Carry-over and consequences of social connections amongst wild birds

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ABSTRACT

CARRY-OVER AND CONSEQUENCES OF SOCIAL CONNECTIONS AMONGST WILD BIRDS

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Ecological factors are known to influence the spatial distribution of individuals, which in turn governs social structure. However, social interactions can have important individual- and population-level consequences and may shape various ecological processes (Chapter 1). In this thesis, I examine the factors shaping social networks amongst wild birds (*Paridae*). I demonstrate that these social connections are biologically important, and influence numerous processes, including spatial structure itself.

First, I demonstrate that both the spatial occurrence and dynamic social decisions of individuals underpin the non-random composition of foraging flocks (Chapter 2). Reciprocally, I show that the spatial arrangement of individuals' breeding locations is predicted by the previous winter's social network, as birds breed nearer to, and share territory boundaries with, those they held the strongest connections to (Chapter 3).

I then use experiments to directly assess the consequences of social structure. I show that birds exhibit compensatory shifts in their social network position upon removal of their flock mates (Chapter 4). Following this, I introduce a novel experimental system that automatically controls which individuals could feed together. These externally-imposed foraging constraints cause social segregation at non-experimental food patches (Chapter 5), which also carries over into breeding site prospecting (Chapter 5). I show that social information transmission, regarding the location of novel food patches, also changes to correspond to the experimentally imposed social network structure (Chapter 6). Furthermore, social foraging associations are found to influence social learning, as birds appear to prioritise learning from those who provide relevant information on a regular basis. Finally, I demonstrate that birds choose to forgo maximising their own food intake to sustain their relationships (Chapter 7). Through prioritising their pair-bond over their own preferences, this also changes the social composition of foraging flocks, indicating how a single relationship can govern wider social network position. Additionally, I show how social relationships can influence individual behavioural plasticity and the learning of foraging strategies.

This thesis thus contributes to elucidating the relationship between spatial structure and social networks within wild populations. It also demonstrates how social systems respond to external changes, and the direct causal implications of this for shaping spatial structure, information flow and individuals' social and foraging strategies. Together, these findings form a foundation for expanding our understanding of the ecological and evolutionary implications of social networks and the mechanisms underpinning this (Chapter 8).

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AUTHOR CONTRIBUTIONS

Main contributors

Josh A. Firth had independent intellectual input into all aspects of the thesis, designed the 'selective feeders' and collected the data, carried out the 'removal' experiments, and contributed to all fieldwork of monitoring the Wytham Woods bird (*Paridae*) community (breeding season fieldwork and winter RFID-tracking). Also conceived, analysed data, wrote drafts, and incorporated comments from co-authors for each chapter.

Ben C. Sheldon (supervisor and co-author of all data chapters) secured funding and provided intellectual input throughout. Also gave guidance on research techniques, experimental design, and analytical methods. Gave detailed comments on all chapter drafts.

Additional contributors

Ross A. Crates (co-author chapter 4) provided support with the fieldwork in chapter 4 and offered feedback on the manuscript draft, also contributed to testing the 'selective feeders' used in chapters 5-7.

Damien R. Farine (joint lead author chapter 2, co-author chapter 6 & 7) carried out the analysis of flock size and stability for chapter 2 (Figure 1 & 2) and helped draft the manuscript, carried out the NBDA analysis for chapter 6 and gave guidance on writing, provided valuable comments on chapter 7.

Social Network Group (co-author chapter 2) performed the fieldwork, contributed to early design and discussion, and provided comments on the draft of the manuscript.

Bernhard Voelkl (co-author chapter 4 & 7) helped with bird ringing and provided advice and feedback on chapter 4, offered advise on the statistical approach and writing of chapter 7.

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Chapter 1

Introduction

Introduction

"*In Nature, Nothing Exists Alone*" – Rachel Carson (1962).

Ecology and sociality

A particularly striking feature across animal taxa is the ubiquity of social behaviour, yet the organization and structure of animal societies show huge variation. More than half a century ago, it began to be widely recognized that such structures were far from simple, indiscriminate arrangements of independent animals. Rather, these social structures appeared to correspond to the environment within which they were found (Crook 1964; Crook & Gartlan 1966; Crook 1970). A myriad of seminal research examining the variation in social structure across species followed, culminating in the formation of a fundamental theory of behavioural ecology: the distribution of resources acts as a forceful selection pressure that governs the spatial distribution of individuals, and this in turn determines social structure (Crook 1970; Barash 1973; Clutton-Brock 1974; Jarman 1974).

It emerged the same principles could be applied to social organization within species (Kruuk 1972). Particularly for mammalian systems, efforts turned towards understanding how environmental features may cause non-kin to form social groups, even in the absence of cooperation (Kruuk 1978a, b; Macdonald 1983). These pioneering descriptive studies highlighted the influence of fine-scale ecological factors, such as food availability, on social structure. They were later validated by experimental work that manipulated resources at the population level and confirmed that social structure responded flexibly to different environmental conditions. For example, increasing the variability of resource dispersion has been shown to increase social interactions in mammalian (Sanchez-Prieto *et al.* 2004; Verdolin 2009) and avian systems (Davies & Hartley 1996).

Along with environmental features, endeavors in deciphering the influence of genetic and developmental factors on sociality also advanced (McBride 1964; Lack 1968). Yet, from the notable intricacies of primate sociality, an innovative approach arose. This considered the structure of societies as a product of social behaviour itself, in terms of

whether interactions were of a cohesive or divisive nature (Carpenter 1942b, a; Sade 1972). Indeed, social interactions themselves may be a prized 'resource', and thereby potentially influential to social structure across a wide range of systems. An obvious, and widespread, example of a valuable interaction is mating, and the distribution of mating opportunities can shape social structure in the same way that environmental resources may (Emlen & Oring 1977; Gehrt & Fritzell 1998; Johnson *et al.* 2002). Concurrently, empirical studies have shown that the opportunity to interact with females can govern the spatial distributions and territory arrangements of males of various species (Gompper 1996; Vangen *et al.* 2001; Kaneko *et al.* 2014). Hence, interplay exists between social structure itself and the social interactions thought to be underlying it.

By the 1970's, the biological importance and implications of social organization had become a topic of substantial interest. Social structure quickly became appreciated as an influential factor for a wide range of ecological and evolutionary processes, such as predation, competition, cooperation and gene flow (Wilson 1975; Hinde 1976; West-Eberhard 1979). The idea that the natural and sexual selection pressures an individual experiences depended on their social environment was soon formalized, and consideration turned towards how the expression of individual behaviour may depend on the fitness implications given its social setting (Alexander 1974; Maynard Smith 1982). Empirical work has demonstrated how fine-scale social structure can have important consequences for individual behaviour. For instance, early studies of foraging behaviour aimed to predict individuals' decision making by assuming they attempt to maximize consumption (Charnov 1976; Pyke 1984; Stephens & Krebs 1986), yet later research revealed how individuals would forgo maximising their own food consumption in efforts to maintain social cohesion (Livoreil & Giraldeau 1997; Giraldeau & Beauchamp 1999; King *et al.* 2008; Kazahari 2014; Firth *et al.* 2015). In such cases, by potentially losing out on maximising their own food intake, animals are able to gain the advantages of social living, such as predator defence/vigilance, discovery of new resources, cooperation and other benefits of grouping (Giraldeau & Caraco 2000; Vasquez & Kacelnik 2000; Bates & Chappell 2002; Krause & Ruxton 2002). Certainly, various advances in our understanding of social behaviour were made through considering how individual behaviour may be affected by the frequency of different behavioural strategies within the population (Maynard Smith 1982). However,

it is becoming increasingly apparent that, by considering the fine-scale connectivity between individuals, we can deepen our understanding of the consequences of the social environment for individual behaviour and the ecological processes that result (Skyrms & Pemantle 2000; Krause *et al.* 2007).

A network approach to social systems

Along with emphasizing the ecological implications of social structure and organization, Wilson (1975) also noted that a social network approach could be an effective tool for studying sociality across various animal systems. The basic principles of social network theory were developed in sociology by applying mathematical graph theory to describe human group structure (Moreno 1934). This allowed interactions (or 'edges') between individuals (or 'nodes') to be placed in the wider context of the entire network. In this way, social network theory provided a single theoretical scaffold for examining individual, dyadic, group and population level patterns (Croft *et al.* 2008). This powerful framework can represent any behaviour, from simple co-occurrences to cooperative, aggressive, or sexual interactions. Edges can be considered as directional (for non-reciprocal behaviours) or symmetrical, and can be 'weighted' to contain information on the rate of interaction between dyads or their propensity to associate with one another. In this way, the connections within the network can convey the existence, strength, frequency and direction of the social interactions or associations in a diverse array of social systems. Furthermore, individual attributes can be assigned to nodes, allowing relationships to be drawn between particular characteristics of individuals and structural components of the network. Hence, given the transferability of this approach originally developed to describe human sociability, social network principles even whilst still in their infancy were quickly adopted and used to describe non-human primate sociality (Sade 1972; Hinde 1976) as well as other mammalian (Clutton-Brock 1982; Le Pendu *et al.* 1995) and avian systems (Ekman 1979, 1989).

Considering social associations or interactions between individuals can be analytically complex and computationally intensive. This initially meant that the applications of social network theory to ecological systems were primarily in visualizing or simply describing social structure (Pearl & Schulman 1983; Krause *et al.* 2007; Croft *et al.* 2008; Brent *et al.* 2011a). Recent advancements in computational and analytical methods now allow the application of network theory for the quantification of social

structure, and fine-scale dissections of its various components, on a large scale (Krause *et al.* 2007; Whitehead 2008). Social networks also inherently require large amounts of data on individuals' associations with one another, which are often difficult to obtain using traditional observational methods. Yet, modern technologies now enable the automated and simultaneous tracking of large numbers of wild animals within populations, allowing social interactions to be inferred on a large scale (Krause *et al.* 2013).

Modern social network analysis has now become a versatile approach for assessing both population social structure and individual patterns of social behaviour (Croft *et al.* 2008; Whitehead 2008). By drawing from the modern analytical techniques, the factors underpinning the emergent social structure can be assessed. These techniques now allow us to elucidate how ecological and social dynamics determine the arrangement of social interactions, and how this subsequently gives rise to structural properties of the network (Hasenjager & Dugatkin 2015). Various potential properties and drivers of social structure, such as spatial structure, individual characteristics and movement patterns, can be scrutinized by comparing the observed network with 'null models'. These null models consist of empirically-parameterized permutations of the observed network to randomise the pattern of interest whilst controlling for structural properties of association as well as factors such as spatial and temporal autocorrelations (Whitehead 2008). Furthermore, examining multiple datasets generated by different permutation methods simultaneously enables inference of which processes may be responsible for the observed patterns, and allow, for example, the disentangling of spatial and social causes of group structure (Farine et al. 2015). Simulations can also be employed to manipulate observed data to determine how the social network (and coupled processes) may change under different circumstances, for example how the loss or addition of individuals may affect the connectivity and fragmentation of the social network (Lusseau 2003; Williams & Lusseau 2006; Manno 2008).

