduce their risk produced high numbers of individuals at more than one feeder. In this case, relocating individuals may be unable to determine the difference between sites, leading to a random probability of picking between these feeders. This is not unlikely given that birds did not remain on the feeders to feed, but potentially spread up to 20m from the feeder, making it difficult to assess the exact number of individuals present.

Within-flock responses to heterospecifics under competition and predation

One of the predominant hypothesis for the evolution of mixed-species flocking is the reduction in interference competition with conspecifics (Beauchamp 2010; Buskirk 1976). Studying mixed-species flocks in this framework provides a clear and testable prediction about how animals respond to a cost-benefit trade-off when joining or leaving groups: increased competition should have a greater impact on conspecific attraction than on heterospecific attraction (Buskirk 1976).

Our results strongly support this prediction. Under competition, the value of S in response to heterospecifics (S=2.2, 95%CI=1.9-2.6) did not differ from the heterospecific parameter in the control treatment (S=2.8, 95%CI=2.4-3.4), but was significantly greater than conspecific attraction in the same treatment. Further, the heterospecific response to predation resulted in a higher estimated S parameter (S=9.9, 95%CI=6.1-16.0) that did not significantly differ to conspecific attraction, supporting dilution of risk as an important benefit of mixed-species group-living. The values for the k parameter were almost identical in heterospecifics (competition: k = 0.17, 95%CI=0.11-0.25; control: k = 0.16, 95%CI=0.11-0.25; predation: k = 0.09, 95%CI=0.04-0.16). Figure 3C demonstrates the probability curves of heterospecific movements under each treatment.

Inferring the emergent properties of dynamic interaction rules

Varying the parameters of interaction rules can have profound implications on the dynamics of social groups (Couzin & Krause 2003), potentially influencing individual fitness. For example, groups of individuals containing mixed personalities may be able to have more effective use of limiting resources whilst maintaining high levels of behavioural synchrony (Farine et al in review), suggesting that heterogeneous group structure may be adaptive. In order to understand whether dynamic interaction rules can lead to potentially adaptive variation in group structure, we simulated individual decisions in mixed-species flocks using the parameters we inferred from our experimental data. For each treatment, we simulated 1000 flocks formed of 12 individuals (the mean group size) distributed amongst 5 species as observed in our data. For each flock, we simulated 100 stochastic within-patch feeder-choice decisions by sequentially selecting a random individual and calculating the probability of choosing each of the four available feeders based on the distribution of both conspecifics and heterospecifics.

We found that the inferred interaction rules under competition led to a random spacing of individuals across the patch in simulated flocks (Figure 4A). This suggests that such a rule could generate an equal spread that is similar to an ideal free distribution. In contrast, heterospecifics remained significantly aggregated (Figure 4B), leading to a high degree of cohesion in overall flock structure (Figure 4C). This provides some evidence that heterospecific associations can stabilize mixed-species flocks under competition. Under natural and high predation risk conditions, the group cohesion increased such that under high predation risk, on average 70% of individuals were found on the same feeder.

DISCUSSION

Variation in the cohesiveness of animal groups, such as in fission-fusion societies (Couzin 2006), is often considered to be an adaptive response to ecological factors (Chapman et al. 1995; Lehmann & Boesch 2004). For example, being in a large group decreases predation risk through dilution (Krause & Ruxton 2002), but maintaining cohesion between group members may be equally important for avoiding predation (for example through the confusion effect, Landeau & Terborgh 1986) as individuals that behave differently may be easier to target (Ioannou et al. 2012). However, cohesion may introduce higher costs, where individuals that feed closer together experience greater interference competition

(Dhondt 2012). Our results suggest that the trade-off between opposing attraction and repulsion forces lead to dynamic shifts in the parameters of cohesion used by individuals. It is therefore possible that the structure of animal groups could be an emergent property of the interaction rules used by individuals (Hoare et al. 2003). This would be a cognitively much simpler process than one involving decision-making based on choosing optimally-sized groups.

Previous studies in captive fish have demonstrated that shoal size can vary in response to environmental cues, such as alarm signals and food (Hoare et al. 2003). Simulations of these shoals using agent-based models then suggested that the observed patterns of shoal size could be replicated by varying the interaction space in which individuals responded to conspecifics, for example increasing the diameter of attraction led to larger shoals (Couzin & Krause 2003; Hoare et al. 2003). In our study, we have shown that in the wild, birds behaved as if they are dynamically varying their interaction rules in response to competition and predation cues. This supports the hypothesis that aspects of population structure, such as group size and constitution, could be driven by a probabilistic decision-making process. For example, disassortment by species can emerge from a disproportionate reduction in the weighting that individuals place on the decisions observed in conspecifics over those observed in heterospecifics. It is important to note that these simulations predicted decisions that were made based on the observation of both conspecifics and heterospecifics together, whereas decisions made based only on heterospecifics could yield high cohesion between conspecifics as a by-product of being attracted to the same location.

How dyadic variation in interaction rules (for example in social networks that are based on complex relationships that include kinship and familiarity, see (Kurvers et al. in press)) can potentially result in phenotypic or genotypic self-organisation at the population level (Farine in revision) remains an unresolved question in population biology.

Despite the potential for pair-wise variation in interaction rules to determine the membership of groups in fission-fusion populations, we have demonstrated how ecological conditions can profoundly influence the magnitude of rules that underlying population structure. Yet, although competition and predation can independently operate on the parameter of social cohesion in animal groups, the model we have used does not explicitly separate different factors that could lead to cohesion (Perez-Escudero et al. 2013). For example, a recent study trained fish to have different, but complementary, preferences in a three-choice design, finding that fish shoals resulted from both information about patch quality and extrinsic factors maintaining cohesion, such as risk minimization (Miller et al. 2013). Given that birds in our study did not actually aggregate on the feeders, it is possible that individuals were observing others in order to gather public information about potential differences in patch quality (Dall et al. 2005; Danchin et al. 2010; Danchin et al. 2004; Goodale et al. 2010), or looking for opportunities to socially learn about novel food sources (Aplin et al. 2013b). Previous work in our system has shown that social information plays an important role in the discovery of ephemeral food resources (Aplin et al. 2012). Thus, in this case the model parameter S could represent an integration of forces operating on grouping behaviour (Beecham & Farnsworth 1999): individuals weight their belief that others make a good choice based on the potential influence of the decision on their direct fitness.

One surprising result in our study was that our experimental treatments did not influence the average size of groups present in the patch. One explanation for this may be that we only left patches out for three days at a time, which may not be sufficient to broadly influence stability in flock size in the system. Alternatively, the flocks may have been able to maintain their size because the cost of competition was high only at single feeders, but not generally in the patch. Thus, the patch design did not drive flock fission. In terms of predation, perceived risk may have been estimated to be locally high but generally unchanged across the entire range of the flocks. Finally, there could be inertia in group size, whereby the shift in individual within-flock spacing (as suggested in our results) did not spread more widely in the population. For example, although individuals in this population exhibit fission-fusion dynamics (Aplin et al. 2013a), they are also constrained by previous residence and territoriality. Whether individuals can perceive behavioural changes in others (for example high cohesion indicating a recent predation event), or a socially-mediated component influencing cohesion parameters, remains unknown.

Given the recent advances in identifying rules of motion and interaction in collective behaviour, investigating the collective ecology of animal groups promises to be an important area for empirical research. Recent evidence has shown animals can exhibit surprising behavioural plasticity to changing conditions at the small scale (such as in this study) and at a larger scale (such as responding to climate change, Charmantier et al. 2008). Agent-based simulations have long predicted that varying interaction parameters can generate plastic social responses at the population level (Couzin & Krause 2003; Hoare et al. 2003). Recent work where live predatory fish were allowed to attack simulated prey provided important empirical evidence that selection can operate on interaction rules that promote group cohesion (Ioannou et al. 2012). By integrating the study of collective animal behaviour with experimental manipulation of ecological conditions, we have provided the first evidence that individuals can dynamically modulate their interaction rules in order to respond to trade-offs between costs and benefits of grouping.

METHODS

Study Population

The study took place at Wytham woods (51°46'N, 1°20'W), Oxforshire, UK. Wytham woods is an 385 hectare broadleaf deciduous woodland surrounded by farmland. The breeding population has been the subject of a long-term monitoring project, with most adults and all nestling marked with uniquely-coded British Trust for Ornithology rings at their breeding nest-box. Although pairs of tits defend territories while breeding, this partially breaks down over autumn and winter as birds form fission-fusion groups of unrelated individuals that search for ephemeral food sources (Aplin et al. 2012). Since 2007, individuals have also been fitted with a PIT tag moulded into a plastic ring as part of on-going research on the social behaviour of birds. In this time, breeding-season marking has been supplemented with autumn and winter catching to maximise population coverage (estimated at over 90%, Aplin et al. 2013a). All handling and ringing was undertaken under license by the BTO, and approved by the University of Oxford's Local Ethical Review Committee.

General data collection method

We deployed four feeders placed in a square representing ephemeral foraging patches. Feeders were positioned 50m apart in order to remain within visual and auditory range. Given that birds only perch briefly on feeders to collect food before manipulating the food on nearby trees, this distance minimised the chance that two or more birds could feed on separate feeders and perch together, thereby confounding our data (Farine et al in review x 2, also see supplementary movie). Each feeder had two access holes that were fitted with RFID antennae connected to data loggers (Francis instruments, Cambridgeshire), which scanned for records of birds every 1/16th of a second. Feeders were positioned after dark on the evening prior to day 1 in order to maximise natural discovery of sites. Each site was monitored in order to ensure that feeders did not fully deplete, and removed after the third day. We ran all three treatments in parallel each week across two groups of three sites, using a fully-balanced design whereby we alternated between the two groups of sites each week, and used each of the six possible order combinations for the rotation of treatments within sites (1->2->3, 2->1->3, etc.).

Control treatment

In control treatments, feeders were filled with sunflower seed and allowing access to both feeding holes. This design replicated previous studies ensuring that the control data we collected were consistent with deployments in years (chapter 8). Sunflower seed were used as they reduced competition at feeders given that birds collect a seed and generally vacate the feeder within one or two seconds. Additionally, by using standard bird feeders we avoided effects of perceived resource depletion that could introduce variation in the quality of sites (Stephens et al. 2007) and therefore introduce personal information into the decision-making process.

Competition treatment

In order to increase perceived resource competition, we altered the control treatment in two ways. First, we replaced the food with peanut granules, which increase the time spent perched on the feeders as birds consumed small pieces of peanuts. Second, we removed access to one of the two holes on each of the feeders, therefore increasing the queuing time at busier feeders and increasing interference competition. Together, these treatments have been shown to result in higher competition at feeders (Aplin et al. 2013b). Beside these exceptions, patches under competition treatments were identical to control treatments.

Predation treatment

We used model sparrowhawks in order to influence the perceived predation risk as a high predation treatment. Each feeder had a sparrowhawk model was fitted to fly along the length of a thin wire passing approximately 1m above the feeder. Sparrowhawk models were contained within a plastic box fitted with an opaque curtain across the front in order to remain invisible when not flying. Launching and receiving boxes were placed approximately 15 meters on either side of the feeder creating a slope along which the sparrowhawk flew at approximately 8ms-1, thus resembling sparrowhawk attack speeds (Macleod et al. 2005). Previous studies have demonstrated that model sparrowhawks can influence perceived predation risk across a range of contexts (Macleod et al. 2005). Although this treatment differed from control treatments by having boxes and a wire over each feeder, we found no difference in average number of records between any of the treatments which suggests that these only influenced within-patch behaviour rather than the choice to feed or not.

Data analysis

Data from each replicate (18 in total across 6 sites and 3 treatments) were analysed to identify within-patch movements by individuals. These movements were defined as consecutive detections of individuals on two different feeders within 240 seconds (see Farine et al in review). For each 'swap' we recorded distribution of either conspecifics or heterospecifics across all four feeders at the departure and arrival times, as well as the departing and arriving feeder. We then combined all swaps within each treatment, using maximum likelihood estimation to find the best-fitting values and 95% confidence intervals of parameters S and k in the Bayesian collective decision-making model (Arganda et al. 2012) at the treatment-level.

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FIGURES

Figure 1. Overview of the experimental design and data collection. (A) Schematic of an experimental habitat patch, where individuals (in this case *k*) were detected leaving a feeder F_i with relative density ρ_i and arrives at feeder F_j with relative density ρ_j. We tested whether individuals had a greater tendency to move towards areas of high density (B), or towards areas of low density (C).

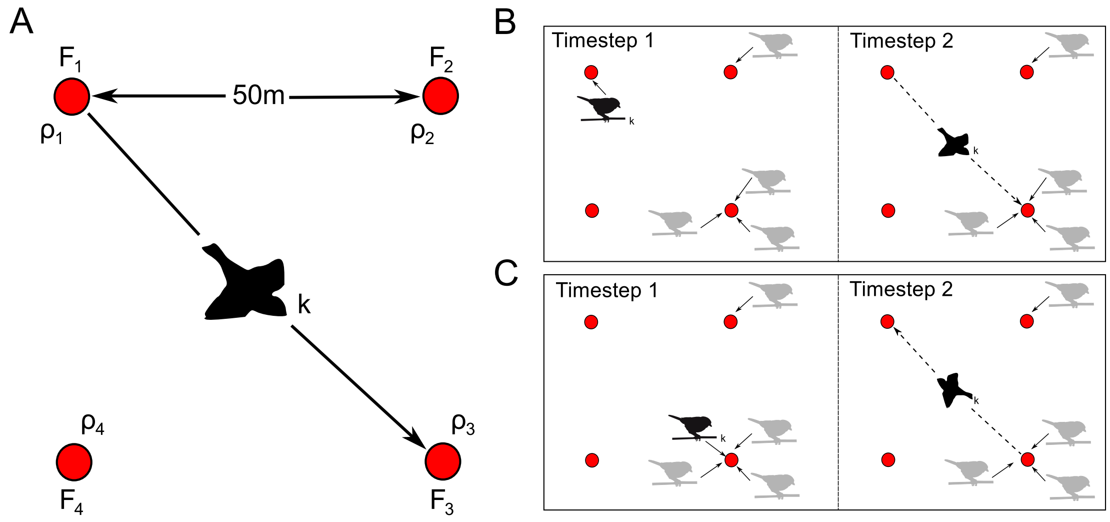


Figure 2. Example of model predictions for (A) whether a site is estimated to be good, and (B) the probability of choosing between two sites after probability matching, under different values for parameters S and k. When $S = 1$, the model makes no prediction, providing an equal probability of choosing either site for all distribution of individuals. As S increases, the probability curve becomes more sigmoidal, creating a sharper threshold between low and high proportion sites. As k decreases, the differences in probability of picking between two sites both containing a relatively high proportion of individuals becomes more similar, which is biologically similar to avoiding low proportion sites.

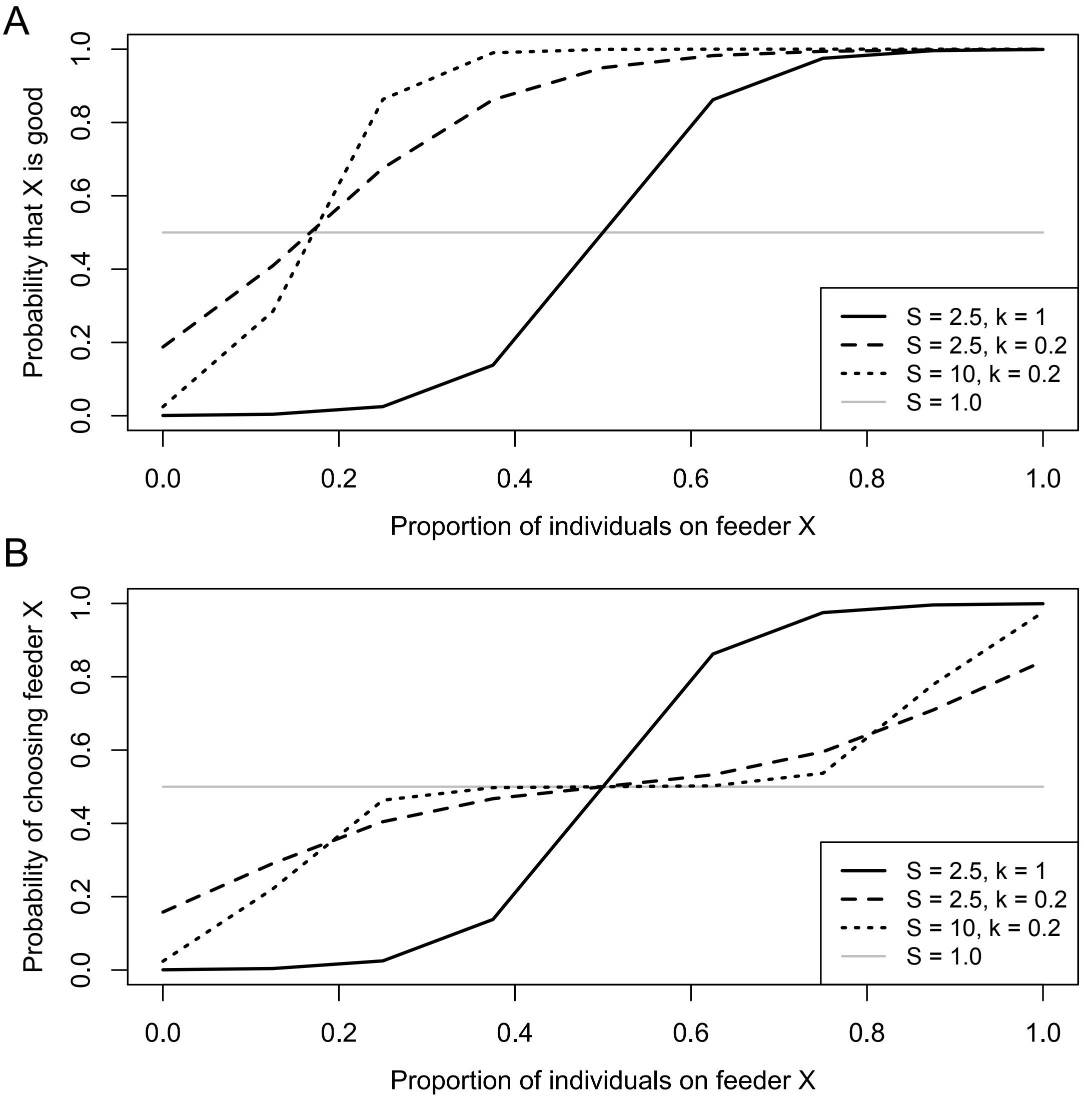


Figure 3. (A) Estimated *S* parameter from maximum likelihood estimation (with 95% confidence intervals) shows a significant increase in weighting of observed behaviour in others by individuals when under high predation risk that suggests a similar response with regards to both conspecifics and heterospecifics. Under high competition treatments, the weighting used for conspecifics was significantly lower than the value of *S* for conspecifics in the control treatment, whereas the heterospecific parameter value under high competition was not significantly different from the heterospecific control. However, there was a significantly lower value for *S* in conspecifics than heterospecifics when competition was high, but not in any other treatment. (B) Probability curves for a site being good with respect to conspecifics under competition, control and predation treatments, compared to asocial decisions (*S* = 1). (C) Heterospecific curves associated with competition, control and predation treatments, compared to asocial decisions (*S* = 1).

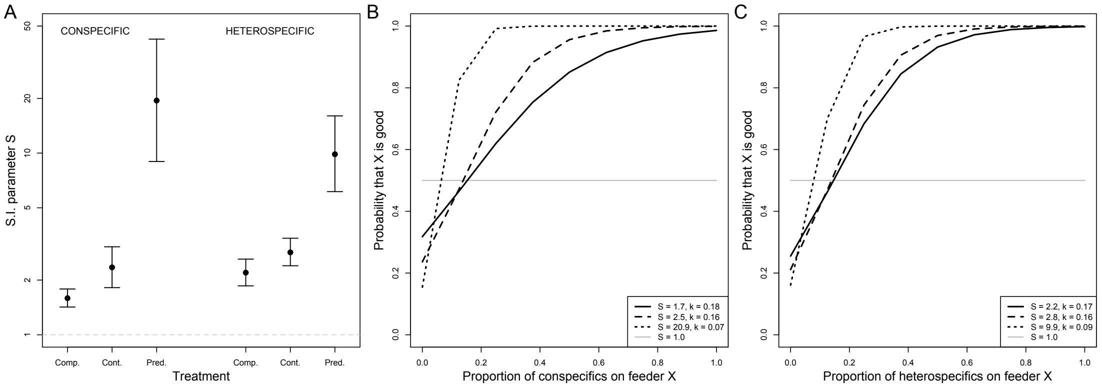
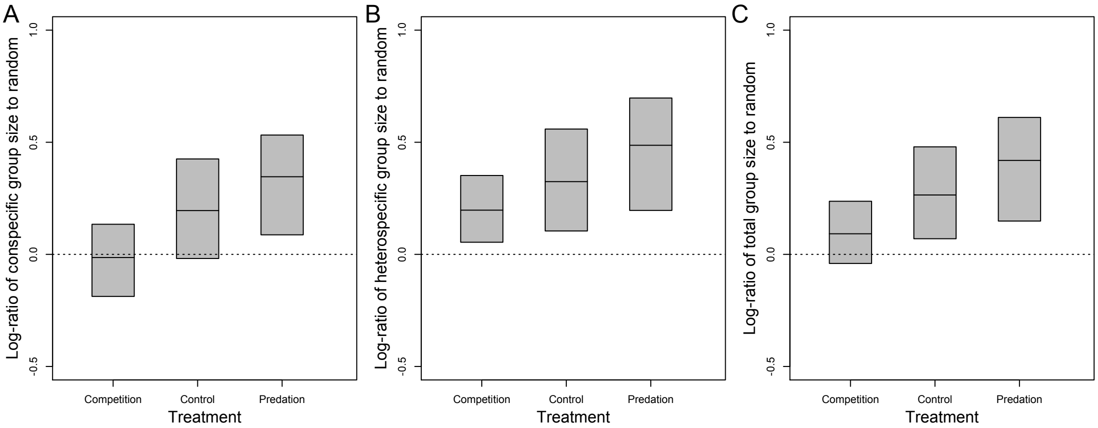


Figure 4. Log-ratio of the mean and 95% range of the chosen group size of (A) conspecifics, (B) heterospecifics, and (C) both combined, associated with each decision. Under competition, individuals on average moved towards feeders where conspecifics were at a density equal an even distribution of individuals (approximately 0.25 when S = 1). In contrast, they always moved towards heterospecific groups that were larger than the expected density, suggesting that heterospecific associations may play a key role in maintaining overall flock coherence.



CHAPTER 10

General discussion

General discussion

Aims and motivations

The primary aim of this thesis was to investigate interspecific social dynamics in mixed-species animal groups. This work was motivated by an emergent body of literature suggesting that heterospecifics may play an important role underpinning behavioural processes in animals (Seppanen et al., 2007; Goodale et al., 2010). The evolutionary drivers of mixed-species associations, particularly in terms of predation and competition, have been investigated for several decades (Krause and Ruxton, 2002; Sridhar et al., 2009). However, the role of heterospecifics in promoting social processes within species has received much less attention, despite the existing evidence, such as for interspecific social learning (Krebs, 1973). One reason for this has been the relative scarcity of studies that apply a bottom-up approach to mixed-species interactions, coupled with logistical difficulties associated with tracking groups of individuals from multiple species within a single framework.

The PIT-tagged mixed population of tits and nuthatches used in this study provides a unique opportunity for investigating social processes both within conspecifics and between heterospecifics. Using a bottom-up approach has opened up a new set of questions and research opportunities, some of which I have outlined in **chapter 2**. For example, individual position in heterospecific networks is linked to body size (**chapter 2**), whereas the patterns of connectivity between species are restricted by niche overlap (**chapter 3**). These results suggest that participation in mixed-species flocks is a complex balance of cost and benefits, mediated by both individual phenotype and group properties.

Motivated by these findings, I developed a framework for investigating mixed-species flocking, and social behaviour more generally, as a set of properties that emerge from individual decision-making processes (Figure 10.1). This approach was inspired by the modelling approaches used in studies of collective animal behaviour (Sumpter, 2010; Sumpter et al., 2012). The framework sets out an adaptive cycle, including selection operating upon phenotypes via individual fitness, the distribution of these phenotypes in physical and social space resulting from individual decision-making, and how the decisions made by each individual can then influence selection through both i) social selection and ii) the emergent properties of social (collective) behaviour via a set of interaction rules.

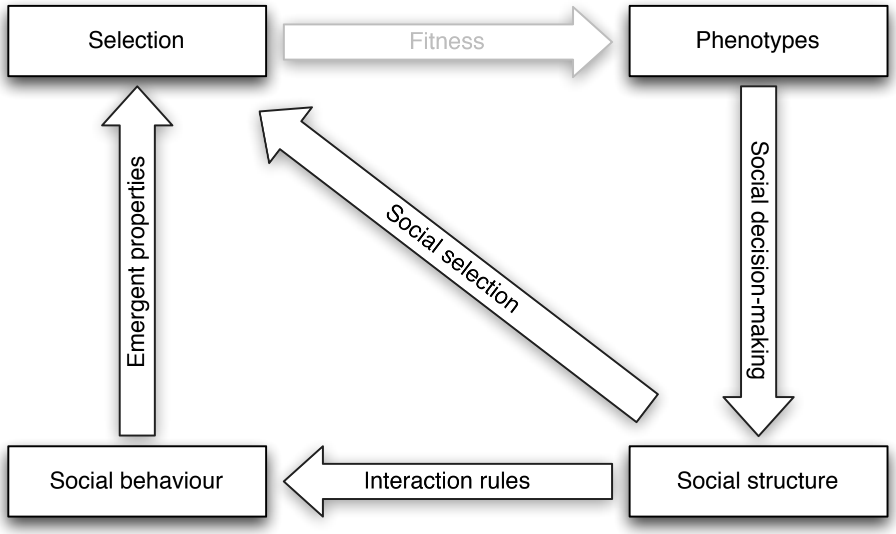


Figure 10.1: Overview of the emergent framework in this thesis. Arrows represent feedback mechanisms, for example feedback from selection on traits via fitness variation determines the phenotypic distribution in the next generation. Black arrows represent areas investigated in this thesis, whereas the grey arrow is one for which no data were collected.

Social decision-making

Individuals often forage socially, and a great deal of theoretical and empirical effort has gone to address questions of optimality in social group size in the context of foraging (Pulliam and Caraco, 1984). However, individuals may also be making decisions about to the phenotypic composition of groups as well as their numerical sizes. For example, there may be significant benefits to be gained by assorting with individuals of the same phenotype, such as in body size shoaling in fishes (Hoare et al., 2000). In **chapter 4**, I developed a measure of assortment that can be used with weighted, rather than binary, networks, and use this measure to investigate patterns of assortment in mixed-species flocks.

Using the weighted assortativity coefficient, I found that the mixed-species social networks of wild tits and thornbills contained significant phenotypic structure. However, this could arise from a number of different processes, for example if individuals are spatially disaggregated by phenotype. In **chapter 5**, I used different null models to identify whether phenotypic structure in great tits was the result of social or spatial decisions. This proved to be a powerful approach, combining long-term social structure with short-term processes in order to gain an understanding of what drives fission-fusion dynamics. Identifying these sorts of patterns, such as spatial effects of dispersal phenotype and social effects on sex ratios, opens up a broad new set of questions, particularly about how social decision-making interacts with selection on individual phenotypes.

In **chapter 5**, I found that immigrating birds were choosing different sites to resident birds, leading to spatial disaggregation by dispersal phenotype. These settling decisions could also result from social decisions if immigrants were responding to local competition. Alternatively, Wytham Woods is almost unique in composition and structure in the Oxfordshire landscape, and it is unlikely that immigrating birds will have previous experience of high-quality habitat, so they may pre-emptively settle for low-quality habitat after comparing it to an incomplete spectrum of previous experience. If the habitat within and around Wytham Woods was quantified along a quality gradient, simulations could be used to generate an expected settling pattern based on all possible arrival routes and potential individuals habitat expectations. The results from these could then be used to disentangle potential explanations for the observed spatial distributions of phenotypes.

Null models are particularly important for understanding the ecology of social decision-making. Firstly, animals rarely use space randomly, even if their social behaviour is random. For example, a random allocation of edges to nodes in a social network would assume that all individuals could associate with each other, whereas in reality individuals generally restrict their movements within a set range. Secondly, null models have the ability to isolate particular ecological mechanisms (Gotelli and Graves, 1996). In **chapter 5**, I isolated local social decisions from spatial decisions using two different randomisations, allowing identification of the scales at which social decision-making was influencing population structure. As technology facilitates the automated tracking individuals over long time periods, null models will become increasingly important for generating meaningful hypothesis tests (Croft et al., 2011).

Social selection

Social selection is an emerging analytical framework that estimates the link between social behaviour and natural selection (Wolf et al., 1999). Here, selection is partitioned into natural selection, that operates on the individual's phenotype, and social selection arising from non-random interactions between an individual's phenotype and the phenotypes of its associates. For example, in a population of wild beetles, Formica et al. (2011) found that selection for large body size (natural selection) was counteracted by negative social selection for males to have small social partners, resulting in a reduced gradient of natural selection. In **chapter 6**, I extended this framework to social network in order to calculate the social component of selection on dispersal phenotype. I found that there was significant selection on early arrival (dispersal) into Wytham woods, with early arrivals being more likely to gain breeding territories, but that late-arriving individuals could counteract this selection by associating in groups of other late arrivals. This may partially explain the findings of **chapter 5** that assortment by dispersal phenotype (immigrant versus non-immigrant) is driven by a non-random spatial distribution of individuals. It suggests that immigrant birds may be avoiding areas with many resident birds in order to reduce the effects of competition for breeding territories, given that social dominance is mediated by residency in great tits (Sandell and Smith, 1991).

Together, **chapters 5 & 6** highlight how decision-making can influence individual fitness at multiple time scales. Perhaps most importantly, they demonstrate a quantitative approach for assessing selection that operates at the social level, such as negative frequency-dependent selection. However, it remains largely unknown how individuals make decisions between available options, given that each individual is likely to experience a different social environment while dispersing. High-resolution tracking of dispersing individuals in a monitored population would be one way to establish whether individuals make settlement decisions based upon short-term or long-term adaptive strategies.

Social interaction rules

Upon joining a group, individuals need to interact with other group members in order to benefit from group-living. For example, individuals need to travel in the same direction as the group in order to gain dilution benefits, and can use information generated by other group members (social information use), trading it off against its personal information if the two do not agree. This trade-off of how much an individual weighs social versus personal information is an example of an interaction rule. Computer scientists were the first to find that complex group patterns, or collective group behaviour, could emerge from simple interaction rules (Reynolds, 1987). In this case, they developed models of self-propelled particles moving in a uniform space, interacting with other particles using zones of attraction, alignment and repulsion (Couzin and Krause, 2003). However, models of collective animal behaviour typically assume that individuals are homogeneous, live in homogeneous space, and use the same rule for all individuals of the flock (but see Bode et al., 2011).

In **chapter 8**, I investigated whether individuals used a common interaction rule (Arganda et al., 2012) for both conspecifics and heterospecifics in mixed-species flocks. I found that the best fitting parameters for this rule were almost identical within and between-species, suggesting that under natural conditions individuals are flocking as a single coherent unit. However, within these flocks, species may show dyadic differences between conspecific dyads or particular pairs of species. I found that some variation existed, with more dominant species using more heterospecific information than subdominant species. Collecting repeated decisions from the same individuals across time would easily provide enough data to infer parameters at a dyadic level in order to test whether pairwise social information use within patches is related to association strength in a winter-long social network. Such data could be used to identify whether individuals vary consistently in their social rules of interaction, which is one potentially under-explored component of social behaviour.