Using a diverse array of analytical techniques, non-random patterns of preferential social connections amongst particular individuals have been discovered within a wide variety of species, ranging from insects to mammals (Hasenjager & Dugatkin 2015). The organisation of social associations have been found to be interlinked with genetics, such as African elephants (*Loxodonta Africana*) maintaining close associations with

relatives (Archie *et al.* 2006), and individual characteristics, such as northern long-eared bats (*Myotis septentrionalis*) preferentially roosting with young individuals (Patriquin *et al.* 2010) (Patriquin *et al.* 2010; Farine *et al.* 2015b), teleost fishes generally shoaling with others of similar size (Hoare *et al.* 2000), and social assortment by behavioural type in Trinidadian guppies (*Poecilia reticulata*) and great tits (*Parus major*) (Croft *et al.* 2009; Aplin *et al.* 2013). Additionally, both social structure and individual social behaviour have been found to show high consistency over time (Brent *et al.* 2013; Shizuka *et al.* 2014; Aplin *et al.* 2015b) and across social contexts (Drewe *et al.* 2009; Firth & Sheldon 2015). This indicates that social structure may have resilient properties, and changes to one time period or context many carry over into other aspects of sociality.

Social networks and biological processes

An important benefit of modern network analysis is that it provides a framework to examine the relationship between social structure and other ecological and evolutionary processes. The social network approach has already proven useful in understanding emergent social processes, such as social hierarchies, collective behaviour and movement (Couzin *et al.* 2002; Nagy *et al.* 2010; Shizuka & McDonald 2012; Strandburg-Peshkin *et al.* 2015). Yet interestingly, individuals' social associations have also been found to be significant predictors of their fitness. For instance, long-tailed manakins (*Chiroxiphia linearis*) that engage in social interactions with lots of conspecifics at a young age experience higher reproductive success as adults (McDonald 2007), while female baboons (*Papio cynocephalus*) with tight social relationships benefit from increased survival, both in terms of their own longevity and their offspring's survival (Silk *et al.* 2003; Silk *et al.* 2009, 2010). Similarly, individuals' social positions within the network have been linked to reproductive success for Assamese and rhesus macaques (*Macaca mulatta, Macaca assamensis*) (Schulke *et al.* 2010; Brent *et al.* 2013), beetles (*Bolitotherus cornutus*) (Formica *et al.* 2012) and degus (*Octodon degus*) (Wey *et al.* 2013). Further, network positions also have been found to be related to survival probability following catastrophic events in feral horses (*Equus caballus*) (Nunez *et al.* 2015) and barbary macaques (*Macaca sylvanus*) (Lehmann *et al.* 2016). Generally, such studies attempting to link network positions to longevity and reproductive success have found that individuals with high amounts of social associations experience increased fitness.

Whilst these observational studies demonstrate a relationship between individuals' positions within the social network and fitness, thus potentially linking social structure and evolutionary processes, the underlying causes of these relationships remain less clear. In primates, social integration may lead to reduced stress, increased 'well-being', and improved thermoregulatory abilities, along with benefits such as greater access to resources and increased cooperation (Crockford *et al.* 2008; Berghanel *et al.* 2011; Brent *et al.* 2011b; McFarland *et al.* 2015). On a broader level, how population level processes operate in relation to the social network may also have important consequences for the individuals within it. For instance, social network structure has been shown to relate to processes that are dependent on contact patterns between individuals, such as competition and sexual selection (Oh & Badyaev 2010; Farine & Sheldon 2015). Further, as the transmission of infectious disease appears to be related to social network structure, such as in giraffe (*Giraffe camelopardalis*) societies where the transmission of Escherichia coli has been shown to correlate strongly with the social network (VanderWaal *et al.* 2014). Therefore, it may be expected that individuals with high social centrality may suffer costs of increased risk of transmission. For example, Gidgee skinks (*Egernia stokesii*) that occupied the most connected positions within the social network were more likely to be infected by ticks and blood parasites (Godfrey *et al.* 2009).

An 'informative' example

A process particularly relevant to social networks is information flow. The process of information transmission and learning within social networks has been relatively extensively examined (reviewed in Hasenjager & Dugatkin 2015), and therefore provides a suitable example of the development, current utility, and remaining challenges in determining the causal relationship between sociality and population-level processes dependent on social interactions. It is also a deserving topic of interest. Indeed, how animals acquire and use information is a key component to understanding animal behaviour, and is also important to furthering knowledge of a broadly interesting topic (information acquisition) from a biological perspective (Dall *et al.* 2005; Hoppitt *et al.* 2010; Hoppitt & Laland 2011). Whilst individuals can gain information from their environment asocially, information is also provided by the behaviour of others (Dall *et al.* 2005). Social information ranges from direct signals, such as calls or displays as

animals communicate (Sherman 1977; Evans & Evans 2007), to inadvertent social cues, such as when an individual's foraging activity divulges information regarding feeding locations to others (Valone 1989; Templeton & Giraldeau 1995b, a), or their reproductive success indicates the quality of the breeding area (Doligez *et al.* 2002; Danchin *et al.* 2004). Through observing others, animals can reduce energy expenditure and risks associated with gaining knowledge asocially, which might explain why social information use has been widely observed throughout the animal kingdom (Rieucau & Giraldeau 2011; Gruter & Leadbeater 2014).

The socially-informed changes in an individual's behaviour can be observed and copied by others, and the social information can thus diffuse through the population (Whiten & Mesoudi 2008). Early examples include Japanese macaques, where washing sweet potatoes seemed to spread through the population (Kawai 1965), along with the apparent social transmission of opening milk bottle tops by British tits (Paridae) (Fisher & Hinde 1949; Hinde & Fisher 1951).

Initially, social transmission was inferred when the cumulative number of informed individuals plotted against time formed an s-shaped curve, as it was assumed that the rate of social information acquisition would increase as the number of informed individuals (i.e. potential demonstrators) increased (Lefebvre 1995). However, this approach has subsequently been shown to suffer from various drawbacks (Reader 2004; Franz & Nunn 2009). For instance, a step-shaped function may be expected if information spreads more quickly through individuals within social groups embedded within the population (Reader 2004). Indeed, social network analyses (Krause *et al.* 2007) have shown that the fine-scale patterns of social interactions are non-random and consistent (Hasenjager & Dugatkin 2015) and that often individuals do form sets of closely associated sub-groups within the population as a whole. Further, it is these patterns of interaction that determine which individuals can exchange social information, and the subsequent rate and path of its diffusion i.e. "directed social learning" (Coussi-Korbel & Fragaszy 1995; Webster *et al.* 2013). The use of the shape of cumulative learning curves to infer social information transmission has now been abandoned. Instead, applying the social network approach to understanding information flow provides a more detailed view of social transmission (Hoppitt *et al.* 2010). Initially, to address the issue that the pattern of diffusion will be influenced by social

structure, a randomization approach was employed to determine whether the order of acquisition was related to the social network between individuals, whereby social transmission was inferred if this relationship differed from random (Boogert *et al.* 2008; Morrell *et al.* 2008). Yet, the strength of social transmission cannot be quantified using this technique, nor can it account for other variables that influence both an individual's asocial acquisition rate along with their network position (e.g. if older individuals associate with one another, and are also more likely to acquire information asocially) (Hoppitt *et al.* 2010; Hoppitt & Laland 2011).

Network-Based Diffusion Analysis (NBDA) was developed first in the social sciences (Franz & Nunn 2009) to quantify the strength of social transmission given the social network. It has recently been adapted to allow the inclusion of individual-level variables (Hoppitt *et al.* 2010; Hoppitt & Laland 2011). This now provides a means of assessing social transmission in natural systems whilst simultaneously allowing the consideration of various ecological, social and genetic factors as predictors of acquisition (Hoppitt *et al.* 2010; Hoppitt & Laland 2011). Although relatively novel, the technique has been relatively well applied within laboratory systems (reviewed in Hasenjager & Dugatkin 2015). Yet, currently NBDA has only been applied to three wild systems, and has been used to demonstrate the social transmission of (i) the discovery of experimental food patches and the acquisition of novel foraging techniques in wild birds (Aplin *et al.* 2012; Aplin *et al.* 2015a; Farine *et al.* 2015a), (ii) a foraging technique ('lob-tail feeding') in humpback-whales (Allen *et al.* 2013) and (iii) tool use in chimpanzees (Hobaiter *et al.* 2014).

Crucially however, such studies rely on observations of social structure. Therefore, the social network may not govern information acquisition but simply correlate with it due to an underlying factor (not included in the analysis) that simultaneously influences social associations and information acquisition. Indeed, not including such factors within NBDA can lead to biased estimates of the strength of social transmission, and might even result in inferring social transmission within systems where acquisition is in fact entirely asocial (Hoppitt *et al.* 2010). When a particular unmeasured variable increases an individual's acquisition rate, for example an individual's age, in scenarios where individuals choose to associate with alike individuals (i.e. social segregation by age), social transmission will be overestimated, whilst if individuals preferentially

interact with dissimilar individuals (e.g. disassortment by age), the estimate will be depreciated.

Manipulating individuals to understand societies

From the example of information flow, it is clear that experiments that manipulate social associations and subsequently test the effect of this on emergent processes are now greatly needed to disentangle causation from correlation. Understanding the causal relationship between social structure and a related process allows other inferences to be made. In the case of information flow for instance, understanding how social structure directly influences information transmission would also allow us to make predictions regarding the future dissemination of information (Webster *et al.* 2013). In the same sense, it would enable increased confidence in forecasting how information transmission may be affected by perturbations causing the loss or gain of individuals or associations (Firth & Sheldon 2015), and even whether selectively seeding particular individuals in the population with information may hasten its diffusion (Makagon *et al.* 2012).

The issue of a lack of experimental evidence for the importance of social associations is not unique to information flow; it also applies to various other potential emergent processes related to social structure, such as collective decision-making, disease spread, fitness and selection landscapes. For example, Oh & Badyaev (2012) showed that male house finches (*Carpodacus mexicanus*) with low-quality plumage were more likely to find a mating partner if they had high 'betweenness' (i.e. movement between flocks/groups). They explained this finding by proposing that such low-quality but socially mobile individuals can increase their mating success through joining groups containing even lower-quality males, rendering them of relatively higher quality. This 'social strategy' can thus have important consequences for sexual selection (Oh & Badyaev 2010). Alternatively, it is possible that the relationship that 'mating-finding' showed with 'betweenness' is a simply product of a correlated trait (e.g. activity levels) acting to increase mating success and promote movement between groups.

In addition to being complicated by individual-level factors, a major component in understanding how social networks may relate to ecological and evolutionary processes involves accounting for spatial distributions of individuals. Whilst statistical techniques

(e.g. permutations) can help estimate the influence of spatial effects to some extent (Whitehead 2008; Aplin *et al.* 2015b; Farine *et al.* 2015b), these often require extensive amounts of data. Furthermore, they do not adequately consider that individuals' locations may be based upon their social phenotypes, and resolving this relationship requires an experimental approach. Similarly, whilst simulations have been useful in forecasting the effect of individual loss on the social connectivity within social networks (Lusseau 2003; Williams & Lusseau 2006; Manno 2008), captive experiments have shown that changes to social group composition may influence individuals' social behaviour in a manner that statistical approaches would struggle to predict (Flack *et al.* 2006). Finally, whilst 'natural' experiments provided some indication of how environmental changes and external factors may influence social networks, for instance for dolphins (Ansmann *et al.* 2012), feral horses (Nunez *et al.* 2015) and Barbary macaques (Lehmann *et al.* 2016), such occurrences are rare and, critically, do not allow replication. This, along with a general lack of understanding of how power or biases in sampling techniques may influence animal social network inferences, means that our confidence in the network approach would be improved considerably through expanding the use of experiments (James *et al.* 2009; Croft *et al.* 2011).