Most models and empirical studies, including my own in this thesis, infer single behavioural rules from observations of many individuals. They assume that individuals are identical or follow the same rule. Yet, individuals may vary their interaction rules for a number of reasons. The first, and simplest, is variation due to mechanical differences between different phenotypes or classes. For example, larger individuals (such as adults or males) may have less manoeuvrability, hence maintaining a larger zone of repulsion or exhibit weaker attraction. Conversely, smaller individuals may have a higher attraction if groups of small individuals require less food, resulting in lower per-individual competition for food resources. These differences could then lead to social structure, such as assortment resulting from differences in ability of pairs or groups to synchronise their behaviours according to traveling speed.

Individuals could also vary according to inherent behavioural states, such as by their acceptance of risk. Group-living may reduce variance in benefits accrued by individuals (for example if the discovery of ephemeral food is socially-mediated Aplin et al., 2012). If individuals are consistent in their grouping tendency, even across environmental conditions, this may create opportunities for alternative social niches. These could allow individuals to follow an asocial strategy that results in higher rewards with higher associated risk. Subsequently, these individuals may provide public information about new resources, acting as leaders. In this way, interaction rules may covary with other behaviours, potentially causing suites of behavioural polymorphisms, contributing to the evolution of animal personalities (Wolf and Weissing, 2010).

Emergent group properties

There is increasing evidence that animal groups behave as complex systems (Sumpter, 2010). For example, group size distributions often exhibit long-tailed power or logarithmic distributions (Griesser et al., 2011). By integrating behaviour across multiple individuals, such by using information from their neighbours, emergent behaviour can arise from individuals that form collective groups. Recent work has shown how the interaction between travelling speeds of neighbouring fish can steer groups towards dark, safe, areas (Berdahl et al., 2013).

In **chapter 9**, I experimentally manipulated the perceived competition and predation risks in mixed-species flocks to investigate whether interaction rules are dynamic, and if changes in these rules can lead to different group properties. I found that individuals increased their attraction towards both conspecifics and heterospecifics when predation risk was high, but reduced their attraction to conspecifics when competition was high. These results provide important evidence that intraspecific competition plays an important role in the formation of mixed-species flocks (Buskirk, 1976). Perhaps more importantly, the results of this study suggest that flock fission-fusion dynamics could be an emergent property of individual-level social interaction rules (Couzin, 2006), where low attraction leads to smaller flocks and high attraction leads to larger flocks. This approach could also be used to examine variance in individual or dyadic behaviour, which may play an role in driving emergent properties of collective behaviour or drive leader-follower dynamics (Farine and Aplin unpublished data). Ultimately, this approach could be used to relate individuals (or phenotypes) to social roles, linking these roles to adaptive behaviour at the group-level, and identify the feedback between the behavioural properties of animal groups and individual fitness. For example, identifying pair-wise attraction under different ecological conditions could provide a test for heterogeneity in dyadic cost-benefit trade-offs for association with conspecifics and heterospecifics. This is a potentially powerful extension to this thesis.

General conclusions

Theoretical and empirical evidence is increasingly suggesting that the process of natural selection operating on social individuals is modulated by a broad set of complex interactions (McGlothlin et al., 2010). In this thesis, I have developed a framework for understanding the linkages between the different contributing factors that generate social structure and animal groups. However, this opens up many more questions than I could answer, particularly in understanding how group properties can shape individual fitness. For example, can the social structure of animal populations be optimised for rapid flow of information (such as the discovery of food, Aplin et al., 2012) in a way that reduces potential spread of disease or pathogens (Hock and Fefferman, 2012)? In other words, can specific social structures increase individual survival when resources are limited, compared to non-social or randomly assorted populations? In this way, understanding the dynamic properties of animal groups will be critical for determining the relationship between natural selection and social behaviour. Further, there is increasing evidence that group dynamics can be vastly different if individual participants, or their dyadic relationships, are not homogeneous, such as in leader-follower polymorphisms (Farine et al., in revision). Mixed-species flocks are a useful way of testing the links between individual direct fitness trade-offs (such as competition and predation risks, which are directly influenced by selection pressure) and emergent group properties (such as the ability to find and optimally exploit food in ephemeral environments). Importantly, they can provide irrefutable evidence that interaction rules and social processes (e.g. social learning) can be applied generally and for gaining direct fitness benefits. In this way, this thesis supports the theory that mixed-species flocking is a mutualistic relationship between participating species (Hino, 1998), albeit one in which some components of individual fitness benefits are likely to emerge from the complex properties of group behaviour. Ultimately, this thesis has demonstrated that it is possible to gain an understanding about ecological adaptation, such as behavioural plasticity, by investigating individual decision-making mechanisms in a social context.

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Appendices

APPENDIX A

Animal Social Network Inference and Permutations for Ecologists in R using asnipe

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APPLICATION

Animal social network inference and permutations for ecologists in R using *asnipe*

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Summary

1. The sampling of animals for the purpose of measuring associations and interactions between individuals has led to the development of several statistical methods to deal with biases inherent in these data. However, these methods are typically computationally intensive and complex to implement.

2. Here, I provide a software package that supports a range of these analyses in the R statistical computing environment. This package includes a novel approach to estimating re-association rates of time between frequently sampled individuals.

3. I include extended demonstration of the syntax and examples of the ability for this software to interface with existing network analysis packages in R.

4. This bridges a gap in the tools that are available to biologists wishing to analyse animal social networks in R.

Key-words: animal social networks, *asnipe*, lagged association rate, permutation test, R

Introduction

In recent years, there has been a proliferation of software packages that provide functionality for analysis of social network data. These have largely been driven by the computational needs to analyse and interpret affiliation data in sociology, where data sets can be collected with high resolution and certainty. However, studying social behaviour in non-human animals entails much greater uncertainty in the probability that a dyad exists, and the measured strength of that connection. This has spawned extensive literature, in particular when testing for statistical significance and non-randomness (Whitehead 1997; Bejder *et al.* 1998; Croft *et al.* 2008; Whitehead 2008; Croft *et al.* 2011). Yet, there remains a general lack of simple to use tools in R (R Development Core Team 2012) that implement methods to perform the specialized analyses on sets of observed co-occurrences of individuals in animal groups.

The jump from analysing high-resolution networks, as typically achievable in human social networks, to networks comprising high levels of uncertainty is one of the largest barriers to robust application of social networks in animal behaviour. Croft *et al.* (2011) provide a comprehensive review outlining the reasons why standard methods, particularly those based on node-based permutations, are not suitable. The need for specialized methods for analyses in this subject was rapidly addressed by statisticians and biologists, culminating in the package *SOCPROG* (Whitehead 2009) that provides routines for many complex analyses. However, numerous studies are still published using packages such as *UCINET* (Borgatti *et al.* 2002) that provide out-of-the-box analyses but typically violate many of the underlying assumptions from data sampling when calculating significance in animal social networks (Croft *et al.* 2011). For example, social networks from human data generally assume that all individuals are equally likely to be observed at all times. Here, I describe a package that provides routines for several specialized tests based on data describing individual membership in groups. The *asnipe* package provides these routines in the statistical environment R that enables the results of these routines to be directly integrated with a wide range of social network packages for generating statistics on the inferred social network. By providing these routines in the R environment, I hope to bridge an existing gap in statistical tools and enable more robust use of social networks in animal behaviour research.

Overview of *asnipe*

asnipe primarily provides tools for analysis of social networks that are performed either on a group by individual matrix or a stack of association matrices represent sampling periods. The former is a matrix where the columns contain the identities of all individuals in the population, and each row describes membership to a distinct group:

	Ind. ‘A’	Ind. ‘B’	Ind. ‘C’	Ind. ‘D’	Ind. ‘E’	Ind. ‘F’
Group 1	1	0	1	0	0	0
Group 2	0	0	1	1	0	1
Group 3	0	1	0	0	1	0
Group 4	0	0	1	0	0	0
Group 5	0	1	0	0	1	0
Group 6	1	0	0	1	0	1

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The latter is a $t \times N \times N$ matrix, where t is the number of sampling periods, and *N* is the number of individuals. Each N x N submatrix in this stack contains 1s and 0s depending on whether individuals were associated during that sampling period. In the case below, all individuals were seen together during the first sampling period, whereas individuals ‘A’ and ‘B’ were not seen together in the second.

Period 1

	Ind.‘A’	Ind.‘B’	Ind.‘C’
Ind.‘A’	0	1	1
Ind.‘B’	1	0	1
Ind.‘C’	1	1	0

Period 2

	Ind.‘A’	Ind.‘B’	Ind.‘C’
Ind.‘A’	0	0	1
Ind.‘B’	0	0	1
Ind.‘C’	1	1	0

Period 3

	Ind.‘A’	Ind.‘B’	Ind.‘C’
Ind.‘A’	0	1	0
Ind.‘B’	1	0	1
Ind.‘C’	0	1	0

This is the approach used by the *Matlab* package *SOCPROG*. The *asnipe* package contains routines for turning most common forms of association data into either of these two formats.

Functionality

At present, *asnipe* includes functions for four key analytical steps that are generally lacking in existing R packages (but available in *Matlab* via *SOCPROG*):

1. Defining a group by individual matrix or generate sampling period co-occurences from association data.

2. Creating an association matrix from observations of individuals co-occurring in time and space.

3. Performing permutation tests on the observation stream following the method originally proposed by Bejder *et al.* (1998) and since refined by other authors (Whitehead 2008; Sundaresan *et al.* 2009).

4. Calculating lagged association rates between individuals or classes of individuals.

In addition to the above, the routines in *asnipe* provide built-in functionality that enables simple incorporation of time, space and classes of individuals. This is important for conducting biologically meaningful statistical tests and enables users to very easily create temporal or spatial networks from their data.

Package functions

CONVERTING GROUP DATA

Commonly, data on group membership will be in a sequential format based on the observation of the groups. *asnipe* provides functions for converting these into either a group by individual matrix or a set of sampling periods. Here, I provide two examples for doing this using the provided functions. First, I provide code to demonstrate how to generate a group by individual matrix from a data frame containing individuals and the groups they are observed in. Note that the input for this function must be in this two-column format.

```
## first load the package
R>library(asnipe)

## define group memberships (or read from file)
R>individuals <- data.frame(ID=
+c(“C695905”,“H300253”,“H300253”,
+“H300283”,“H839876”,“F464557”,“H300296”,“H300253”,
+“F464557”,“H300296”,“C695905”,“H300283”,“H839876”),
+GROUP=c(1,1,2,2,2,3,3,4,5,5,6,6,6))
R>individuals
```

```
                ID              GROUP
1               C695905         1
2               H300253         1
3               H300253         2
4               H300283         2
5               H839876         2
6               F464557         3
7               H300296         3
8               H300253         4
9               F464557         5
10              H300296         5
11              C695905         6
12              H300283         6
13              H839876         6
```

```
## get group by individual matrix
R>gbi <- get_group_by_individual(individuals,
+data_format=“individuals”)
R>gbi
```

```
  C695905 H300253 H300283 H839876 F464557 H300296
1 1       1       0       0       0       0
2 0       1       1       1       0       0
3 0       0       0       0       1       1
4 0       1       0       0       0       0
5 0       0       0       0       1       1
6 1       0       1       1       0       0
```

An alternative approach is to record each group and all of the members it contains. This will need to be in the form of a list (and can be directly imported from file as shown in the previous section). Lists are collections of elements that can vary in size or form, making it suitable for groups with different number of members. These can then be converted into a group by individual matrix using the same function as listed above.

```
## define group memberships (or read from file)
R>groups <- list(G1=c(“C695905”,“H300253”),
+G2=c(“H300253”,“H300283”,“H839876”),
+G3=c(“F464557”,“H300296”),
+G4=c(“H300253”),
+G5=c(“F464557”,“H300296”),
+G6=c(“C695905”,“H300283”,“H839876”))
```

```
R>groups
$G1
[1]“C695905″“H300253″
$G2
[1]“H300253″“H300283″“H839876″
$G3
[1]“F464557″“H300296″
$G4
[1]“H300253″
$G5
[1]“F464557″“H300296″
$G6
[1]“C695905″“H300283″“H839876″

## get group by individual matrix
R>gbi<-get_group_by_individual(groups,
+data_format=“groups″)
```

Both of these input formats can also be used to generate sampling periods. The key difference is that sampling periods must explicitly contain the time when each group was observed, and the period over which data should be represented. Using the two input files from above, the sampling periods can be generated as follows:

```
## individuals in groups format
## include times for each individual
R> individuals <- cbind(individuals,
+DAY=c(1,1,1,1,1,2,2,2,3,3,3,3,3))

## now get sampling periods
R> SPs <- get_sampling_periods(individuals[,
+ c(1,2)],individuals[,3],1,
+ data_format=individuals)

## sampling periods indexed over the first element
R>SPs[1,,]
```

```
        C695905 H300253 H300283 H839876 F464557 H300296
C695905 0       1       0       0       0       0
H300253 1       0       1       1       0       0
H300283 0       1       0       1       0       0
H839876 0       1       1       0       0       0
F464557 0       0       0       0       0       0
H300296 0       0       0       0       0       0
```

```
## list of groups format
## create a time variable
R>days <- c(1,1,2,2,3,3)

## now get sampling periods
R> SPs <- get_sampling_periods(groups,
+days,1,data_format=“groups″)
```

These sampling period matrices can then be used to generate association matrices and to perform network randomizations that control for individual gregariousness (see Whitehead 2008, p. 130). In some cases, randomization procedures may need to control for spatial, such as swapping only individuals within the same locations. In that case, the sampling period function also provides the functionality to input location information and calculates independent sampling periods for each location in each time period. Although in the rest of this manuscript, I will be using group by individual matrices to demonstrate functionality, using sampling period data is identical. When entering sampling period data, the *data_format* flag is changed from ‘*GBI*’ to ‘*SP*’.

GENERATING NETWORKS

The main step involved with performing social network analysis is the creation of the social network. Whitehead (2008) provides extensive discussion of the methodology for observing associations, groups and measuring interactions. Yet with the exception of *SOCPROG* (Whitehead 2009), I am unaware of another package that will accept group data and generate a social network with a chosen measure (see Whitehead 2008, for information on index ratios). In *asnipe*, I provide a method that calculates the association matrix from either sampling periods or a group by individual matrix. Perhaps, the most powerful aspect of this function is the ability to subset data within the function and therefore generate temporal or spatial networks using a single loop.

In the following examples, I will be using the data from Farine *et al.* (2012). This data set is provided with the package and can be loaded using the *data* function as shown below. Once the group by individual matrix has been loaded, the association matrix can be calculated using the function *get_network*:

```
R>data(“group_by_individual″)
R>network <- get_network(gbi, data_format=“GBI″)
```

However, the *get_network* function has further functionality that can automatically subset data internally. In the example below, the network is calculated separately for the first and second half of the time. The results are stored in a three-dimensional cube where the first index is the network number, second is the association matrix rows, and the third is the association matrix columns:

```
R>data(“times″)

## define to 2 × N × N array that will hold
## the two N x N association matrices
R>networks <- array(0, c(2, ncol(gbi), ncol(gbi)))

## calculate network for first half of the time
R>networks[1,,] <- get_network(gbi,
+ data_format=“GBI″, times=times,
+ start_time=0, end_time=max(times)/2)
Generating 151 × 151 matrix

## calculate network for second half of the time
R>networks[2,,] <- get_network(gbi,
+ data_format=“GBI″, times=times,
+ start_time=max(times)/2,
+ end_time=max(times))
Generating 151 × 151 matrix
```

These association matrices can then directly interface with other packages to calculate network statistics:

```
## convert to igraph network and calculate
## degree of the first network
R> library(igraph)
R> net <- graph.adjacency(networks[1,,],
+ mode=undirected, diag=FALSE,
+ weighted=TRUE)
R> deg_weighted <- graph.strength(net)
R> detach(package:igraph)

## alternatively package SNA can use matrix stacks
##directly
R> library(sna)
R> deg_weighted <- degree(networks,gmode=“graph”,
+ g=c(1,2), ignore.eval=FALSE)
R> detach(package:sna)
```

NETWORK PERMUTATIONS OF THE DATA STREAM

An important finding in the animal social network literature is that the randomization methods used for creating null models in community ecology (for example Manly 1997) can easily lead to biases and overestimates of statistical significance (Bejder *et al.* 1998). It was proposed by Bejder *et al.* (1998) that to avoid biases in sampling, randomizations should be performed on the data stream rather than on the association matrix. This is where most software packages are incompatible with the requirements when analysing animal social networks as they typically rely on node-based permutations (with the exception of *SOCPROG*). Several authors have also suggested improvements to the data stream permutation method, such as randomizing while controlling for space, time or type of individual (Whitehead 1999; Whitehead *et al.* 2005; Sundaresan *et al.* 2009).