Study system

The research took place in the context of a larger study examining the social ecology of a population of wild, forest dwelling, passerine birds including great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*) and European nuthatch (*Sitta europaea*) in Wytham Woods, Oxford, UK (51°46'N, 1°20'W). The area comprises 385ha of mixed deciduous woodland, enclosed by arable land and pasture (Savill et al. 2010). It includes ~1210 nestboxes in fixed positions with known GPS co-ordinates. Around 60% of these are occupied during the breeding season (April-May), primarily by great and blue tits. During these months, and for many years previously (Lack 1947, Perrins 1965; 1979), these have been visited regularly to record breeding attempts, and capture adults (between days 6-14 of nestling phase) and nestlings (after day 15) to mark with a unique BTO (British Trust for Ornithology) metal leg ring. Parent characteristics (sex and age-class) are also determined using previous ringing records, presence of brood patch, and plumage characteristics

(Svensson 1992). Breeding performance is also documented, as first egg date, egg number and weight, chick number and fledgling success is recorded which gives multiple measures of reproductive success. Extensive mist netting from September to February allows individual marking and recording of morphometric information of immigrant birds, as well as primarily natural cavity nesting species (nuthatches, coal tits and marsh tits). Additionally, blood samples have been collected from a limited subsample of adult great tits between 1985-2004, and for a much larger proportion until 2009, and a smaller proportion thereafter. Currently, 2644 of these individuals have been genotyped on an Illumina iSelect BeadChip ('SNP chip') of 9193 SNPs (van Bers et al. 2012). Therefore, potential also exists for research requiring detailed genetic information on individuals, some of which contributed to the appendices of this thesis.

More recently (beginning in 2007), birds have also been fitted with a plastic leg ring containing a unique passive integrated transponder (PIT tag). PIT tags contain a small (<0.1g) electronic passive microchip that is dormant until activated when it comes within the electromagnetic field generated by a Radio Frequency Identification (RFID) antenna. Upon activation, the PIT tag transmits a unique alphanumeric ID code, allowing the individual wearing the tag to be identified. Such tags have a lifetime that far exceeds that of the studied birds, and are also inexpensive (~€2), which allows large-scale deployment of tracking wild individuals throughout their whole lives. Though deployed in a range of ways, PIT tags have previously been found to have no effect on behaviour or fitness of birds (Bonter & Bridge 2011). In great tits, even the use of subcutaneous PIT tags was found to have no negative consequences for survival, recruitment or body condition (Nicolaus *et al.* 2008). Similarly, neither subcutaneous or leg-ring applied PIT tags had any effect on the fitness of house sparrows (*Passer domesticus*) (Schroeder *et al.* 2011). Along with PIT tags proving to be a safe and low-interference monitoring technique, they have also been shown to be an accurate method for measuring bird behaviour (Bonter & Bridge 2011). For instance, RFID data which assessed Wryneck (*Jynx torquilla*) nest provisioning closely matched that gathered from both direct observations and timed photography (Freitag *et al.* 2001). Further, quantifying Magellanic penguins' (*Spheniscus magellanicus*) foraging trip duration using PIT tag detections was almost equivalent to using data gathered from satellite transmitters on the same individuals (Boersma & Rebstock 2009).

During the winter, the study species form mixed species foraging flocks that are relatively loose in composition and experience reasonable turnover, as individuals regularly join, leave and return to intermingling flocks (Hinde 1952; Farine *et al.* 2015b). Those individuals who form part of the same flock are often observed together regularly throughout the winter (Saitou 1978), and the flocks also contain a subset of strongly bonded individuals such as mated pairs (Ekman 1989), which can maintain their relationship with one another over multiple years. Indeed, in great tits, individuals who co-occur together one day are significantly more likely to be observed in the same flock the very next day (Aplin *et al.* 2013). Over longer time periods, on-going work suggests 'social communities' (i.e. loose aggregations of the intermingling flocks) show high stability, with >80% probability that birds in the same social communities one year will also share the same community in the following winter (Farine *et al.* In prep).

In the study system, the PIT tags fitted to the birds' legs allowed detection of the time, date and location of each individual's feeding attempts at sunflower feeding stations equipped with RFID antennae on both access holes (Dorest ID, Aalten, Netherlands). These were placed in 65 fixed locations in a stratified grid throughout the study area from September to February opening every weekend for both days, scanning for PIT tags from pre-dawn until after dusk. I have previously found that individuals differ consistently in their usage of this supplementary food, particularly in terms of males consuming more seeds than females. However, all measures of individual fitness were found to be unrelated to seed consumption, suggesting the limited temporal availability of the resource reduces any potential individual-level carry over effects of this method of tracking individuals (**Appendix A**).

The PIT-tag detection records provide a spatiotemporal data stream, typically comprising of 'quiet' periods broken up by intermittent bursts of activity as flocks of individuals come in to feed. As expected, these feeding events often differ in length, intensity, and density of individuals due to the stochastic nature of bird flock feeding behaviour. Therefore, classifying individuals into groups using an arbitrary time frame around observations is difficult due to the inflexibly of this approach and the prior assumptions needed. To the human observer, some discrete feeding events appear easily detectable by eye, whilst others are more difficult to judge from visually assessing the datastream alone. Further, such judgment is somewhat subjective, and impractical given

the scale of the data. Hence, a machine learning algorithm was developed as a consistent and objective method of identifying feeding events based on measurable attributes of the data (Psorakis *et al.* 2012). This process automatically recognizes segments of temporally clumped activity with the datasteam using a Gaussian Mixture Model (GMM), and statistically assigns each individual detection of a bird to the cluster in which it is most likely to belong (Psorakis *et al.* 2012). Whilst relatively computationally intensive, this method has been found to be highly robust, and preferable over various approaches using set time windows (Psorakis *et al.* 2012; Psorakis *et al.* 2015). Indeed, using simulation approaches, it has been shown that the social associations subsequently derived from this process are highly similar to those initially specified (Psorakis *et al.* 2015). Therefore, in this way we are able to estimate distinct 'gathering events' as flocks of PIT tagged birds arrive and forage at the RFID antenna equipped feeders. These 'gathering events' (or 'flocks') are used as the basis of co-occurrences between individuals. Standard methods of estimating social association rates based on the propensity of each dyad to co-occur with one another can then be used to estimate social networks over the entire population (Cairns & Schwager 1987). By assuming a social association between all individuals detected within the same gathering event, we utilize a 'gambit of the group' approach (Whitehead & Dufault 1999). Whilst such an approach has some potential drawbacks, this approach is particularly well-suited to this study system due to the extensive sampling employed, the creation of weighted networks, as well as the use of null models for statistical analysis (Croft *et al.* 2008; Franks *et al.* 2010; Croft *et al.* 2011).

On a more general note, the use of RFID technology enables the collection of large-scale, high-resolution and non-subjective data sets, yet the simplicity of the raw records (i.e. the time and place of individuals' occurrence) provides less detail than human observations can offer. For instance, whilst it may be possible to infer social associations (as described above), the RFID records themselves cannot provide direct information about the nature of the social interactions taking place, such as whether it was aggressive, affiliative, or neutral. On the other hand, human observation is prone to being subjective, and also often suffers from sampling constraints due to the relatively large amounts of effort needed. Indeed, recent studies of avian behaviour have actually used data gathered from RFID technology to validate and optimise human observation efforts (Lendvai *et al.* 2015). Ideally, the combination of these two complementary

approaches should be applied when possible (Bonter & Bridge 2011). Within our own system, human observations have shown that >99% of visits to RFID feeders from PIT tagged birds are successfully recorded by the automated system. Further, throughout the thesis, I take the approach of attempting to understand the biological significance of the inferred social associations by comparing these to data gathered using various other methods (e.g. morphological records, observations during the breeding season), as well as testing the consequences of manipulating the social associations occurring at the feeding stations.

Thesis Outline

In this thesis, I investigate the carry over and consequences of social structure, using the extensively monitored wild bird community described above as a model system. I first detail the patterns of social associations amongst individuals, and then use null models (empirically-parameterised permutations of the data) to determine the contributions of spatial features and fine-scale social dynamics towards the observed structure. Following this, I build upon these approaches to demonstrate how null models can be combined with linear modeling to enable relationships between social connections and spatial decisions to be elucidated, and to determine the carry-over of prior social networks onto the subsequent spatial arrangements of the population.

Experiments are then carried out to explicitly test the carry-over and consequences of social connections, which firstly begin with removals of individuals. I then introduce a novel experimental design whereby the foraging associations amongst individuals can be directly manipulated. The data generated from these experiments are used to assess the consequences of foraging associations for (i) sociality itself, in terms of individual social behaviour and social associations within other contexts, (ii) social transmission of information and (iii) individual behaviour with regards to spatial foraging choices and the development of flexible scrounging strategies. Within this work, I aim to further reveal the underlying structure of social networks amongst wild animals, enhance current understanding of their response to external changes, and, importantly, provide novel insights into the consequences of social connections for wider biological processes.

The importance of ecological factors and fine-scale social dynamics in shaping the interactions between individuals is a fundamental aspect of understanding social structure. In **Chapter 2**, I separate out these often-overlapping components of population structuring by comparing the observed data to different null models. In this way, I was able to reveal the scale and relative contributions of spatial and social choices in determining the association patterns between individuals of different demographic classes. The results suggest that both dynamic preferential attachment and avoidance strategies, as well as dispersal and settlement decisions, consistently shape phenotypic structure even within a fluid ('fission-fusion') social system.

Spatial structure in populations is key to many ecological processes. Although much work has focused on the role of abiotic effects and conspecific density in contributing to population spatial structure, the role of specific social relationships in determining this is much less studied. However, there is increasing realisation that the links between social and spatial structure are central to many emergent properties of populations, and may also determine important aspects of individual life histories. Therefore, in **Chapter 3,** I examine the complex relationship between spatial and social structure. I demonstrate how social structure throughout the fission-fusion winter flocking period can determine future spatial structure of wild great tits during the crucial breeding period. I show that birds breed closer to those they held stronger social connections to during the winter, and also arrange their territory boundaries around these individuals. These patterns were found to be consistent across classes of individuals (first-year birds, males and females, etc) and over all years. Importantly, as spatial structure mediates a wide range of population-level processes, this work presents how prior social networks may carry over to influence a broad range of individuals in various ways, including their future interactions.

Large-scale observational data combined with various analytical techniques is certainly an invaluable aspect of understanding of social systems. Indeed, almost all work to date is non-experimental, in the sense that the social network itself is not manipulated. In **Appendix B**, I use the observational data to show that individuals are consistent in their social phenotypes over short and long time frames, and apply null models to illustrate that this repeatability is more than expected from individuals' spatial locations alone. In **Chapter 4**, I monitor the social associations amongst birds, whilst experimentally

removing individuals from the network. I illustrate that birds alter their social behaviour in response to experimentally imposed loss of their flock members, and adopt more central network positions, which may enable them to compensate for this reduction in their social associates. I also discuss the potential applications of this for understanding the effects of individual loss from wild populations.

Whilst manipulating social networks through the removal (or addition) or individuals is a useful approach, they are limited in their versatility and do not allow assessment of how external factors may alter the social connection patterns amongst the same set of individuals. To this aim, in **Chapter 5**, I present a newly developed and novel experimental design that enables the subtle social manipulation of wild animals. I developed 'selective feeders' which use an automated RFID system to automatically respond to the detected individual. Using these, I was able to control which individuals could access which feeding stations. In this way, I experimentally imposed social segregation between individuals of the arbitrary phenotype of "tag type" (i.e. whether their unique, randomly assigned, PIT tag number was an odd or even). In **Chapter 5**, I use this system to show how external factors can impose social segregation between spatially affiliated individuals, independent of intrinsic factors. Further, I illustrate that these effects are carried over into other contexts (uncontrolled foraging sites and associations during breeding territory acquisition), thus illustrating how constraining interactions within a single context can ultimately influence numerous aspects of sociality. Finally, by continued monitoring of the foraging social network after ceasing the externally imposed assortment, I show that the fission-fusion dynamics of the system allows the network to quickly recover from the prior segregation. Hence, this work has broad significance in that it (i) demonstrates a novel method to directly manipulate social networks; (ii) allows inferences of causal effects of networks across contexts; (iii) tests the recovery of networks to external perturbation.

In **Chapter 6**, I move beyond examining the resilience and carry over of social associations, to also consider how these changes to the social network influence pathways of information flow within the mixed species community. Furthering the understanding of social information transmission remains a particularly important application of modern social network analysis, as it also offers potential insight into social learning as well as the emergence and spread of culture. Therefore, using newly

developed techniques for examining the diffusion of information through various components of the network, I show that the experimentally-imposed social structure carries over into patterns of information flow. Social connections between those who were of the same tag-type (allowed to feed together) subsequently became more important for gaining information regarding new food resources. Additionally, birds demonstrated a social learning strategy whereby they prioritised learning from those who provided relevant information on a regular basis. These findings show how changes to social networks cause corresponding changes to social information flow, and add to the limited existing knowledge surrounding social learning strategies within wild animal networks.

Chapter 7 focuses on strong social relationships within the system, which are fundamental components of many complex animal societies. Whilst individuals' behaviour may determine which relationships form, it could also be the case that individuals choose to shape their behaviour around maintaining social relationships. Although potentially crucial in explaining variation in behaviour, the influence of social relationships as a driver of behavioural variation is often overlooked, and poorly understood. Using the selective feeders, I was able to experimentally test the importance of this alternative view of the relationship between individual behaviour and social structure. I show that mated pairs prioritised sustaining their relationship with their partner over their own foraging preferences. Through staying with their partner, these key social relationships also resulted in individuals forming flocks with other birds they would not normally associate with. This demonstrates how the strong social bonds an individual holds may structure their wider social network. I further show that the conflict between social relationships and an individual's own interests also have important consequences for learning and behavioural flexibility, as individuals quickly learn a flexible scrounging strategy to alleviate the constraints resulting from maintaining their relationships. These findings are particularly novel because they demonstrate experimentally how animals base their own decisions on their social relationships, and how this then feeds back onto wider social structure and can influence the learning of flexible behaviours. Such results were only attainable through an experimental approach involving the deployment of new technologies within an intensively studied population.

Ultimately, I end the thesis with a discussion (**Chapter 8**) of the findings made throughout this work and their relationships to one another. I synthesize the primary findings to illustrate how the work has contributed to the understanding of the interplay between ecology and sociality, and provided novel insights into the consequences of social networks for population level processes. Additionally, I comment on the potential utility of furthering our understanding of animal social networks for various practical applications, such as animal conservation and welfare. Finally, I highlight several outstanding questions, and discuss how the advancements made within this thesis now provides a foundation for using this study system to addressing various unresolved challenges. This is particularly in reference to examining the causal relationship between social networks and fitness, as well as the mechanisms underpinning this, in hopes of elucidating the evolutionary implications of social structure.

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Chapter 2

The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds

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The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds

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1. Summary

Both social and ecological factors influence population process and structure, with resultant consequences for phenotypic selection on individuals. Understanding the scale and relative contribution of these two factors is thus a central aim in evolutionary ecology. In this study, we develop a framework using null models to identify the social and spatial patterns that contribute to phenotypic structure in a wild population of songbirds. We used automated technologies to track 1053 individuals that formed 73 737 groups from which we inferred a social network. Our framework identified that both social and spatial drivers contributed to assortment in the network. In particular, groups had a more even sex ratio than expected

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and exhibited a consistent age structure that suggested local association preferences, such as preferential attachment or avoidance. By contrast, recent immigrants were spatially partitioned from locally born individuals, suggesting differential dispersal strategies by phenotype. Our results highlight how different scales of social decision-making, ranging from post-natal dispersal settlement to fission–fusion dynamics, can interact to drive phenotypic structure in animal populations.

2. Introduction

Group dynamics are an important part of an individual's social landscape. Group size can impact predation risk through dilution [1], selfish herd dynamics [2] or predator confusion effects [3]. The social links between individuals can also be important for gathering information about the environment [4–7], such as finding food [8–10]. Group-living often is typified by a trade-off between these benefits and costs incurred through competition [1]. However, costs and benefits of joining groups may vary according to the environment [11], individual phenotypic characters (such as those influenced by dominance or sex [12]) or with the existing composition of the group (similarity or difference in phenotype, for example the oddity effect [3]). If the benefits of being in a group vary with the phenotypes of its members, we should then expect regular patterns of associations to emerge between phenotypes in a way that maximizes the individual fitness of participants (such as kin structure in cooperative breeders [13]). How these patterns emerge in populations, whether from social (attraction or avoidance) or spatial (acceptance or exclusion) effects remains largely unexplored [14].

Fission–fusion societies are common across taxonomic groups. These are typified by groups that have short-term structural stability and high turnover in membership. Classic examples of animals that exhibit this social dynamic include primates [15–17], bats [18,19], elephants [20,21], red deer [22], as well as birds [23–26]. This dynamic structure is thought to result in linkages across all levels of these populations, from pairwise to landscape community interactions [27]. Such behaviour could be adaptive if simple pairwise interactions facilitate the emergence of complex patterns at the population scale [28,29]. For example, larger groups may be better at tracking environmental gradients [30]; 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 [11]. In particular, fission–fusion dynamics are thought to facilitate behavioural plasticity, which could play a critical role in successful individual responses to environmental variability.

Individuals may also be able to influence particular selection pressures by choosing their social environment [31]. 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 [32]. 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 the identities that individuals associate with in groups can change, the phenotypes of their associates may follow consistent non-random patterns [33]. For example, large fish may consistently interact with other large fish. Thus, unlike mechanisms relying on repeated interactions between individuals, such as cooperation [34], selection could influence individual fitness, regardless of the specific identity of participants in the groups [35].

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 are over time, (ii) how groups varied in size according to population density and time of year, (iii) whether group composition reflected the local availability of individuals, and finally (iv) whether social or spatial variation in the distribution of phenotypes led to phenotypic assortment over the length of an entire winter. In doing so, we investigate the potential for social dynamics (i.e. group formation) to contribute to evolutionary processes, as non-random association of phenotypes can lead to variable selection [33].

3. Material and methods

The study took place at Wytham Woods, Oxford (51°46′ N, 1°20′ W). The breeding great tits (*Parus major*) in this 385 ha woodland are the focus of a long-term study, with over 1000 nest-boxes monitored annually.

Since 2007, all breeding adults and chicks have been caught and fitted with PIT tags, in addition to the standard British Trust for Ornithology metal ring. Morphometric measurements, including age and sex were recorded for every bird caught as adults (93% of all birds in this study). This marking protocol 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 [8,36,37]). This approach enabled us to maintain in excess of 90% of the population fitted with PIT tags [23]. Recent studies suggest that social network analysis is robust against biases that may arise from small proportions of untagged individuals [38].

3.1. Field observations

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. In order to sample the social and phenotypic structure of these groups, we deployed 65 automated feeding stations in a stratified grid from 3 December 2011 to 26 February 2012. Each feeding station was fitted with two radio frequency identification antennae (one on each access hole) and filled with sunflower seeds. These were automatically opened for all daylight hours for 2 days per week, providing synchronous snapshots of the association patterns in the population. Feeders were filled with sunflower seed in order to minimize queuing (and therefore competition) as individuals picked up a seed and processed these in a nearby bush or 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 one-third of a second from pre-dawn until after dusk and detected more than 99% of tagged individuals' visits to feeders. In all, we collected 26 days of data over 13 sampling periods.

3.2. Inferring group membership

Feeding stations provided a highly resolved spatio-temporal data stream of individual visits. As individuals fed in groups, or flocks, the pattern of visits 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 machine learning algorithm based on Gaussian mixture models [39]. 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 dataset, resulting in a more accurate social network than other approaches [40]. By fitting a Gaussian distribution over closely spaced visits, visits can then be assigned to a burst, or group, to which they have the highest probability of belonging. This method returns a matrix of groups and the individual's membership of these groups.

3.3. Stability

We used a measure of temporal group stability that is similar to the lagged rate of association proposed by Farine [41]. 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. $S(\tau, X) = 0.5$ is equivalent to a group fusing with another group twice the size, or if two-thirds of a group remains the same in two evenly sized groups, over 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. To estimate how the observed stability

differed from random, we calculated $S(\tau, X)$ for groups in a spatio-temporally restricted null model (see below). This model constrains the distribution of group sizes and uses the ratio of the observed to permuted data to estimate the period τ in which non-random associations persist.

3.4. 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 3–5).

3.5. Within-group membership

We explored how the composition of the groups varied with regard to group size for three different state variables (sex, age and residency status), all of which are binary states (male or female; juvenile or adult; immigrant or locally born, respectively). Sex was determined when birds were recaptured (93% of individuals were sexed) using plumage characteristics (the width of the breast stripe is much larger in males). Juveniles are defined as birds that were born in the breeding season immediately prior to the winter (in this case in spring 2011). Immigrants are defined as birds that were born outside of the study area (dispersed into Wytham Woods), whereas locally born birds were ringed as nestlings within the study area (the proportion of nestlings born in natural cavities is estimated to be very low [42]). The demographic structures of groups were calculated as the proportion of individuals from each class occurring in each separate group, and pooling these data as the mean for each group size. We then compared these means to groups in permuted data (described below).

Further, we also examined whether group size was associated with the body size of individuals within them. As a multivariate measure of size for individuals, the first principal component (PC1) of a principal components analysis using wing and tarsus length (available for 84% of all individuals) was used. As males were significantly larger in both measures (t-test; wing: $t = 28.82$, d.f. $= 931$, $p < 0.001$, tarsus: $t = 13.63$, d.f. $= 885$, $p < 0.001$), 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's correlation coefficient; male wing $= 0.998$, male tarsus $= 0.323$, female wing $= 0.998$, female tarsus $= 0.288$). 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.