I incorporate all of these in the function *network_permutation* to test where the observed data fits on a distribution based on permutations (Fig. 1). This method swaps either individuals between groups (when using group by individual matrices) or associations (when using sampling periods). It then recalculates the network after each swap, creating a stack or set, of p matrices where p is the number of permutations, and each slice in that stack is an $N \times N$ association matrix. These swaps can maintain the variance in individual gregariousness and size of each group constant (Bejder *et al.* 1998). This function enables the swaps in the data stream to be limited between individuals that occur on the same day, in the same location, or are of the same class (such as sex or age class). These variables are not confined to data types and can therefore provide the ability to restrict permutations within any two types of group-level characteristics (*days* and *locations* that can represent any time and/or space variable) and one type of individual characteristics (*classes* that can be any variable describing a characteristic of individuals). In the case of group-level characteristics, these must be explicitly incorporated into the sampling periods if using that method.

```
## calculate the weighted degree of the two networks
## calculated previously. The degree function
## accepts stacked graphs as an input.
R> library(sna)
R> deg_weighted <- degree(networks, gmode=“graph”,
+ g=c(1,2), ignore.eval=FALSE)

## perform the permutations constricting within hour
## of observation using the days parameter
R> network1_perm <- network_permutation(gbi,
+ data_format=“GBI”,
+ association_matrix=networks[1,,], times=times,
+ start_time=0, end_time=max(times)/2
+ days=floor(times/3600), within_day=TRUE)
R> network2_perm <- network_permutation(gbi,
+ data_format=“GBI”,
+ association_matrix=networks[2,,], times=times,
+ start_time=max(times)/2, end_time=max(times),
+ days=floor(times/3600), within_day=TRUE)
## calculate the weighted degree for each permutation
R> deg_weighted_perm1 <- degree(network1_perm,
+ gmode=“graph”, g=c(1:1000),
+ ignore.eval=FALSE)
```

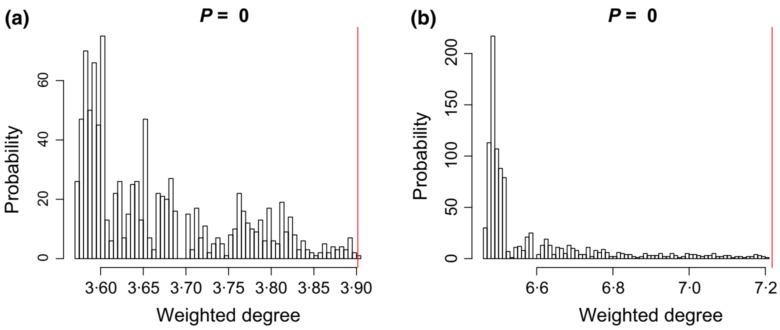

Fig. 1. Results from the example permutation show that the observed weighted degree, or strength, in the population was significantly higher than expected by chance in both the morning (A) and afternoon (B). The red line (observed weighted degree) is higher than 100% of the values from permutations in both cases. The plots also suggest a shift in behaviour in the afternoon that leads to an overall increase in associations.

```
R>deg_weighted_perm2<-degree(network2_perm,
+gmode=“graph”,g=c(1:1000),
+ignore.eval=FALSE)
R>detach(package:sna)

##plot the distribution of permutations with the
##original data overlaid
R>par(mfrow=c(1,2))
R>hist(colMeans(deg_weighted_perm1),breaks=100,
+main=paste(“P=”,sum(mean(deg_weighted[,1])<
+colMeans(deg_weighted_perm1))/ncol
+(deg_weighted_perm1)),
+xlab=“Weighted degree”,ylab=“Probability”)
R>abline(v=mean(deg_weighted[,1]),col=‘red’)
R>hist(colMeans(deg_weighted_perm2),breaks=100,
+main=paste(“P=”,
+sum(mean(deg_weighted[,2])<colMeans
+(deg_weighted_perm2))
+/ncol(deg_weighted_perm2)),
+xlab=“Weighted degree”,ylab=“Probability”)
R>abline(v=mean(deg_weighted[,2]),col=“red”)
```

USING PERMUTATIONS WITH LINEAR MODELS

Linear models, and variants such as general linear models and generalized linear mixed models, are frequently used in ecology and animal behaviour to test the strength and significance of biological effects. The Bejder *et al.* (1998) permutation method is a useful way of estimating the significance of parameter estimates against biologically relevant null models, because permutations can control for spatial, temporal and individual variation. Here, I demonstrate how this can be used to show that there is a significant effect of time of day on the weighted degree as shown by the shift in histograms from Fig. 1. In this case, the coefficient estimate for the magnitude of the slope from the original data is compared with the coefficient estimate based on the weighted degrees of individuals from each permuted network. The one-tailed significance is then calculated based on the position of the observed slope estimate relative to the distribution of slopes calculated from the randomized data.

```
##build dataset with all data in one column of a data
##frame
R>input<-rbind(data.frame(Degree=
+deg_weighted[,1],Time=“MORNING”),
+data.frame(Degree=deg_weighted[,2],
+Time=“AFTERNOON”))

##build model of strength (weighted degree)
##of each individual as a function of time of day
R>model<-lm(Degree~Time,data=input)

##get parameter estimate of slope
R>e<-coef(summary(model))[2,1]
R>e
[1] 3.316351

##get an estimate of the slope for each permutation
##matrix
R>e_perm<-rep(NA,1000)
R>for (i in 1:1000){
R>input_perm<-rbind(data.frame
+(Degree=deg_weighted_perm1[,i],
+Time=“MORNING”),data.frame
+(Degree=deg_weighted_perm2[,i],
+Time=“AFTERNOON”))
R>model_tmp<-lm(DegreeT˜ime,data=input_perm)
R>e_perm[i]<-coef(summary(model_tmp))[2,1]
R>}

##calculate P value from how many of the slopes
##estimated in the randomized data
##are larger than the observed
R>P_value<-sum(e_perm>e)/1000

R>P_value
[1] 0.001
```

This result suggests a significant effect of the time of day on association patterns because the parameter estimate from the model based on the original data (in this case a slope of 3·316) was greater than the estimate from the randomized data in all but 1 of the 1000 permutations. Thus, the increase in the strength of associations from the morning to afternoon was significant when compared to a null model that randomized the pattern of associations within these same time periods ($P < 0{\cdot}01$). Although here I demonstrate the use of this approach using 1000 permutations, this approach does often require some verification that the P value has stabilized, which may only occur after many more permutations. This approach could be extended to incorporate individual identities as random effects using generalized linear mixed models or species as random effects. Here, I demonstrated the approach using linear models for maximum clarity.

CALCULATING LAGGED ASSOCIATION RATES

Lagged association rates are a measure of the probability of being observed re-associating in a given time lag (Whitehead, 1995, 2008). This allows biologists to test for temporal persistence of associations between individuals. The original approach given by Whitehead (1995) measures the average probability of *any* re-association between individuals during the given time window (see Whitehead 2008, section 5.5.1).

```
R>data(“group_by_individual”)
R>data(“times”)
R>data(“individuals”)

##calculate lagged association rate for great tits
R>lagged_assoc<-LAR(gbi,times,3600,classes=
+inds$SPECIES,which_classes=“GRETI”),
+which_classes=“GRETI”)
```

```
R>lagged_assoc

                 [,1]               [,2]
2           0.6931472          0.7210728
3           1.0986123          0.6745192
4           1.3862944          0.7021277
5           1.6094379          0.6911413
6           1.7917595          0.6666667
7           1.9459101          0.6539924
8           2.0794415          0.6181102
9           2.1972246          0.5121951
```

This function returns a 2 × N matrix with $\log(\mathit{time})$ in the first column and the lagged association rate for each time period τ in the second that can be used directly for plotting the results (Fig. 2). However, this approach generally requires an estimate of the error to be generated. Whitehead (1995) suggests that the Jackknife technique is appropriate. This can easily be implemented by creating subsets of the data, removing one or more observations and calculating the lagged association rate for the new data. By repeating across all possible subsets, the standard error can be estimated and plotted onto the graph.

```
# create an empty variable to store results, and
# store the result after each group has been removed
R>lagged_assoc_perm<-matrix(NA,
+nrow=nrow(lagged_assoc),ncol=nrow(gbi))

# create a loop to run each simulation, and run on the
# dataset having removed one row at a time. Here we are
# only interested in the second column of the result.
R>for (i in c(1:nrow(gbi)){
R>lagged_assoc_perm[,i]<-LAR(gbi[-i,],
+times[-i],3600,classes=inds$SPECIES,
+which_classes="GRETI")[,2]
R>}

# calculate the standard error
R>N<-nrow(gbi)
R>means<-rowMeans(lagged_assoc_perm)
R>se<-sqrt(((N-1)/N)*apply((means-
+lagged_assoc_perm)^2,1,sum))

## plot the results
R>plot(lagged_assoc,type='l',axes=FALSE,
+xlab="Time (hours)",ylab="LAR",ylim=c(0,1))
```

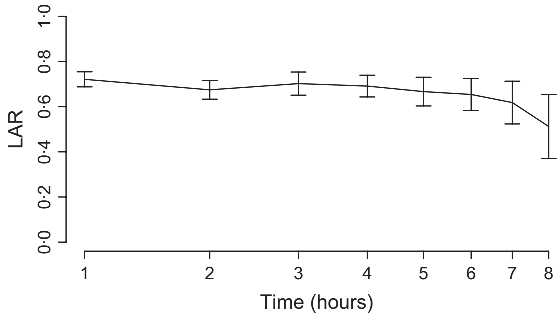

Fig. 2. Lagged association rate for individuals in the study by Farine *et al.* (2012) shows little decline over the course of one day.

```
R>arrows(lagged_assoc[,1],lagged_assoc[,2]-se,
+lagged_assoc[,1],lagged_assoc[,2]+se,
+angle=90,code=3,length=0.1)
R>axis(2)
R>axis(1,at=lagged_assoc[,1],
+labels=c(1:nrow(lagged_assoc)))
```

The lagged rate of association

One significant advance in the study of animal social networks is the greater sampling rates that are achievable through tracking of individuals, giving greater temporal resolution to their behaviours and subsequent associations. However, repeated sampling of individuals within short time periods is likely to upweight random interactions that are driven by spatial overlap, and therefore confound long-term lagged association rates of populations studied at a landscape scale. For example, if individuals are sampled 100 times per day over 3 months and the minimum τ is set to one day, then any dyad needs to be observed just once per day or approximately 90 times, in order to get a constant lagged association rate of 1. Yet the association rate between these individuals could be as low as 0·01 (if associating just once per day).

In this package, I present an alternative measure of the temporal rate of re-association that incorporates the frequency at which dyads are observed to associate for a given time lag τ. This measure is given for individuals X and Y by:

$$g(\tau, X, Y) = \sum_{j,k|(t_k - t_j)=\tau} \frac{a_j(X,Y) \cdot a_k(X,Y)}{a_j(X,Y) \cdot a_k(X,X)} \tag{1}$$

where $a_j(X,Y)$ is the number of observations of the dyad X and Y in time period j, and $a_k(X,X)$ is the number of observations of individual X in time period k. This results in a measure for τ that is more closely related to the association rate of individuals calculated by the simple ratio index. The *LRA* function calculates the lagged rate of association using the above formula. Alternatively, it can be used to return a lagged rate of association that is qualitatively similar to Whitehead (1995) but calculated independently for each dyad by setting the *association_rate* flag to FALSE. Setting *association_rate* to FALSE ignores the number of observations of individuals within sampling periods (both together and apart), setting their value to 1 if they were seen at least once and 0 if they were never seen together. The mean of this dyadic lagged rate of association may differ to the regular lagged association rate from the function *LAR*, but can be used to estimate association rates within or between classes of individuals.

```
R>data("group_by_individual")
R>data("times")
R>data("individuals")

## calculate lagged association rate between great
##tits
R>lagged_rates<-LRA(gbi,times,3600,
+classes=inds$SPECIES,which_classes="GRETI"
+association_rate=TRUE)
```

```
## calculate the mean rate for individuals at each tau.
## note the difference to the values generated from LAR
## above
R> apply(lagged_rates,3,mean,na.rm=TRUE)
[1] 0.6100229 0.5473871 0.6131421 0.6426655
0.6293223 0.5905218 0.5775401 0.5121951

R> str(lagged_rates)
num [1:51, 1:51, 1:8] NA NaN NaN NaN 0.333 ...
- attr(*, “dimnames”)=List of 3
..$ : chr [1:51] “1” “2” “3” “4” ...
..$ : chr [1:51] “1” “2” “3” “4” ...
..$ : NULL
```

This function returns the lagged rate of association for each dyad in a stack of $N \times N$ matrices with each slice representing one increment in τ. Dyads not observed associating are returned the value *NaN* to distinguish this from a probability of zero. The function also provides an alternative output style that is a data frame consisting of each dyad, τ, and probability of re-association. This format is useful for fitting models from other packages or plotting data as a surface.

```
R> lagged_rates <- LRA(gbi,times,3600, classes=
+ inds $ SPECIES, which_classes=“GRETI”
+ output_style=2)
Timesteps=9

R> str(lagged_rates)
‘data.frame’ : 3680 obs. of 4 variables:
$ ID : Factor w/ 45 levels “1”,“10”,“11”,..:
+ 1 1 1 1 1 1 1 ...
$ ASSOCIATE : Factor w/ 51 levels
+ “1”,“10”,“11”,..: 45 49 50 3 5 6 ...
$ TIME : num 1 1 1 1 1 1 1 1 1 1 ...
$ RATE : num 0.333 0.5 0.667 0.667 0 ...
```

In order to demonstrate the difference between the lagged association rate and the lagged rate of association, I calculated both values for a population of wild blue tits sampled repeatedly over 13 consecutive weeks in Wytham Woods, near Oxford, UK. Individuals fitted with passive integrated transponder (PIT) tags were detected on average 226 times (range 1–942) in a stratified grid of 65 feeders fitted with antennae to detect visits by individuals. These feeders were all opened and shut on the same two days per week using the same methods described by Farine *et al.* (2012) to provide 26 daily samples over a period of 86 days (3 December 2011 to 26 February 2012). Running the two methods demonstrates that the lagged association rate is significantly higher than the lagged rate of association in this population (Fig. 3). Importantly, these two methods have a very different estimate with respect to a null association rate. The lagged rate of association null was calculated using the mean group size experienced by individuals divided by the mean number of total associates for each individual (the mean binary degree). It differs from the null lagged association rate proposed by Whitehead (1995) that used $N-1$ in the denominator, which assumes equal probability of mixing between all individuals and may not be appropriate for large populations. The standard lagged association rate suggests a high rate of re-associations. This is largely because individuals were detected many times within each sampling period, and this measure requires only one re-association in order to give that time period a value of 1. Therefore, individuals that co-occur in space but are not associates might be repeatedly found co-occurring simply by chance arrivals at the same feeder at the same time. The new method proposed in this package will therefore be most appropriate for data-rich studies using automated sampling, while the traditional lagged association rate will be most suitable for studies in which individuals have fewer observations per sampling period.