3.6. Within-group assortativity

After determining the content of groups in regard to the different demographic states (above), within-group assortativity for each demographic state 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 among 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, while 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 [23]), where high kurtosis scores indicate a peaked distribution (i.e. assortativity), while low scores indicate a flat distribution (i.e. disassortativity).

3.7. Null models

We used randomization techniques in order to create two contrasting null models. The first assumed random interactions between individuals but a fixed observation stream, which we call the phenotypic

null model. In this method, we created 1000 random networks by shuffling the node labels associated with each individual's phenotype. The second maintained spatio-temporal distributions of phenotypes; we call this the spatio-temporally controlled null model. These two randomizations used two general methods of data randomizations. Phenotypic randomizations consisted of randomly re-allocating the phenotype of individuals, maintaining the same observation patterns and the same distribution of phenotypes. Spatio-temporally controlled randomizations used a restricted permutation test following the methods originally described by Bejder *et al*. [43] with subsequent improvements by numerous authors (see [44, 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 dataset. In our case, we restricted swaps to occur only between groups that were observed at the same location (same feeder) and on the same sampling period (weekend). 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 [45]. If the patterns between the two randomizations 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 in the spatio-temporally controlled null model, but not in the phenotypic null model. If the observed data then match the spatio-temporal but not the phenotypic null model, then any assortment in this phenotype is attributable to spatial effects. If the data differ from both, then we attribute assortment to be due to social effects given that phenotypes are randomly distributed in space.

Comparing the observed patterns of group membership with null models derived from permutation allowed us to reduce the potential impact of pseudoreplication in our data. Both the null models maintained the same underlying structure of interactions, such as group sizes, number of observations for each individual and the temporal properties of group structure (group size increases as a proportion of time of day [36]). Although our data comprise many repeated observations of the same individuals and occasionally even the same groups, these repetitions are repeated in the permuted data. Taking the ratio of measures calculated on both observed and permuted data provides a measure of how non-randomly groups and occurrences are repeated.

We repeated the phenotypic randomization 1000 times. We ran 1 000 000 iterations of the spatio-temporal randomizations, as only a single observation is swapped on each iteration (whereas phenotypic randomizations shuffle all nodes; see [44, p. 130]). Where possible, we compared our data to the distribution of the spatio-temporal randomizations (taken after every 1000th iteration), but where this was not possible (for example for the group stability measure that is highly computationally intensive) we used only the final randomized group membership matrix after the 1 000 000th iteration.

3.8. Social network analysis

We used the R [46] package *asnipe* [41] 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 [47], which is derived from the Pearson correlation coefficient for weighted-edge networks in the R package *assortnet* [14].

4. 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 individuals of unknown sex (that were never caught post-fledging and not included in subsequent analyses). Across 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 unique detections of individuals over the 13 sampling periods, forming 73 737 unique groups with a mean size (±s.e.) of 4.7 ± 0.01 individuals and a typical group size (i.e. group size experienced by the average individual, ±s.e.) of 7.5 ± 0.01 individuals per group.

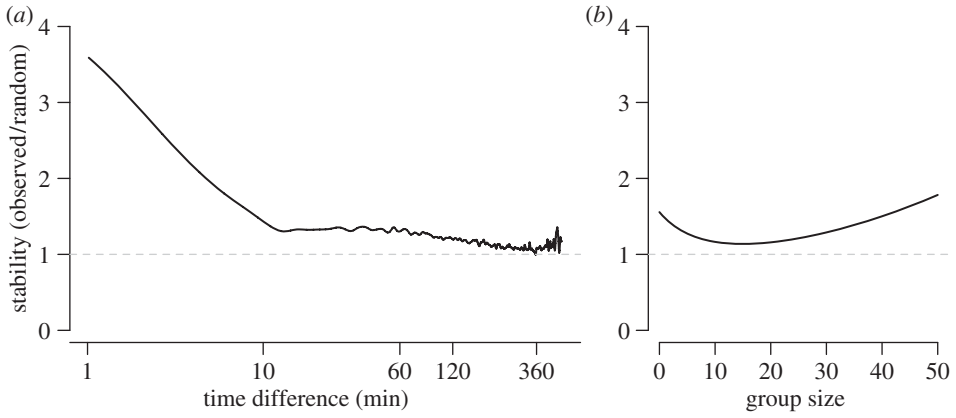


Figure 1. Groups show higher stability than expected from random, both in terms of (*a*) the (log) time-gap between groups and (*b*) the size of the initial group. Groups were most stable in the period of 1–10 min, after which stability was non-random, but much lower, up to approximately 2 h (see electronic supplementary material, 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 randomized data.

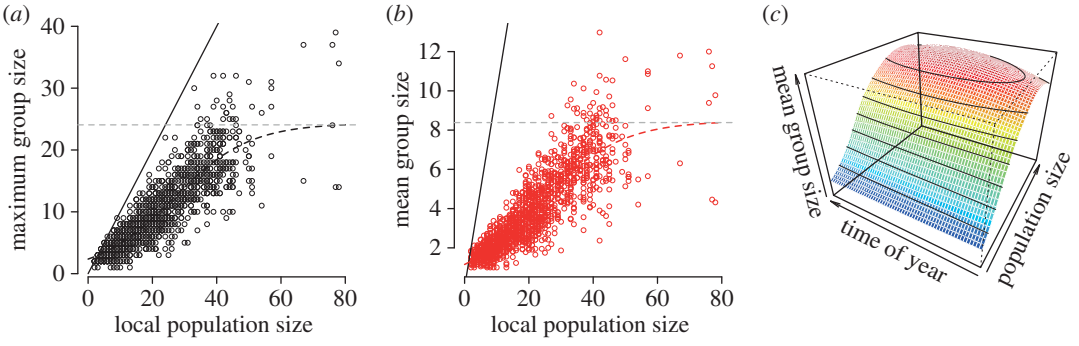


Figure 2. Group size was proportionately smaller as local population size increased. For each location, we calculated the number of individuals recorded at the site in each sampling period. We found that both (*a*) maximum group size and (*b*) average group size saturated with increasing population size. (*c*) We found no effect of season on this relationship, where time of year represents the period ranging from 3 December 2011 to 26 February 2012.

4.1. Stability of group membership

We found that groups had significantly higher stability in the first 10 min after being observed when compared with the same data after 1 million randomizations of the spatially and temporally restricted null model (figure 1*a*). 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 stable over short periods of time (less than 10 min), with only a few stable associations being maintained over longer periods (see also [23]). Stability also varied according to group size, with small and large groups being more stable than expected by chance (figure 1*b*).

4.2. Group size distributions

We found a strong divergence from a 1 : 1 relationship between the number of individuals present on a given day and the group sizes observed (figure 2*a*). Logistic models of the mean and maximum observed groups sizes had significantly greater support than linear models applied to the same data (electronic supplementary material, table S1). This suggests that the relationship between population size and mean or maximum group size saturated, in this case at a maximum of eight and 24 individuals per group, respectively (figure 2*a*,*b*, horizontal dashed lines). Further, the relationship between mean group size and population size appeared to remain rather stable between weeks over the winter (generalized linear mixed model controlling for population size with location as a random effect suggests a very weak decrease in group size each week: $t = -1.85$, $B \pm \text{s.e.} = -0.012 \pm 0.006$, $p = 0.06$; figure 2*c*).

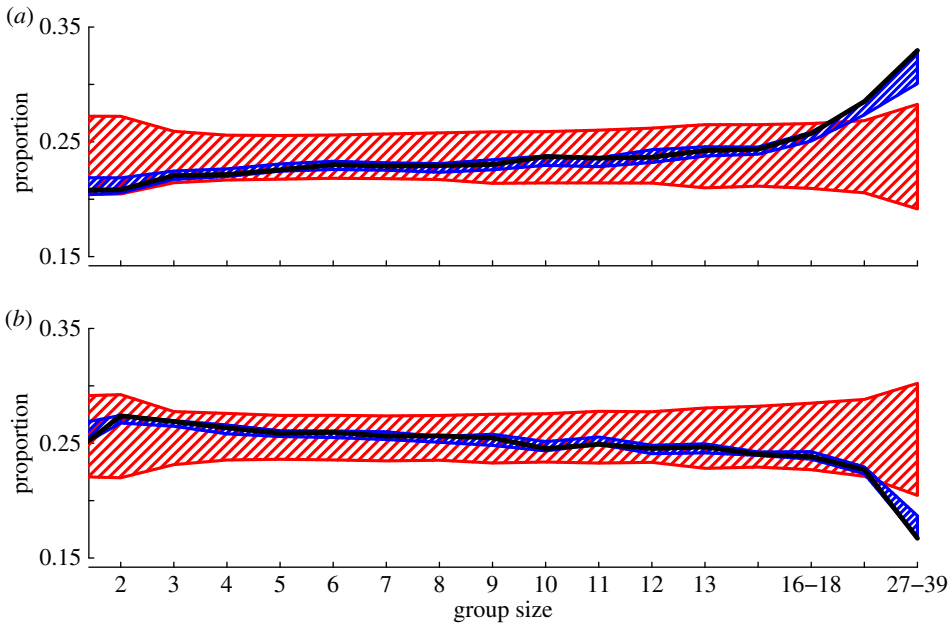


Figure 3. There was a significantly greater proportion of females in large groups that were juvenile (*a*) and lower proportion of males in large groups that were adults (*b*). The black lines show the observed data, the blue polygons show the 95% range of permutation data from the 'spatio-temporally controlled null model', and the red polygons show the 95% range of permutation data generated from the 'phenotypic randomization null model'. In groups of over 18 individuals, the observed proportions of the age classes of males and females in each differ from the phenotypic randomization null model only. This suggests that juvenile females were disproportionately found in areas with large flocks, whereas adult males were absent from areas containing large flocks.

4.3. 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 randomization' null model) or socially driven, i.e. active decisions by individuals regarding group membership (inferred here from the observed data differing significantly from the 'spatio-temporal controlled' null model, or both). Indeed, we found evidence for all three situations in regards to the demographic states considered here.

Although groups of all sizes contained the expected proportions of adult females and juvenile males (electronic supplementary material, figure S2), we found that large groups contained more juvenile females but fewer adult males than expected by the phenotypic randomization 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 randomization. As the spatio-temporal null model matched the observed data (figure 3), this suggests a spatially driven pattern, such that 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 (less than 8), which was significantly lower than the phenotypic randomization null model but predicted very well by spatio-temporally controlled permutations (figure 4), suggesting a non-uniform distribution of juvenile immigrants across the study area. However, no such pattern of non-random group content based on residency status was observed among adult birds (electronic supplementary material, figure S3).

As well as the proportion of individuals of different phenotypes included in groups, we also found non-random assortment in regards to different demographic characteristics. Groups were found to be more evenly distributed with regard 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 5*a*). By contrast, groups tended to show assortativity by age, as the proportion of either adults

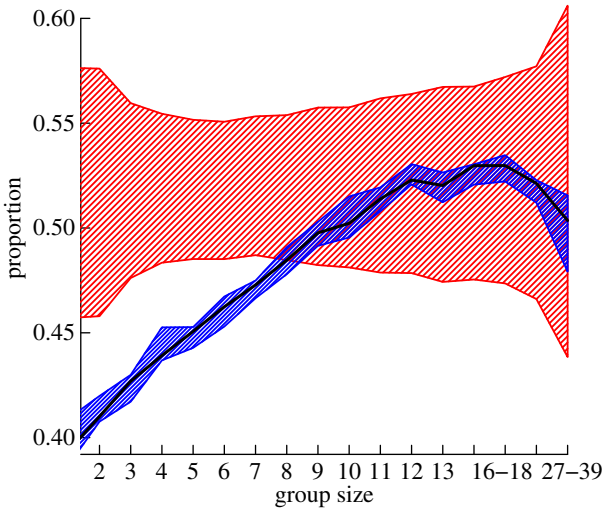


Figure 4. There was a significantly smaller proportion of immigrant juveniles in groups of less than 8. The observed data (black line) differ significantly from the phenotypic randomization null model (red polygon), but not the spatio-temporally controlled model (blue polygon), suggesting that immigrant juveniles are found in areas of Wytham Woods where large flocks occur.

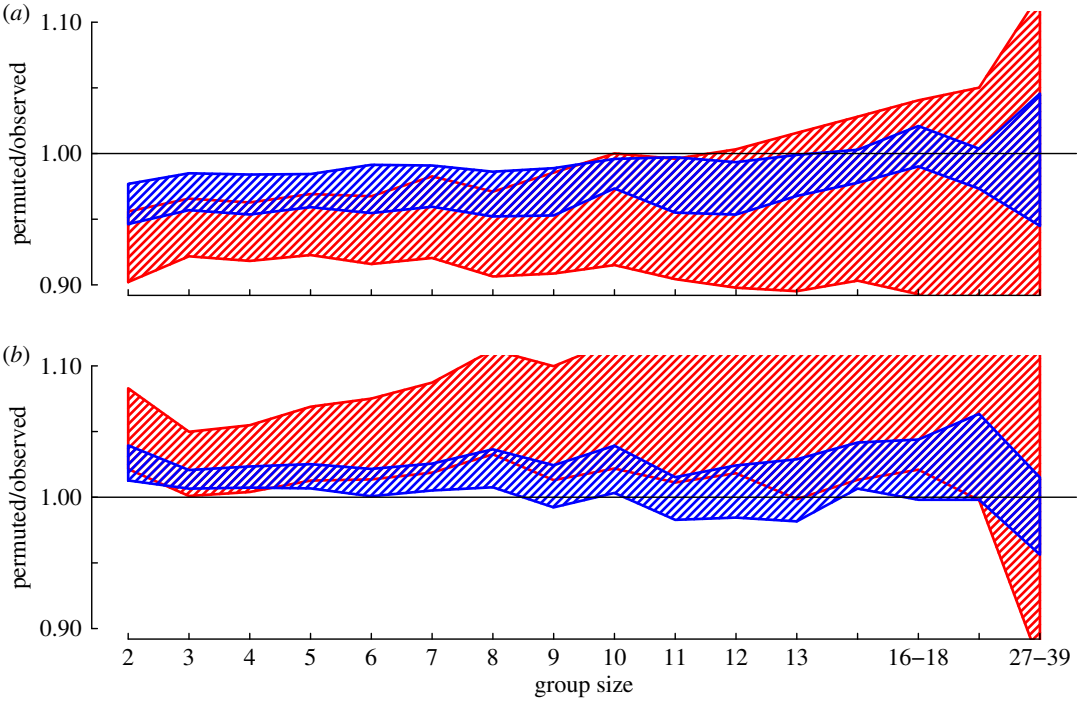


Figure 5. Groups were significantly (*a*) more evenly distributed by sex but (*b*) more assorted by age class than expected from the randomized datasets. In these plots, the *y*-axis shows the ratio of the null models to the observed data (observed data are $y = 1$). The phenotypic null model is shown by the red polygon and the spatio-temporally controlled null model is shown by the blue polygon. The sex ratio of groups up to a size of 10 is significantly closer to even (observed is more than random) than both the spatio-temporally restricted and the phenotypic randomizations (see electronic supplementary material, figure S6, for these shown as binomial probabilities). These groups also tend to contain more individuals that are either adults or juveniles than expected (groups are significantly less mixed than expected, observed is less than random). Plots show the ratio of the 95% confidence intervals of the randomizations to 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 electronic supplementary material, figure S6).

or juveniles in each group was higher than expected by chance (figure 5*b*), and again appeared largely driven by local social group structure rather than variation due to spatial disaggregation.

The mean size of individuals within groups did not differ from either the spatial or population-wide distributions of phenotypes (electronic supplementary material, 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 (electronic supplementary material, figure S4). We also found no major patterns of phenotypic assortment in groups according to individual size among any of the different demographic classes (electronic supplementary material, figure S5), suggesting that these did not differ dramatically from either the spatial or population-wide distributions of phenotypes.

4.4. 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 $r = -0.034 \pm 0.0009$), which indicates that mixed-sex dyads had a higher probability of both occurring and reoccurring. Age (in years) was significant assorted ($r = 0.047 \pm 0.0014$), suggesting that individuals of the same type, particularly juveniles, had a stronger tendency of repeatedly associating during the winter. Finally, we found significant overall assortment by immigration status ($r = 0.037 \pm 0.0019$), which was mostly driven by assortment in adults ($r = 0.11 \pm 0.0034$).

5. Discussion

We used an automated detection system to collect data on the patterns of association between individuals in a large free-ranging bird population to understand how individuals of different types associate and what mechanisms produce non-randomness in association. We showed 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, our results suggest that the patterns of group membership arose through association preferences by individuals, potentially based on both their own phenotypes but also the existing composition of the group. In others, group structure appears to be shaped by the variation in the distribution of phenotypes across space. For example, adult males (which are often more dominant [48]) tended to avoid large groups, whereas juvenile females (generally subdominant phenotypes [49]) were found in larger groups more often than expected.

These findings have important 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 [35]. For example, in species such as great tits, where residency is an important predictor of dominance [48], 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 [28]) may play an important role in shaping the evolution of this social system.

Although phenotypic assortment may be relatively common in nature, no study has, to our knowledge, linked short-term group membership dynamics to long-term association patterns in a social network. In fish, several studies have found that groups will assort by size (reviewed in [50]), often in preference to species identity [51,52]. Also, assorted group composition appears to play a particularly important role in avoiding predation, either by minimizing an individual's risk relative to the group [53] or by maintaining movement synchrony [54]. 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 [55].

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 [56] found that groups of bullfinches (*Pyrrhula pyrrhula*) were more mixed by sex than expected by chance. By 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 [57]. The authors concluded that assortment may play an important role in developing skills needed for breeding in that species [57].

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 [35]. 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 [48,58]. 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 [48]. 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 [59,60], and consequently have been found to be more closely associated in this population [23].

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 and 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.

Ethics statement. All work was subject to review by the Department of Zoology (University of Oxford) ethical committee and adhered to UK standard requirements. Birds were ringed and PIT-tagged as pulli, when caught at breeding nest-boxes or when caught using mist nets. All research was conducted under BTO licences (e.g. DRF licence C5714) as part of ongoing research in this population.

Data accessibility. Data are available to download from Dryad (http://dx.doi.org/10.5061/dryad.885c0).

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Author contributions. D.R.F., J.A.F. and B.C.S. conceived of the study. All authors contributed to the study design and field data collection. J.A.F. and D.R.F. analysed the data. D.R.F. drafted the manuscript with input from J.A.F. All authors helped draft the final manuscript.

Conflict of interests. The authors declare no competing interests.

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SUPPLEMENTARY INFORMATION

Farine*, Firth* et al. The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds

SUPPLEMENTARY TABLES

Table S1. 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

SUPPLEMENTARY FIGURES

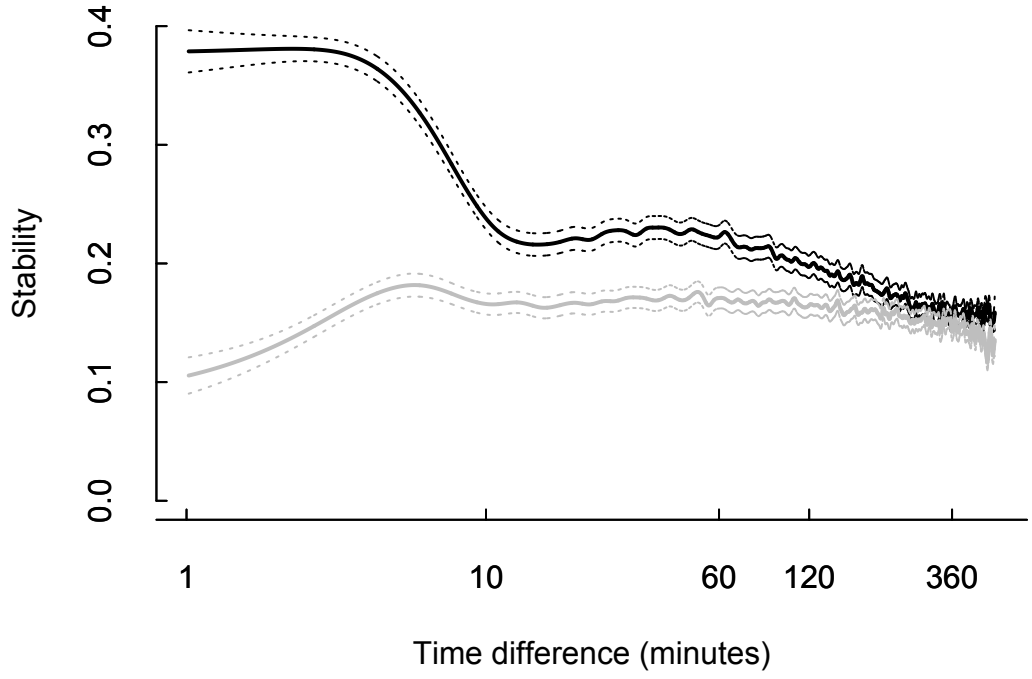


Figure S1: Group stability shown for the observed data (top black line) and randomised (bottom grey line) data after 1 000 000 iterations, shown with 95% confidence intervals calculated using jackknife.