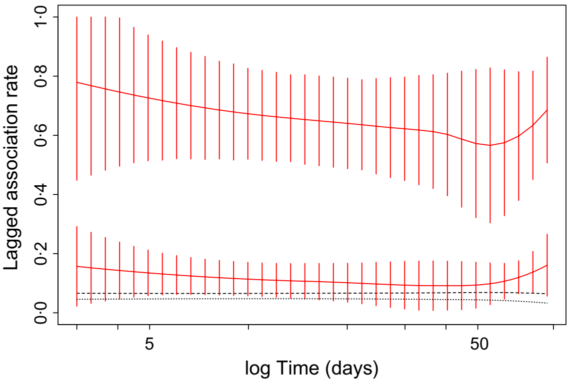

Fig. 3. Lagged association rate (top) and lagged rate of association (bottom) will typically show little difference in shape. However, the lagged rate of association estimates a much lower rate of re-association that does not differ significantly from a null expectation (dashed line) in this population. This more strongly reflects the mean (non-zero) association rate of 0·04 for this period (standard deviation = 0·04, range 0·001–0·45). The lagged association rate in this case overestimates the social affinity over time for this population, suggesting it is significantly higher than the null expectation (dotted line). Standard errors were calculated via jacknife where each sampling location was removed one at a time.

Closing comments

A major goal in introducing *asnipe* is to provide the functionality for specialized analysis of animal social networks, while maintaining access to the wide range of tools for more general analysis of network structure that are available in R, such as *sna* and *igraph*. This article provides examples of all the steps required to perform network analysis on data capturing the group membership of individual animals. I hope that by providing a tool that is freely available in a widely used statistical computing platform, this will encourage greater uptake of R by biologists studying animal social networks and further development of tools tailored to the needs of this type of analysis.

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I sincerely thank the members of the EGI social networks group, and in particular Josh Firth, Colin Garroway, and Reinder Radesma for their comments on early drafts of the manuscript, Ioannis Psorakis for continued debate of the merit of statistical approaches in social networks. I also thank Hal Whitehead and one anonymous referee for valuable comments. This work was funded by a European Research Council grant (AdG 250164) awarded to Prof. Ben C. Sheldon.

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APPENDIX B

Social networks predict patch discovery in a wild population of songbirds

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Social networks predict patch discovery in a wild population of songbirds

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Animals use social information in a wide variety of contexts. Its extensive use by individuals to locate food patches has been documented in a number of species, and various mechanisms of discovery have been identified. However, less is known about whether individuals differ in their access to, and use of, social information to find food. We measured the social network of a wild population of three sympatric tit species (family Paridae) and then recorded individual discovery of novel food patches. By using recently developed methods for network-based diffusion analysis, we show that order of arrival at new food patches was predicted by social associations. Models based only on group searching did not explain this relationship. Furthermore, network position was correlated with likelihood of patch discovery, with central individuals more likely to locate and use novel foraging patches than those with limited social connections. These results demonstrate the utility of social network analysis as a method to investigate social information use, and suggest that the greater probability of receiving social information about new foraging patches confers a benefit on more socially connected individuals.

Keywords: social network theory; social information; Paridae; group foraging; scrounging; local enhancement

1. INTRODUCTION

For many animals, food can be difficult to find, with locally abundant but ephemeral foraging sites scattered patchily across the landscape. In these cases, foraging individuals face a challenge they can attempt to overcome through a variety of strategies. Personal information and experience may be used to optimize search patterns, e.g. by re-checking previously successful sites using 'traplining behaviour' [1]. Alternatively, individuals may use search strategies similar to the Lévy walk model, where clustered searching is alternated with long directional travel [2]. Individuals may also be able to maximize efficiency by searching in groups, particularly if they differ in their personal experience [3–5]. Finally, rather than depending on optimized searching or personal experience, foragers may use social information to locate food.

Social information is a broad concept, encompassing all information resulting from the behaviour of others, whether related to activities as diverse as habitat selection, predator avoidance or mate choice [6–8]. In the context of finding patchy food resources, social information refers to information used by naive individuals to locate resources that they have obtained via the behaviour of successful patch finders [9]. Three such behaviours are generally accepted to occur: recruitment at roosts or colonies, active recruitment to food and local enhancement. The information centre hypothesis proposes that individuals transmit information about food patches when they leave or return to communal roost sites [10]. More commonly, successful individuals may actively recruit others at the foraging site itself. Here, the signaller pays a cost in producing the signal and increasing competition, but may gain greater benefits from reducing predation risk [11]. Finally, and perhaps most simply, individuals may be attracted to inadvertent cues produced by feeding conspecifics or heterospecifics. Such coarse-level local enhancement has been shown in a wide range of taxa, including invertebrates, fish, mammals and birds [9,12,13], and is thought to be the mechanism by which most animals use social information when searching for food sites [12,14].

While it is generally accepted that many species can use social information of some kind to find food patches, little consideration has been given thus far to between-individual variation in access to information, or that information may spread non-randomly between dyads. Assumptions of free mixing and indiscriminate sharing of information in populations are unrealistic when considering the social processes connected with the spread of information [15,16]; social interactions rarely occur completely at random, and individuals often differ in their number and strength of connections to other individuals [17]. Social network theory seeks to explain this variation by measuring individual contact patterns and incorporating them into a descriptive framework that integrates all levels from individual behaviour to population processes [16]. With recent methodological advances, social network analysis has become a promising new way to investigate the effect of individual and community heterogeneities on information transmission dynamics. Network-based diffusion analysis (NBDA) is one such method, designed to identify social learning processes in animals [18–20]. We propose that if individuals exploit social information in the discovery of food sites, then this information should

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be more likely to be transferred between associating individuals, and thus follow routes through a social network. Following this logic, individuals that occupy different network positions should also differ in the speed and reliability with which they receive information.

NBDA infers social transmission of information if the pattern of behavioural change over time follows association patterns in the relevant social network. It assumes that the rate at which social transmission occurs between a naive-informed dyad is linearly proportional to the association between them [20]. Hoppitt *et al.* [19] successfully retrospectively applied this method to the spread of innovation in a flock of captive starlings [21]. However, the only two studies to test NBDA in the wild (both in small groups of lemurs) obtained ambiguous results [22,23], with no evidence found for social transmission despite obtaining positive results from using a more traditional 'two-action control' paradigm.

We investigate social information use and social networks in three species of sympatric tit (family Paridae) in two relatively isolated sub-populations. The ecology of these species makes them excellent candidates to study food-searching behaviour. Tits and chickadees are a family of passerines that mostly live in open woodland and feed on a mixed opportunistic diet, forming roaming mixed species fission–fusion flocks in the non-breeding season. A long history of captive studies has demonstrated that tits can be attracted to new food patches through local enhancement [24,25]. Recent wild studies have also shown that tits use social information when making habitat selection and dispersal decisions, and that this information use differs between individuals [26,27]. Fewer studies have examined social information and food patch discovery in wild tits and chickadees, but it appears that some species may also actively recruit flock-mates to food sites [28,29].

Here, we report the first application of NBDA to a large-scale experiment in wild animals. By measuring the association matrix of two wild sub-populations of tits and then recording arrival of individuals at novel food patches, we attempt to identify whether these populations use social information to find patchy food sites. We then ask whether individuals with differing network positions vary in their probability of finding new food sites after an initial discovery event, that is, whether some types of individuals differ in their access to information [30,31].

2. MATERIAL AND METHODS

(a) *Study area and population*

The study was conducted in two small areas of broadleaf deciduous woodland near Wytham woods, Oxfordshire (51°46′ N, 1°20′ W). These areas form part of a long-term project on great tits, and are surrounded by arable land [32]. We included the most common Paridae species in these woodlands: blue tit (*Cyanistes caeruleus*), great tit (*Parus major*) and marsh tit (*Poecile palustris*), all of which commonly forage together [33]. Birds were caught using mist-nets from October 2010 to January 2011, fitted with a unique British Trust for Ornithology metal leg ring, aged as juvenile or adult and sexed based on biometrics. Birds were also fitted with a plastic ring containing a uniquely identifiable passive integrated transponder (PIT) tag. While there was some movement between our study areas and the main Wytham area, intensive mist-netting of birds throughout the 2010–2011 winter in Wytham woods meant that immigrants were also likely to be ringed and PIT-tagged.

(b) *Association matrix*

Sunflower feeders with two access points were fitted with radio-frequency identification (RFID) antennae (Francis Instruments Ltd., Cambridge) and installed at two locations in each area. The feeders were filled with food for 3 days and left empty for 3 days on a repeated cycle during January 2011 in Higgins Copse and from December to January 2011 in Cammoor/Stimpsons Copse. A data-logger at each feeder recorded the 15-s time block in which each bird visited and the individual's PIT-tag code. Combining the records from both locations at each area resulted in a total of 7790 records at Higgins Copse, and a total of 11 866 records at Cammoor/Stimpsons Copse. The total number of visits each individual made was used as a measure of both individual propensity to visit artificial feeders and overall site residency.

Associations were calculated between individuals using a 75 s moving time window, where an association occurred between two individuals when one individual visited the same feeder within 30 s on either side of the 15 s time block in which the other individual visited. Directionality of interactions could not be inferred, and a gambit of the group approach was used [34]. The results were also analysed using a 135 s time window and were robust to this variation. Twenty-four birds were seen fewer than five times and were excluded from the analysis to avoid a sampling bias that could affect edge weights. An association matrix of all other individuals was then constructed using a simple ratio index [35], whereby edges are scaled between 0 (never associated) and 1 (never observed apart). Two networks were generated (weighted and non-directional), one for Cammoor/Stimpsons and one for Higgins Copse.

An important concept in social network analysis is centrality, with measures reflecting the extent and manner to which individual nodes are connected to others. Here, we concentrate on two measures of centrality most appropriate to local enhancement [30]. 'Eigenvector centrality' extends the concept of degree centrality (the number and strength of a node's connections) by also measuring the relative connectedness of an individual's associates. 'Betweeness centrality' (unweighted) is a measure of an individual's role in connecting otherwise distinct groups of individuals, and is calculated by counting the number of shortest paths between nodes that pass through the focal node. Both centrality measures were calculated in the SNA package (v. 2.2-0) in the software program R (v. 2.12.2) [36].

(c) *Patch-discovery experiment*

Fourteen days after the end of the association matrix data collection, one sunflower feeder fitted with two RFID antennae was placed at a random location within each area to function as a new artificial food 'patch'. A data-logger recorded patch arrival times for each individual. The same feeder design as that used for the social network was used to reduce any effect of neophobia, and feeder installation was undertaken at night to avoid inadvertently producing information about the site [37]. The artificial food patch was removed after 3 days, and the process repeated at a new randomly chosen site, with 7 days between trials. Four trials were completed at the Cammoor/Stimpsons Copse and three at Higgins Copse. In each of the seven trials, different individuals first located the food patch; initial discovery appeared to show a trend towards great tits (four of seven) and first-years (six of seven).

In summary, the association matrix measured undirected relationships from multiple observations of flock composition, and the discovery experiment recorded individual order of arrivals to the food site (with no implied sociality)—the two should only be related if social behaviour is involved in patch discovery. While the methods of data collection for the association matrix and patch-discovery trials were superficially similar, they differed in two important ways. First, the association matrix was measured over a period of one to two months at four set locations, with the feeders as well-established food resources. For the patch discovery, one feeder was installed at a completely novel location such that no individual had any pre-existing knowledge. Second, visits were recorded for the association matrix over an extended period, with individual dyadic feeding co-occurrences accumulated over numerous feeding bouts. Timing of arrival was not differentiated, nor directionality implied. In the patch-discovery experiment, only the time of first discovery for each individual was measured, and group arrival was controlled for in the NBDA.

(**d**) ***Data analysis***

Two alternative methods were used to ask whether the measured network predicted the pattern of patch discovery observed. NBDA seeks to identify social transmission by assuming that if social transmission is occurring, then the spread of behaviour should follow the patterns of associations between individuals, with the rate of social transmission being linearly proportional to the strength of association [18–20]. Second, network centrality parameters were used to try and identify individuals with a higher probability of both finding foraging patches and arriving at patches earlier (after the initial discovery).

Data were inputted using the NBDA code v. 1.2 [19] in R [36]. The time of first arrival at the artificial food patch for each individual was entered using the 'time of acquisition diffusion analysis' function. All individuals that discovered patches but were not in the social network were excluded from the analysis; this equated to 23 individuals at Higgins and 21 at Cammoor/Stimpsons. To allow for the possibility that some individuals were more effective 'transmitters' than others, weights were assigned to each individual of its total number of visits in each trial. This assumes that the rate of social transmission from individual A is proportional to the number of times they visited in the trial. Additionally, individuals who arrive at the new food patch together close in time may be recorded as transferring information, while actually simultaneously acquiring the knowledge as a group. This was accounted for by adding 'ties' between all individuals who first arrived at the food patch less than 10 min apart, with no possible information transfer permitted between tied individuals—this should provide a conservative but robust estimate [19].

Within one area, all trials were assumed to have similar rates of transmission and analysed together on the same network, though we allowed the asocial rate of acquisition to vary between each. Five individual-level variables were incorporated into the models: sex, age (first year per adult), species (marsh tit per great tit per blue tit), site where the individual was first caught (either of the two study plots, or two adjacent areas that are part of the Wytham woods area) and propensity to use feeders (total number of visits by each individual at network feeders). All possible models were fitted.

Individual network centrality measures were analysed in two ways. First, a binomial family-generalized linear model in R was used to compare individuals who did or did not discover any food patches (where all trials were combined), in terms of sex, age, species, propensity to use feeders per site fidelity, eigenvector centrality and betweeness centrality. Second, a linear-mixed model in R was used to determine whether the order of first arrival of all individuals to the novel patches was predicted by the same explanatory variables detailed earlier. Individual identity and trial were included as random intercepts.

(**e**) ***Model selection procedures***

For all analyses, Akaike's information criterion (AICc; corrected for sample size) was used to select the best predictive model from a set of *a priori* models constructed from initial data exploration. The ΔAICc values were used to compare competing models with all models within ΔAICc of 2 having good evidence of fit [38]. AICc weights were also calculated to assess the probability that each model is the one with best K-L information (predictive power) [38]. For the general linear model of patch finding probability, we assessed the severity of any multicollinearity between coefficients by calculating the variance inflation factors using the car library in R. As all $\sqrt{}$GVIF values were less than 2, we considered that there was no evidence for multicollinearity [39].

3. RESULTS

At Higgins Copse, 81 birds were included in the social network (a median of 40 records per bird, maximum of 294 records). At Cammoor/Stimpsons Copse, 73 birds were included in the network, with a median of 78 records per individual and a maximum of 1440 records. Eleven birds (7.1%) were observed in both study areas. Over both areas, 102 individuals were blue tits, 43 great tits and seven marsh tits (summary network statistics are detailed in the electronic supplementary material, table S1). At Higgins Copse, 68 per cent of individuals in the social network found at least food patches (median = 2 patches). In Cammoor/Stimpsons Copse, 59 per cent of individuals found one or more food patches (median = 2 patches; figure 1) (see the electronic supplementary material, figure S3 for Higgins Copse).

(**a**) ***Network-based diffusion analysis***

A full model-fitting procedure was carried out on the network and all patch-discovery trials for each area. The most parsimonious models for each area contained social transmission and had a non-constant, declining rate of acquisition. Two models had good support at Higgins Copse, an additive model with no individual-level variables (AICcWgt = 0.37), and a multiplicative model incorporating site and species (AICcWgt = 0.30). The best model for Cammoor/Stimpsons Copse was multiplicative and included age, site and species (AICcWgt = 0.89). In both areas, there was little or no support for models containing purely asocial acquisition mechanisms (table 1). Parameter estimates are reported in the electronic supplementary material. In the top multiplicative

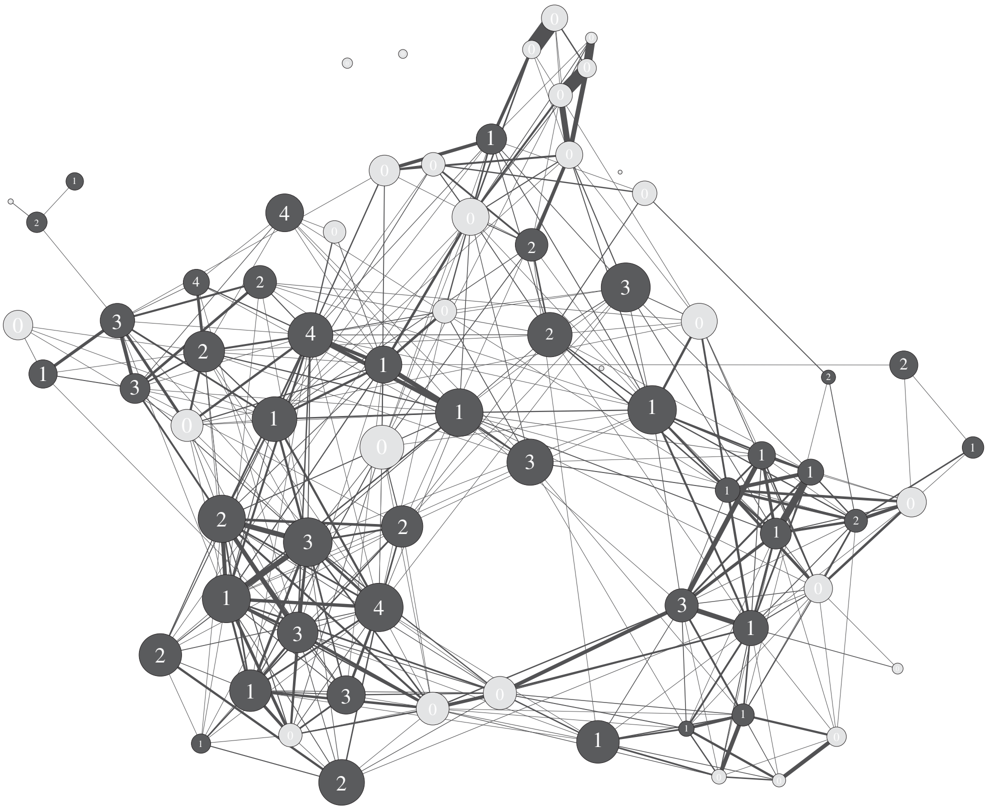

Figure 1. Social network for Cammoor/Stimpsons Copse, contrasting the network positions of individuals with differing patch-discovery success. Dark nodes represent individuals who found food patches; numbers inside nodes indicate how many patches found. Increasing node size indicates increasing eigenvector centrality, and edge (line) weight indicates association strength. Edges are thresholded to weights above 0.02.

Table 1. Summary of model selection statistics for NBDA performed in both areas. si, site of first capture; sp, species; a, age, v, feeder use; se, sex. Average association strength for Higgins = 0.027, Cammoor = 0.022. Additive models assume individual-level variables affect only asocial rate, in multiplicative models differences also influence social transmission [19]. Constant (c) baseline rate denotes rate of asocial discovery constant over time; non-constant (n-c) denotes systematic increases/decreases in rate of asocial discovery [20]. Transmission rate(s) denote rate estimate of social transmission per unit of connection relative to rate of asocial learning.

model type and rate	parameters	S.T. effect (s)	ΔAICc	AICcWt	cum. wt
Higgins Copse—models with social transmission and asocial learning					
additive, n-c, declining		0.01	0	0.37	0.37
multiplicative, n-c, declining	$P_{si} + P_{sp}$	0.01	0.33	0.30	0.67
Higgins Copse—top asocial model					
constant	$P_v + P_{si} + P_{sp}$	0	2.76	0.08	0.75
Cammoor/Stimpsons Copse—models with social transmission and asocial learning					
multiplicative, n-c, declining	$P_a + P_{si} + P_{sp}$	0.27	0	0.89	0.89
multiplicative, n-c, declining	$P_a + P_v + P_{si} + P_{sp}$	0.1	6.38	0.04	0.93
Cammoor/Stimpsons Copse—top asocial model					
n-c, declining	$P_a + P_{se} + P_{si} + P_{sp}$	0	23.39	0	1

model, great tits discovered patches at a rate of 1.01 higher than blue tits at Higgins Copse, and 1.65 times higher at Cammoor/Stimpsons Copse. Adults also discovered at a higher rate than first years at Cammoor.

(b) *Network centrality*

A generalized linear model was run using patch discovery (yes or no) as the binary response variable. At Higgins Copse, the variable with the highest predictive power was betweeness centrality (AICcWgt = 0.13; figure 2*a*). However, there was also good support for total feeder visitations, betweeness + eigenvector centrality, betweeness + sex and betweeness + age (ΔAICc = 1.00, 1.47, 1.62, 1.81). Although the magnitude of difference between the best model and competing models was small, betweeness centrality was present in four of the five top models. At the Cammoor/Stimpsons Copse study area, the

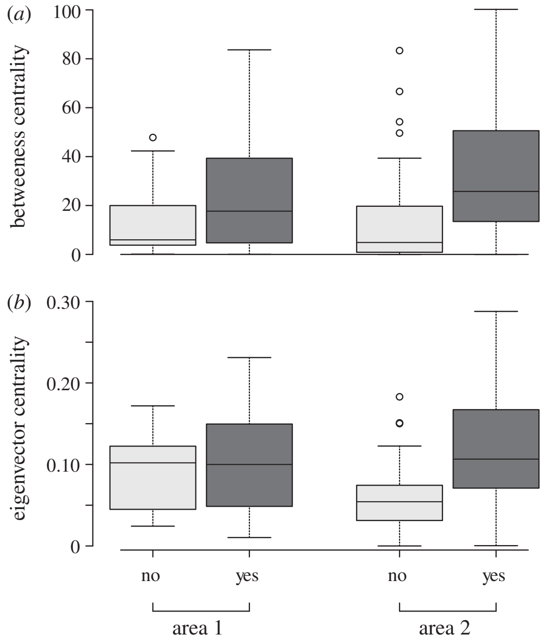

Figure 2. The relationship between two measures of network centrality and the patch-discovery success (no or yes) in area 1 (Higgins Copse); and area 2 (Cammoor/Stimpsons Copse). For a comparison of the observed and expected average network measures for each area, see the electronic supplementary material, table S1 and figure S2.

best model was eigenvector centrality (AICcWgt = 0.21; figure 2*b*). There was also good evidence for models containing eigenvector centrality + age (ΔAICc = 1.35) and eigenvector centrality + betweeness centrality (ΔAICc = 1.89), but eigenvector centrality was present in all of the top five models. The set of models with ΔAICc weights collectively totalling 95 per cent are detailed in the electronic supplementary material, table S6.

There was no relationship between network measures and the relative patch arrival time of individuals. Rather the total number of visits to the network feeder was the best predictor of arrival time (AICcWgt = 0.27 for Higgins Copse, AICcWgt = 0.28 for Cammoor/Stimpsons Copse). Models containing species + feeder visitations and age + feeder visitations also had strong support at both study areas (Higgins Copse: ΔAICc = 0.27, 1.30, Cammoor/Stimpsons Copse: ΔAICc = 0.68, 1.06). Therefore, birds that visited the initial network feeders more frequently were more likely to discover novel food patches earlier. Adults tended to arrive at patches earlier than birds in their first year, and marsh tits and great tits were earlier than blue tits.

4. DISCUSSION

Our study population of tits, as with many parid species, form loose roaming flocks of unrelated individuals in the non-breeding season, during which time they depend on clumped ephemeral food resources such as beech mast (seeds of *Fagus sylvatica*) [32]. Such resources vary in time and space, and while individuals may benefit from optimized search patterns and personal experience, we offer evidence using a novel social networks approach that tits also use social information to locate new foraging resources in the wild. This is consistent with a long history of accumulated evidence from captive studies [24,25], and related studies on food-associated communication in Parids [28,29]. However, our results are novel because they demonstrate that the flow of this information is not random between individuals, but rather that it flows in accordance with the structure of the social network of the population.

NBDA found strong evidence for social transmission. Under this model of patch discovery, the first individual to find the food patch did so by chance (mediated by individual differences in searching behaviour), and subsequently arriving individuals discovered the patch by a combination of chance and receiving social information from connected individuals. Which set of individuals eventually found and exploited the patch therefore largely depended on the identity of those that were first to discover it.

While the study of the movement of information in social networks is rapidly growing in human studies, it is still in its infancy in the field of animal behaviour. NBDA [18–20] offers the most comprehensive model to date to identify information transmission in animal populations. This model uses the theory of directed social learning, i.e. that information is transmitted at different rates depending on association patterns [22,40]. Although supported by simulations and theoretical work [18,41,42], there has been very little empirical evidence for either NBDA or directed social learning. We suggest that the successful application of NBDA may depend on two factors: (i) a large enough sample size for there to be sufficient variation in association strengths and (ii) a social network of sufficient relevance to the type of information transferred [42]. Our study had both these factors, with two networks of 73 and 81 nodes and a network built using foraging associations.

In both our study areas, marked individual variation in patch discovery was observed. On average, 60 per cent of individuals found the novel foraging patches, and of the individuals who found new patches, most only found one or two. None of the morphological or behavioural characteristics we measured, including sex, species, age or site fidelity explained this variation, either in patch-discovery probability or in the number of patches found. Rather at both areas the best model for patch discovery identified was a network characteristic—eigenvector centrality at Cammoor/Stimpsons, and betweeness centrality at Higgins. These two network centrality measures are considered related to information and disease transmission [30,31], with central individuals having a ‘high susceptibility risk’. Few empirical studies have tested these hypotheses in animals, although Godfrey *et al.* [43] found that Gidgee skinks (*Egernia stokesii*) with a higher degree had a higher parasite load. Christley *et al.* [31] simulated epidemics on networks, and similarly found that centrality measures predicted risk of infection. Our study appears to extend this pattern to the transfer of social information.

It is interesting to speculate why the two areas appeared to highlight different centrality measures as important in social information transfer. Perhaps the differing topography of the two areas is implicated; in Higgins, birds appeared to roam freely, whereas in Cammoor (a long strip of woodland), birds might be more restricted in their movements. In this case, information may be more likely to pass ‘grapevine’ style along immediate associates [30]. There was also evidence of a higher social transmission rate for Cammoor using NBDA. However, the exact mechanisms by which individuals transfer information in this study system are unknown. We suggest that basic mechanisms such as local enhancement (resulting from auditory and visual cues produced during feeding) would be sufficient to produce these patterns; yet, if deliberate food-contact calls occur, this could add an intriguing complexity to the relationship between the social network and patch discovery.

Finally, there was no relationship in this study between social network measures and the order of arrival of individuals at an artificial food patch, despite NBDA finding that the order and timing of arrival reflected associations between individuals. While these results are not necessarily contradictory (network centrality cannot predict a discovery order so highly dependent on the identity of first discoverer), centrality measures may be further obscured by additional factors. The NBDA model suggests that species and age differences in social information use may influence discovery rate. Another such factor may be personality; previous studies on parids have found a correlation between personality and patch discovery, with bold individuals arriving faster to new feeders [37,44]. Our study did not measure personality, so the effect of this variable is unknown. However, there is some evidence that personality is correlated with social information use in tits [45], and that personality may affect an individual’s social network position [46]. If so, social network position in our study may be correlated with both personality and patch discovery—this merits further study.

In conclusion, we report the successful use of NBDA to detect social information transfer in the wild, with closely associating individuals being more likely to transfer information about new food sites. Furthermore, we found that individuals with higher social network centrality measures have a higher probability of finding new food patches. Thus far, the weight of evidence in social network research has highlighted the negative impacts to being well connected (between and within communities), with such individuals suffering greater parasite loads and a higher risk of disease infection [31,43,47]. In contrast, our study suggests that the greater probability of receiving social information about new foraging patches may rather confer a benefit on better socially connected individuals.

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Aplin et al. Social networks predict patch discovery

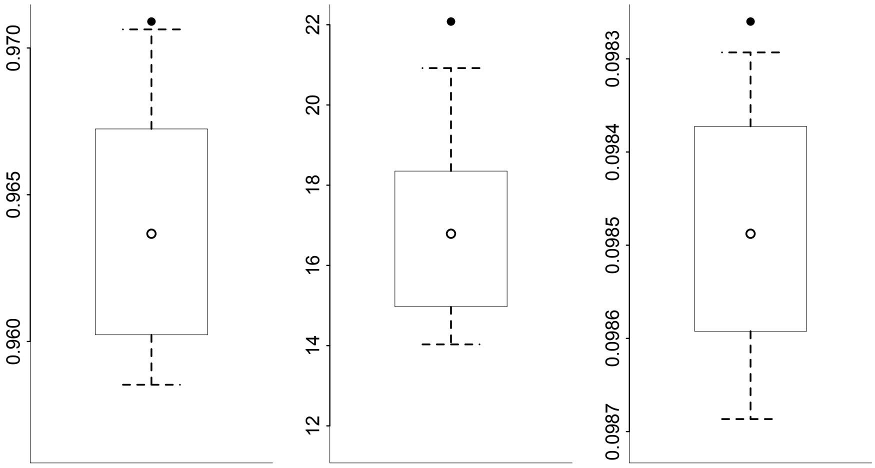
SUPPLEMENTARY MATERIAL:

S1. Average network measures for Higgins Copse (*n* = 81) and Cammoor/Stimpsons Copse (*n* = 73). K_i = degree, S_i = association strength, E_i = eigenfactor centrality, C_i = clustering coefficient, B_i = betweeness.

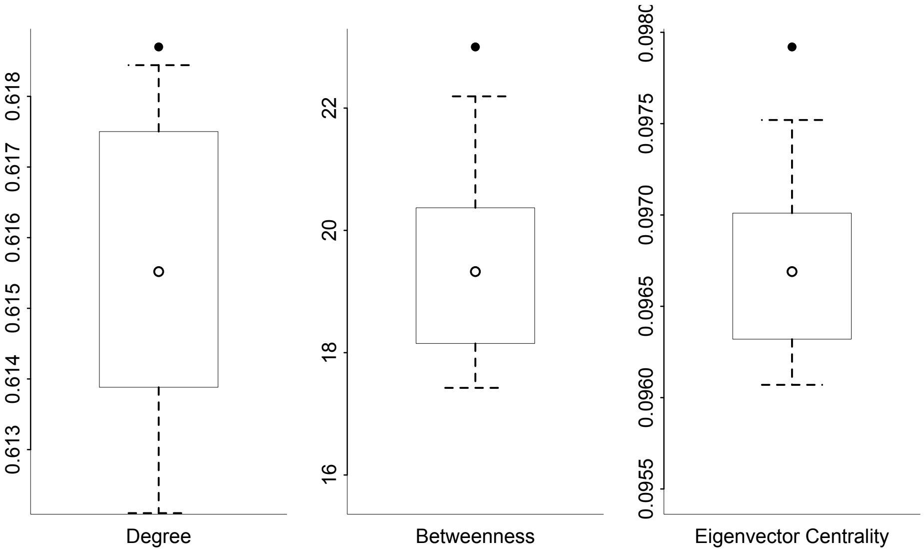
I	K_i	S_i	E_i	C_i	B_i
Higgins Copse	36	0.97	0.099	0.748	22.09
Cammoor/Stimpsons Copse	28	0.62	0.098	0.756	23

S2. Comparing the observed average of three centrality measures (weighted degree, betweeness centrality and eigenvector centrality) with the average network measures expected by chance for (a) Higgins Copse and (b) Cammoor/Stimpsons Copse. The raw data streams were randomized 1000 times by randomly redistributing individual identities. The filled circle shows the observed average centrality value, the clear circle and box show the average and 25% - 75% quartiles of the randomized data. The dotted lines show the 95% confidence interval of the randomized data.