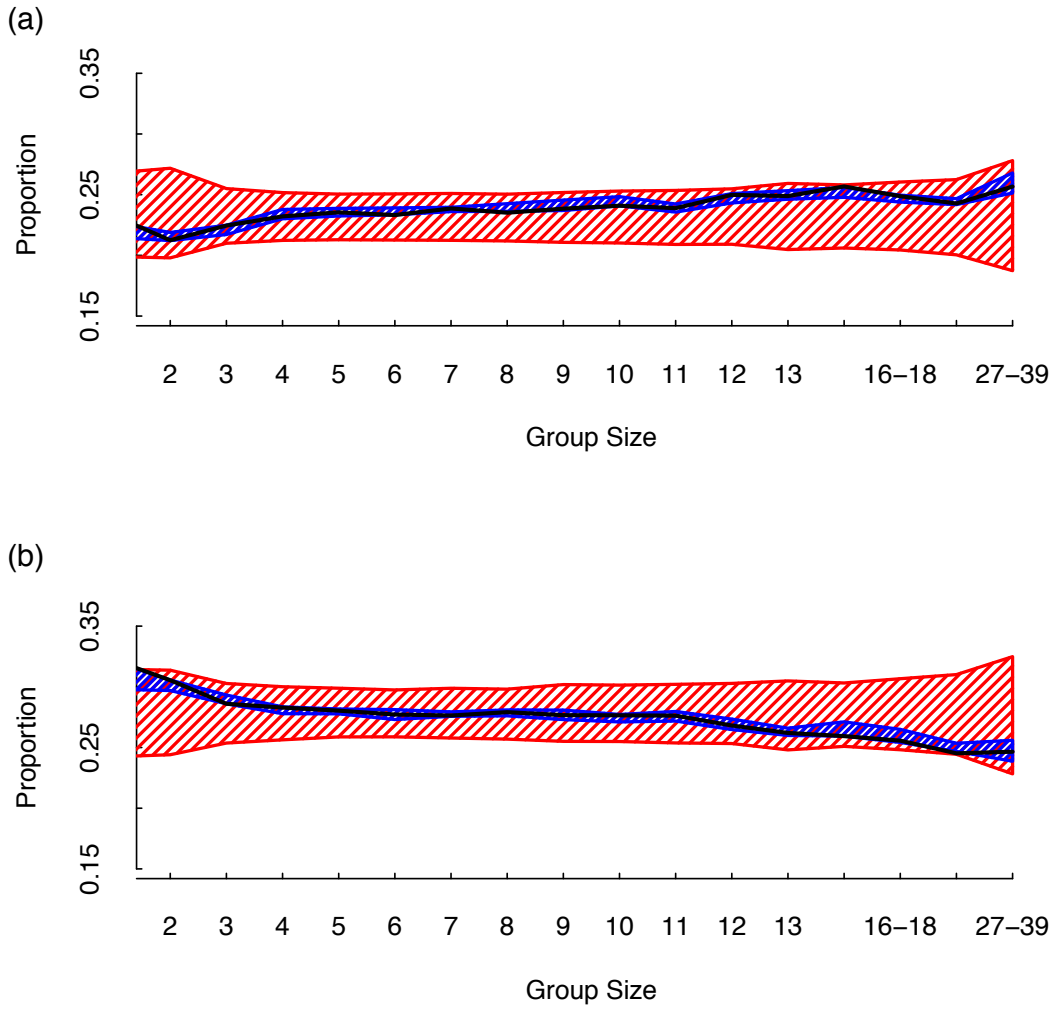


Figure S2: The proportion of a) Juvenile males & b) Adult females in the observed data match that expected from both the phenotypic randomisation null models and the spatiotemporal model.

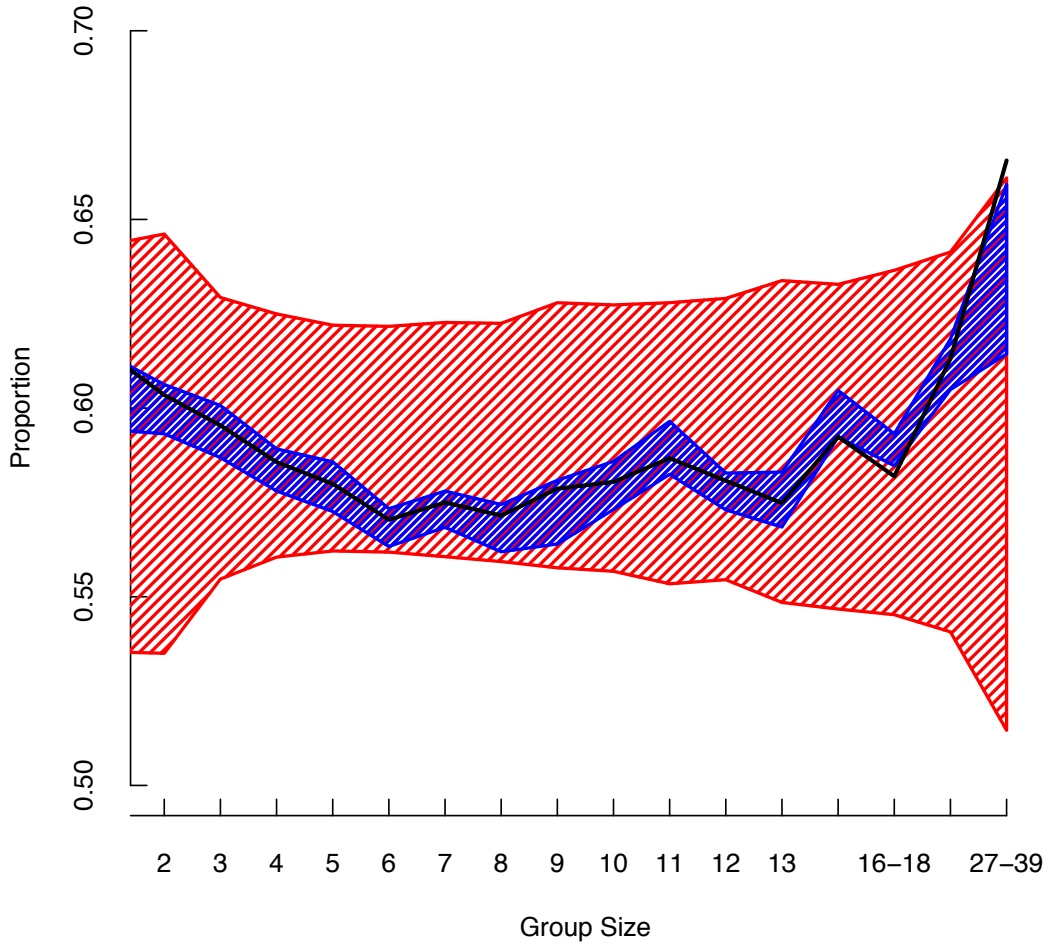


Figure S3: The proportion of adults that are immigrants in all groups matches that expected by both null models.

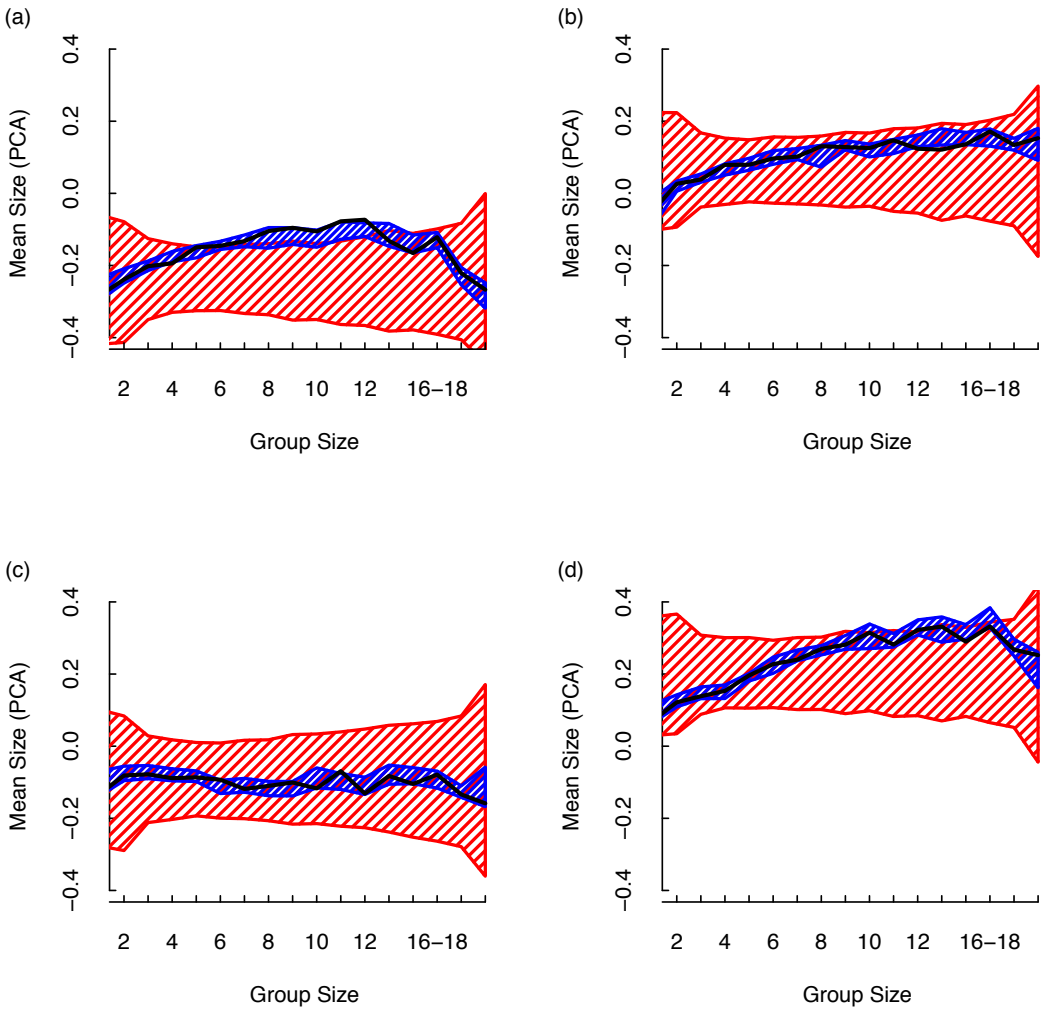


Figure S4: The mean size (PCA1 – see Methods) of individuals within a group for the four classes; (a) Juvenile Male, (b) Adult Female, (c) Juvenile Female, (d) Adult Male. In all cases, the observed data matches the null models, apart from JM, where mid-sized groups (6-12 individuals) contains individuals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