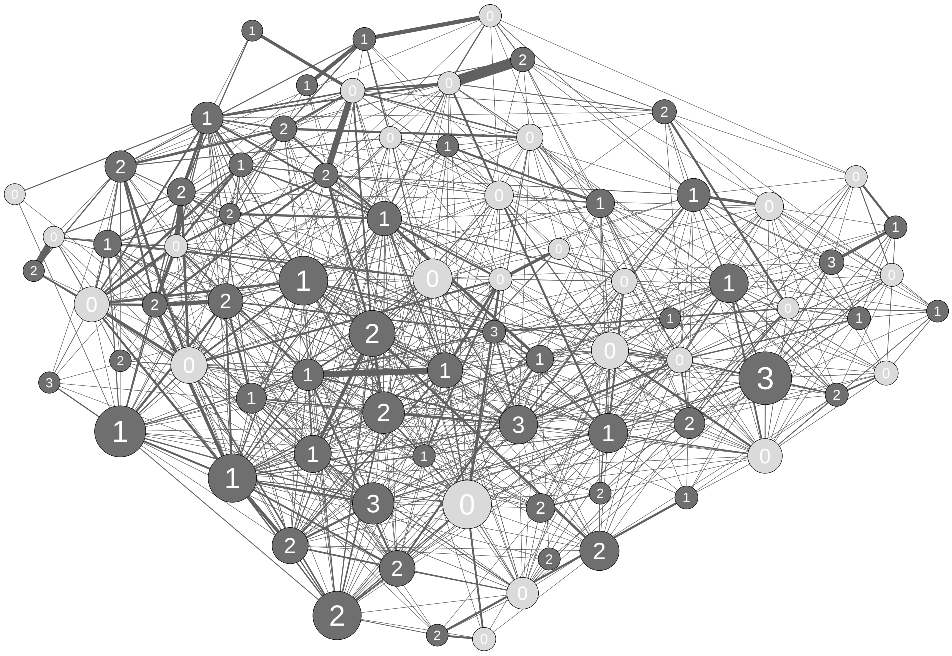
(a)



b)



S3. Social network for Higgins Copse, contrasting the network positions of individuals with differing patch discovery success. Dark nodes represent individuals who found food patches; numbers inside nodes indicate how many patches it found. Increasing node size indicates increasing betweeness centrality, and edge (line) thickness indicates association strength. Edges have been thresholded to only show those above 0.02 in strength.



S4. Parameter estimates for the top four NBDA models, cumulatively totaling 0.83 in AICc weight for (a) Higgins Copse and 0.98 in cumulative AICc weight for (b) Cammoor/Stimpsons Copse. Unweighted model-averaged parameter estimates for both areas are listed in table (c).

(a)

	Model 1 social + asocial add., n-c	**Model 2** social + asocial multi., n-c	**Model 3** asocial	**Model 4** asocial
AICcWt	0.37	0.30	0.08	0.08
Parameters:				
Site	-	-1.411	-0.392	-0.306
Species	-	0.012	0.292	-
Sex	-	-	-	-
Age	-	-	-	-
Feeder use	-	-	0.005	0.005

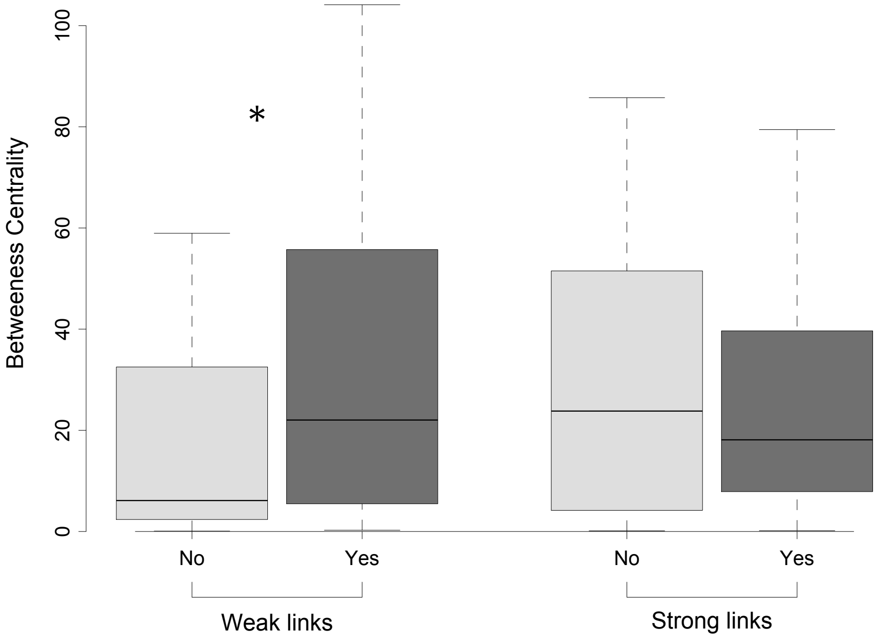
(b)

	Model 1 social + asocial multi., n-c	**Model 2** social + asocial multi., n-c	**Model 3** social + asocial multi., n-c	**Model 4** social + asocial multi., n-c
AICcWt	0.89	0.04	0.03	0.02
Parameters:				
Site	-0.725	-0.810	-0.610	-0.812
Species	0.504	0.294	-	0.299
Sex	-	-	-	0.094
Age	0.821	0.637	0.831	0.629
Feeder use	-	0.001	-	0.001

(c)

	Site	Species	Sex	Age	Feeder Use
Higgins Copse	-0.578	0.028	0	0	0.0008
Cammoor/Stimpsons Copse	-0.713	0.466	0.0019	0.794	0.0001

S5. Comparing the betweeness of individuals in Higgins Copse who discovered food patches ("yes") and those that did not ("no") with two levels of thresholding – "weak links": where edge-weights above 0.3 in strength were removed from the analysis, and "strong links": where edge-weights below 0.03 were removed from the analysis. Weak links seem to be more important for patch discovery than strong links, with discoverer's having a higher betweeness once strong links are removed (*p=0.04), but with no difference in betweeness if weak links are removed (p=0.37).



S6. Summary of model selection statistics for a general linear model of patch discovery at (a) Higgins Copse (n=81, three trials) and (b) Cammoor/Stimpsons Copse (n=73, four trials); (sp) = species, (a) = age, (v) = feeder use, (se) = sex; (ec) = eigenvector centrality, (b) = betweeness

(a)

n	model	**Δ** AICc	AICcWt	cum.wt
1	P_b	0	0.13	0.13
2	P_v	1.01	0.08	0.21
3	$P_b + P_{ec}$	1.47	0.06	0.27
4	$P_b + P_{se}$	1.62	0.06	0.33
5	$P_a + P_b$	1.81	0.05	0.39
6	$P_b + P_v$	2.05	0.05	0.43
7	$P_v + P_{se}$	2.40	0.04	0.47
8	$P_a + P_v$	2.70	0.04	0.51
9	P_{ec}	2.94	0.03	0.54
10	$P_a + P_{ec} + P_b$	3.09	0.03	0.56
11	$P_{ec} + P_b + P_v$	3.13	0.03	0.59
12	$P_{ec} + P_b + P_{se}$	3.35	0.03	0.62
13	$P_a + P_b + P_{se}$	3.38	0.02	0.64
14	$P_{sp} + P_b$	3.48	0.02	0.66
15	$P_b + P_v + P_{se}$	3.53	0.02	0.71
16	P_{se}	3.66	0.02	0.73
17	$P_a + P_b + P_v$	3.69	0.02	0.75

(b)

n	model	**Δ** AICc	AICcWt	cum.wt
1	P_{ec}	0	0.21	0.21
2	$P_a + P_{ec}$	1.35	0.11	0.32
3	$P_{ec} + P_b$	1.89	0.08	0.40
4	$P_{ec} + P_v$	2.06	0.07	0.47
5	$P_{ec} + P_{se}$	2.17	0.07	0.54
6	P_v	3.05	0.05	0.59
7	$P_a + P_{ec} + P_b$	3.26	0.04	0.63
8	$P_a + P_{ec} + P_v$	3.43	0.04	0.67
9	$P_a + P_{ec} + P_{sex}$	3.51	0.04	0.70
10	$P_{ec} + P_b + P_v$	4.11	0.03	0.73
11	$P_{ec} + P_b + P_{se}$	4.15	0.03	0.75
12	$P_{ec} + P_v + P_{se}$	4.30	0.02	0.78
13	$P_a + P_v$	4.40	0.02	0.80
14	$P_{ec} + P_{sp}$	4.42	0.02	0.82
15	$P_b + P_v$	4.72	0.02	0.84
16	$P_{se} + P_v$	5.17	0.02	0.86
17	$P_a + P_b + P_v + P_{ec}$	5.53	0.01	0.87

S7. Summary of the total Akaike weights in both areas across the NBDA Model: additive vs multiplicative (whether individual level variables affect only asocial learning or whether they affect social transmission also); and a baseline rate of transmission which is either constant or non-constant (an unchanging rate of acquisition or a declining/increasing rate of asocial acquisition). (a) Higgins Copse; (b) Cammoor/Stimpsons Copse.

a)

	Social + Asocial: Multiplicative	 Additive	*Asocial:*
Baseline rate:			
Constant	0	0	0
Non-constant	0.99	0.1	0

b)

	Social + Asocial: Multiplicative	 Additive	*Asocial:*
Baseline rate:			
Constant	0	0.03	0.24
Non-constant	0.33	0.37	0.03

APPENDIX C

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

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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 (*Peocilia 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 (Psion 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: $z_{868} = -3.2$, $P = 0.001$); 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 otherwise disparate flocks and forage with more 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-

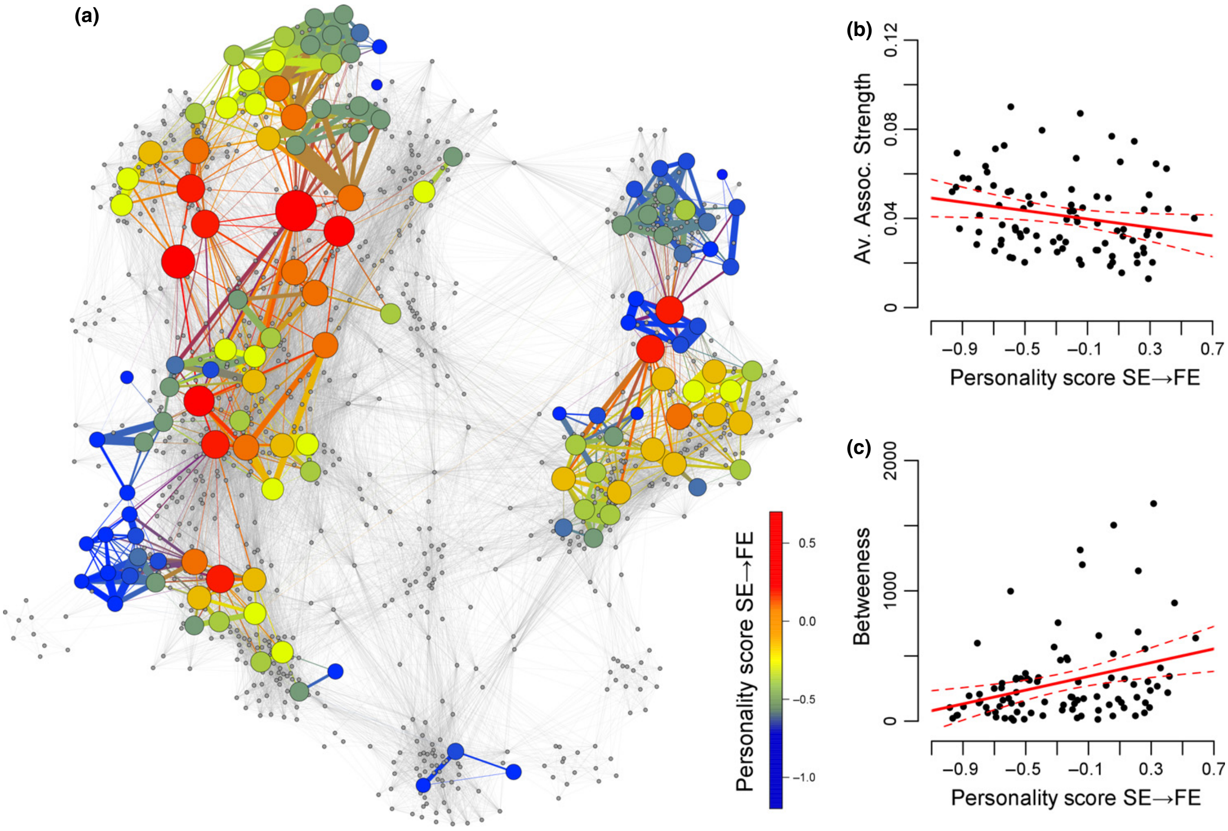

Figure 1 The relationship between personality and social network position in wild great tits. (a) Social network where colour represents personality score ranging from most reactive (SE) phenotypes in blue to most proactive (FE) phenotypes in red; the range of the colour distribution has been slightly 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.

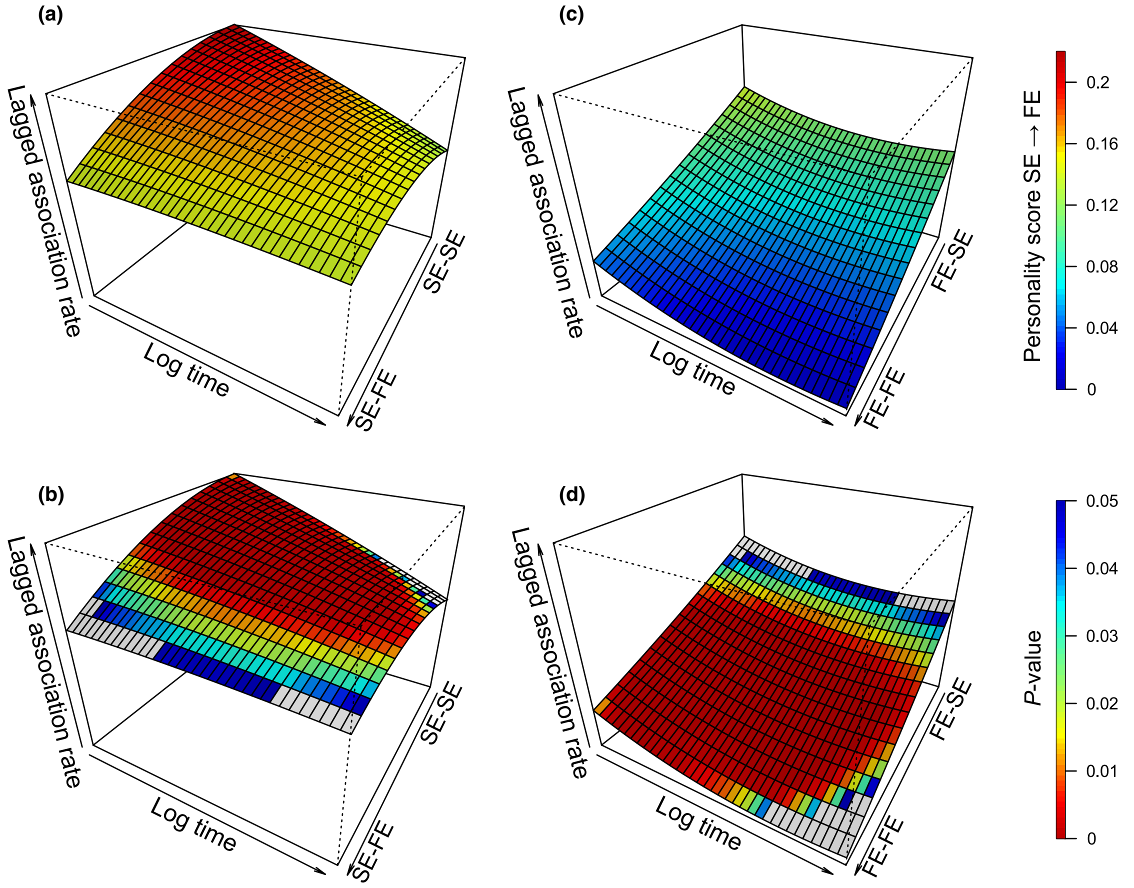

Figure 2 Lagged association rates between individuals of differing personality. (a) Directed re-association rates between individuals with bottom third of personality scores (SE) and all other individuals from most SE at back of plot to FE at front. Lagged association rates vary from blue (no probability 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-

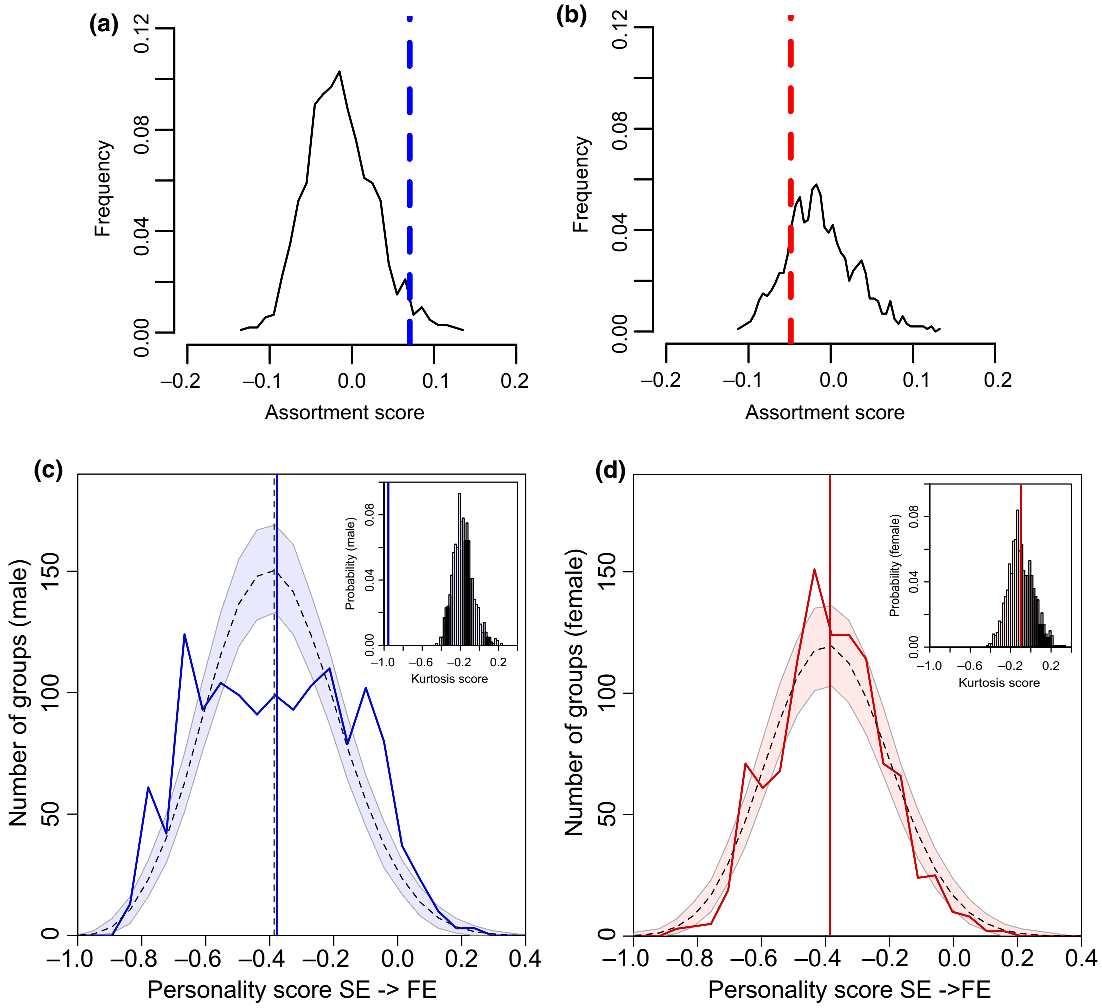

Figure 3 Within group mixing patterns in relation to personality and sex. (a) Assortment in males is significantly higher than expected from data node-randomised 1000 times. Assortment scores of node-randomised data are shown by the distribution, assortment score of observed data is given by vertical 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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SUPPORTING INFORMATION

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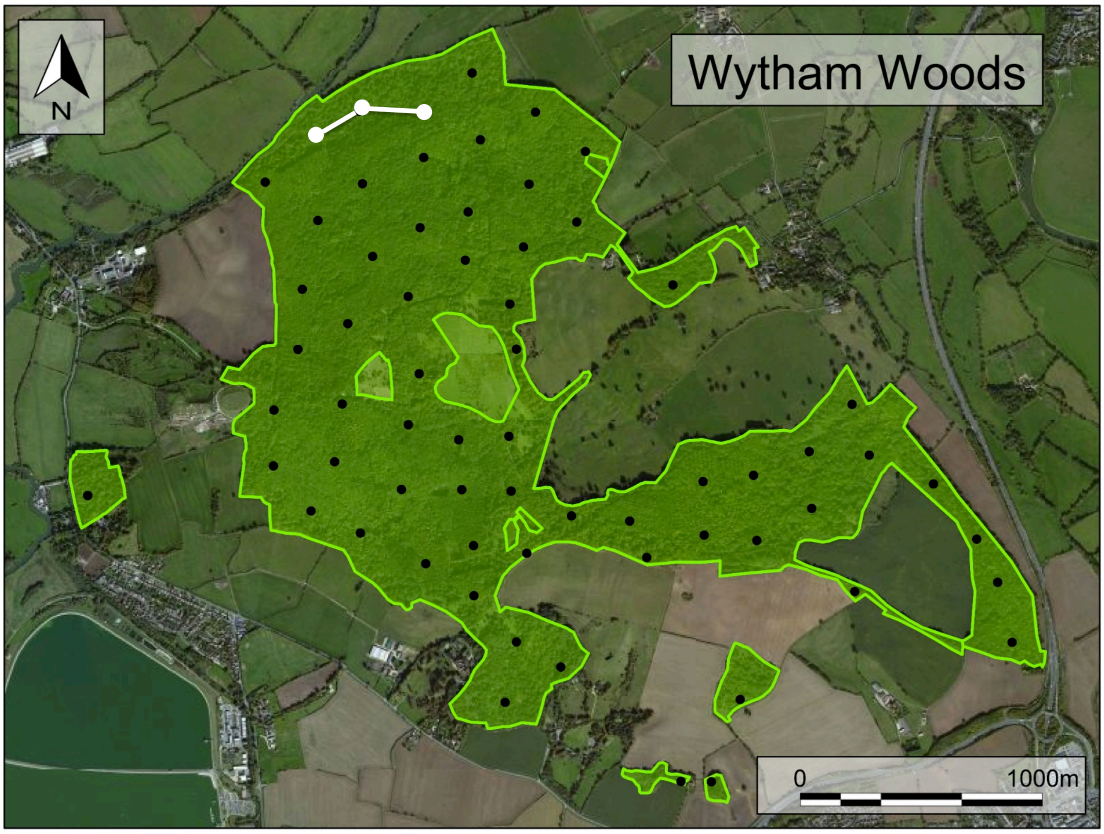
Supplementary Information

Figure S1) Map of Wytham Woods study site, Oxfordshire, United Kingdom (51°46'N, 01°20'W). Black points show the position of feeding stations fitted with PIT-tag detecting antennae. 61 such stations are installed approximately 250m apart. There are also four feeding stations in external habitat patches. While Wytham Woods is not a closed population, the woodlands are a greatly preferred habitat compared to surrounding farmland. An average winter home range encompasses three feeding stations, with an example given by the white nodes.



S2) Overall proportion and distribution of PIT-tagged individuals

The great tit population in Wytham Woods is comprised of two components: i) birds born in a nest box and fitted with PIT tags as nestlings; and ii) immigrant birds caught and fitted with a PIT tag as an adult. There are c. 1200 nest boxes in Wytham Woods that are monitored each spring in which almost every chick and adult caught breeding have been fitted with a PIT tag since 2007. In addition, intensive periods of mist-netting have been conducted throughout the winter in order to catch and PIT tag immigrant birds. In the winter of 2010/11, mist-netting was conducted 5 days per week for three months in an attempt to capture all individuals present and ensure near 100% coverage. In the following winter, mist-netting was conducted one week per month to maintain this coverage. In order to quantify the proportion of individuals fitted with PIT tags in the population, we calculated the proportion of unmarked birds in the breeding season after the 2011-12 winter, when the current research was conducted. This gives the best estimate since each individual is surveyed only once, but is likely to slightly over-estimate the proportion of untagged birds due to an final movement of immigrants into the woods just before breeding. In the spring of 2011, 8% of birds were untagged. We therefore estimate that more than 90% of the great tit population in Wytham Woods were tagged over the 2011-12 winter period.

Figure S2) Great tit, showing BTO metal ring on right leg. The left leg is fitted with a plastic molded ring containing a uniquely identifiable passive integrated transponder (PIT) tag. (Photo credit D.R. Farine)

Table S3) Summary results for network centrality analysis. Linear regressions were run comparing network degree, betweenness and average association strength as response variables against personality, age, the number of periods observed and the number of spatial movements. Sex, weight, body size and number of visits showed no significant correlation and were excluded after exploratory analysis.

Table S3A) Multiple regression on factors affecting network degree.

	F statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	6.33	1	0.01	21.19	8.42
No. of periods observed	3.70	1	0.06	1.49	1.72
Age(in years: 2-7)	0.12	1	0.73	-1.47	3.25
No. of spatial movements	48.19	1	<0.01	1.74	0.26

Table S3B) Multiple regression on factors affecting network betweenness.

	F statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	4.66	1	0.03	440.85	204.18
No. of periods observed	0.18	1	0.67	2.01	41.77
Age(in years: 2-7)	0.07	1	0.80	-66.73	78.88
No. of spatial movements	6.83	1	0.01	15.30	6.27

Table S3C) Multiple regression on factors affecting network betweenness. Model is as above, however three outliers that exerted undue influence on the model fit have been removed.

	F statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	5.01	1	0.03	176.61	78.89
No. of periods observed	0.89	1	0.35	1.11	15.53
Age(in years: 2-7)	2.22	1	0.14	19.09	29.76
No. of spatial movements	32.77	1	<0.01	12.95	2.36

Table S3D) Multiple regression on factors affecting average association strength.

	F statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	4.03	1	0.05	-0.008	0.004
No. of periods observed	0.35	1	0.56	0.001	0.001
Age(in years: 2-7)	0.19	1	0.66	<0.001	0.001
No. of spatial movements	41.17	1	<0.01	-0.001	<0.001

Figure S4) Whole winter social network showing the eleven identified communities. Communities were found in the population using eigenvector community detection, as calculated on the weighted network (see methods). All individuals are assigned to one community only, and eight communities contained individuals upon whom personality assays had been conducted. Colors represent different communities. The links between nodes are shown weighted proportional to time spent associating, with those below a 0.05 threshold removed for visual clarity.

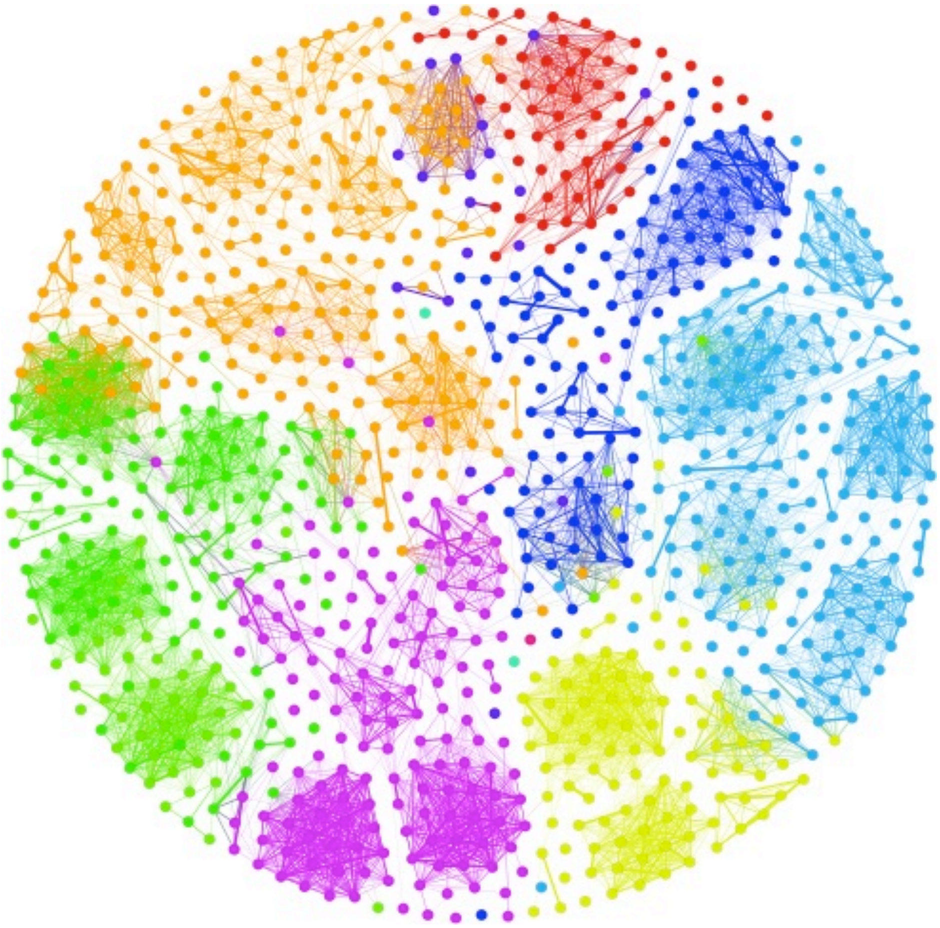


Table S4) All individuals were assigned to one community (community 1-8), with communities identified using weighted eigenvector community detection (see Fig. S4). A separate social network was constructed for each community, and network centrality metrics then calculated for all matrices independently. Linear mixed regressions were run using the *lmer* function in *R* comparing network degree, betweenness and average association strength as response variables against personality, age, the number of periods observed and the number of spatial movements. The community identity for each individual (A-H) was fixed as a random term. Sex, weight, body size and number of visits showed no significant correlation and were excluded after exploratory analysis.

Table S4A) LMM on factors affecting community-level network betweenness.

	t statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	2.13	1	0.04	11.17	5.25
No. of periods observed	2.01	1	0.05	2.17	1.08
No. of spatial movements	4.33	1	<0.01	0.74	0.17
Age(in years: 2-7)	0.65	1	0.52	1.37	2.09

Community ID was fitted as a random term (estimated variance component ± SD: 157.31±12.54)

Table S4B) LMM on factors affecting community-level network betweenness.

	t statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	2.26	1	0.03	25.20	11.17
No. of periods observed	0.60	1	0.55	1.36	2.27
No. of spatial movements	2.80	1	<0.01	1.34	0.35
Age(in years: 2-7)	0.20	1	0.84	0.87	4.35

Community ID was fitted as a random term (estimated variance component ± SD: 130.75±11.43)

Table S4C) LMM on factors affecting community-level average association strength.

	t statistic	*df*	*P*	Coeff. Est.	S.E.
Personality score	-1.97	1	0.05	-0.010	0.005
No. of periods observed	2.62	1	0.01	0.003	0.001
No. of spatial movements	-4.45	1	<0.01	-0.001	<0.001
Age(in years: 2-7)	-0.39	1	0.70	-0.001	0.002

Community ID was fitted as a random term (estimated variance component ± SD: 0.0001±0.01)

Table S5) Probability of associating one day (24 h) after initial association for all focal individuals. To convert continuous into categorical data, the population was divided into three terciles (Slow, Average, Fast), and the mean of each tercile taken. Table is ordered with the direction of relationships running across, such that the first row is Slow -> Slow, Slow -> Average, Slow -> Fast. Snapshot of re-associations shows the effect of temporal dynamics is synergistic. Most associations between individuals of different personality score have a similar probability of re-occurring, with the variation largely explained by preferential re-associations in Slow -> Slow interactions, and a strong re-association avoidance in Fast -> Fast interactions.

	Slow Explorer	Average Explorer	Fast Explorer
Slow Explorer	0.25	0.13	0.14
Average Explorer	0.15	0.14	0.13
Fast Explorer	0.12	0.11	0.01