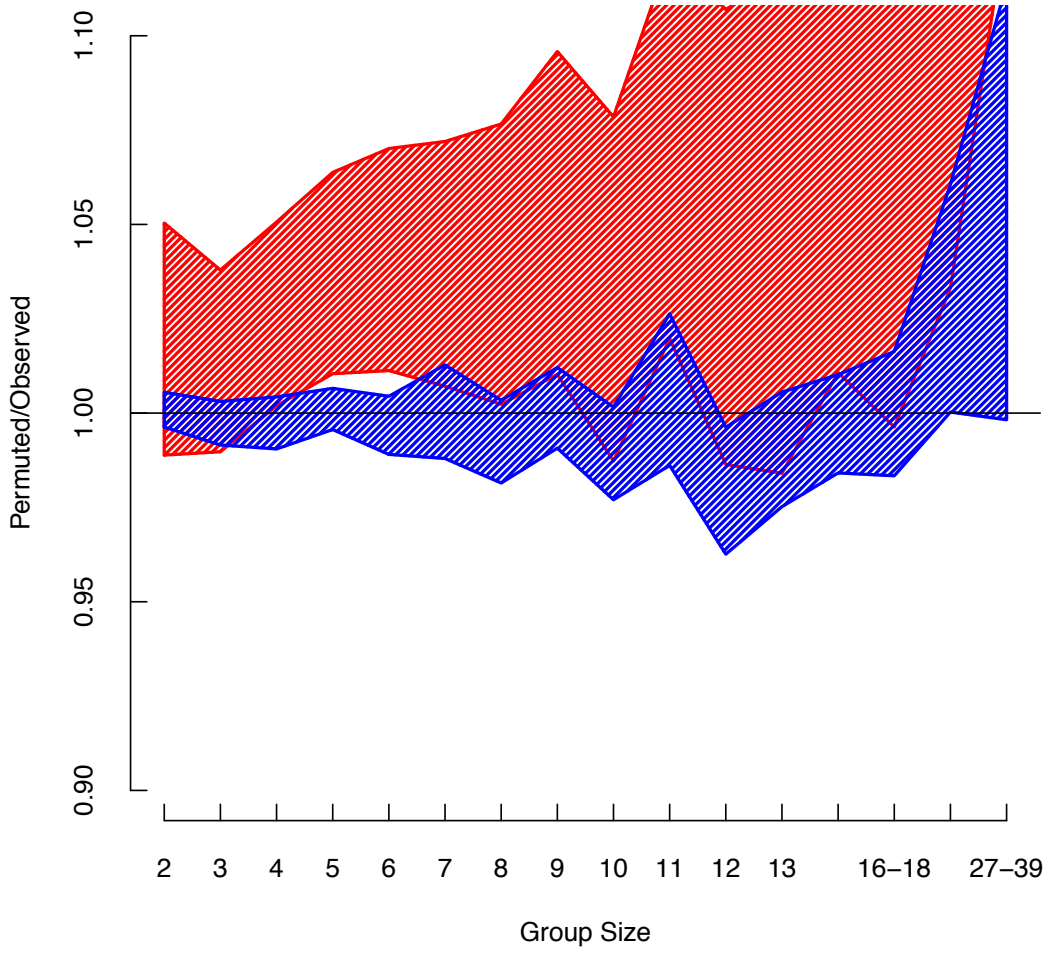


Figure S5: Assortativity for residency status. Over all group sizes, the observed data is very similar to the spatiotemporally controlled null model. However, the observed residency assortativity for groups between 4-9 individuals appeared higher than that expected by the phenotypic randomisation model.

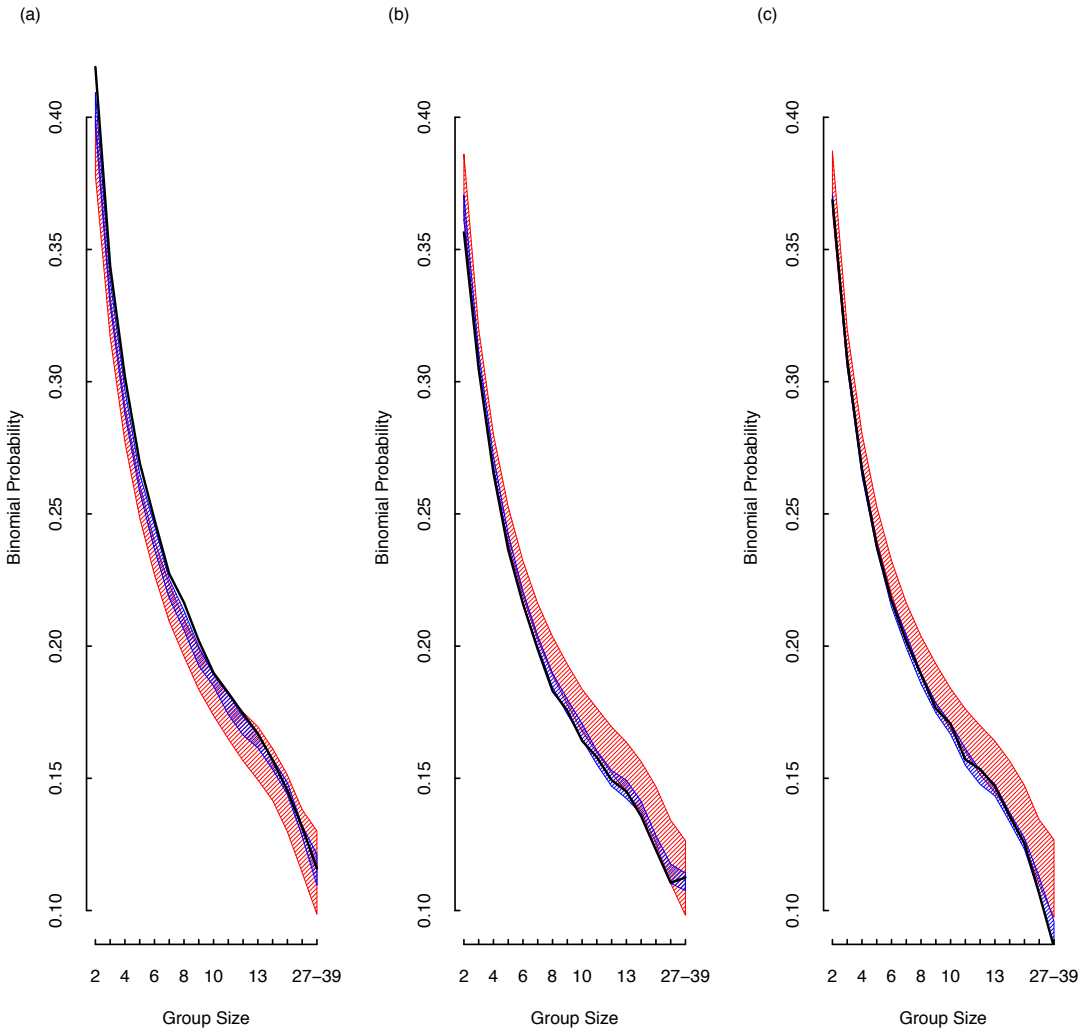


Figure S6: Observed, spatiotemporal controlled null model, and phenotypically random null model binomial probabilities (i.e. Assortativity index) for a) Sex, b) Age and c) Residency Status, over the different group sizes. This data is presented in the manuscript as Permuted/Observed values, due to the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

Chapter 3

Social carry-over effects underpin trans-seasonally linked structure in a wild bird population

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LETTER

Social carry-over effects underpin trans-seasonally linked structure in a wild bird population

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Abstract

Spatial structure underpins numerous population processes by determining the environment individuals' experience and which other individuals they encounter. Yet, how the social landscape influences individuals' spatial decisions remains largely unexplored. Wild great tits (*Parus major*) form freely moving winter flocks, but choose a single location to establish a breeding territory over the spring. We demonstrate that individuals' winter social associations carry-over into their subsequent spatial decisions, as individuals breed nearer to those they were most associated with during winter. Further, they also form territory boundaries with their closest winter associates, irrespective of breeding distance. These findings were consistent across years, and among all demographic classes, suggesting that such social carry-over effects may be general. Thus, prior social structure can shape the spatial proximity, and fine-scale arrangement, of breeding individuals. In this way, social networks can influence a wide range of processes linked to individuals' breeding locations, including other social interactions themselves.

Keywords

Carry-over effects, habitat selection, social networks, social relationships, spatial structure, territory choice.

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INTRODUCTION

The spatial structure within populations is an important aspect of many biological processes (Tilman & Kareiva 1997; Lion & van Baalen 2008). For example, fine-scale spatial positions of individuals within heterogeneous landscapes can govern the environmentally imposed selection pressures they face (Blondel *et al*. 1999; Richardson *et al*. 2014; Hadfield 2016). Further, the heritability of phenotypic traits, and thus responses to selection, can also vary over small scales (Garant *et al*. 2005), and therefore spatial structure can have consequences for adaptation over time.

An individual's spatial position also determines which other individuals it encounters, thereby influencing its social environment (Crook 1970). Therefore, where individuals are spatially located shapes processes dependent on social interactions, such as cooperation (Nowak & May 1992; Lion & van Baalen 2008) and mating (Emlen & Oring 1977). For instance, individuals inhabiting areas where they encounter conspecifics more often may thus experience a higher intensity of sexual selection (Taff *et al*. 2013), and males may increase their reproductive success if their local competitors are systematically less-competitive individuals (Oh & Badyaev 2010; Farine & Sheldon 2015).

Despite its broad significance for a wide range of ecological processes, elucidating the drivers of individuals' spatial distributions with respect to one another is challenging. It has previously been recognised that individuals may base themselves in areas that best suit their own attributes (Clobert *et al*. 2009; Wey *et al*. 2015) and base their decisions on external environmental features, such as habitat quality and predation risk (Cody 1985), and local population factors, such as mating opportunities and competition (Clobert *et al*. 2001, 2004; Bowler & Benton 2005). Yet, how social associations between individuals (the social landscape) shapes where they locate themselves remains largely unknown (Shizuka *et al*. 2014; Wey *et al*. 2015).

Individuals may benefit from positioning themselves near familiar individuals, as close social associates offer potential benefits, such as access to information (Lachlan *et al*. 1998; Aplin *et al*. 2012; Firth *et al*. 2016), reduced aggression (Temeles 1994) and increased reciprocation of cooperation (Croft *et al*. 2006; Grabowska-Zhang *et al*. 2012a; Carter & Wilkinson 2013). This may result in fitness benefits of holding strong social connections to local individuals; previous examples include increased growth in fish species (Hojesjo *et al*. 1998; Seppa *et al*. 2001) and improved reproductive output of birds (Beletsky & Orians 1989; Grabowska-Zhang *et al*. 2012b). In this way, selection may act to shape individuals' choice of spatial location around their close social associates. Elucidating this process would aid in understanding both the importance of maintaining social associations, as well as how social associations can underpin future fine-scale spatial positioning and the resultant consequences of this.

As with many other bird species, great tits (*Parus major*) choose a single spatial location for nesting, egg laying, incubation and raising their brood over the breeding season. Breeding positioning is also known to profoundly influence various ecological processes (Chalfoun & Schmidt 2012), and previous research within our study population has demonstrated relationships with mating, cooperative interactions, response to selection, phenology and timing of breeding (Garant *et al*. 2005; Grabowska-Zhang *et al*. 2012a; Patrick *et al*. 2012; Cole *et al*. 2015; Firth *et al*. 2015a; Hinks *et al*. 2015). Yet, as with

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other ecological systems, the underlying forces driving fine-scale spatial structure remain largely unexplored. Here, we monitored winter social associations among wild great tits, as individuals join flocks and move relatively freely around the woodland. We assess how these social networks, formed when individuals are not required to base themselves at a fixed position, carry-over into shaping the set locations at which they breed during the spring. Hence, we determine how prior social structure relates to future spatial positioning, to understand the potential importance of previous social associations and the possible implications for processes governed by population spatial structure.

MATERIAL AND METHODS

Study system

The work was carried out in Wytham Woods, Oxford, UK (51°46′ N, 1°20′ W), on a great tit population that has been monitored using standardised protocols since the 1960s (Perrins 1965). The great tits breed almost exclusively in the nestboxes located in 1020 fixed positions with known GPS coordinates throughout the woodland (Wilkin *et al*. 2006, 2007). Most breeding birds (> 98%) are only recorded at one nestbox in any single year, and their breeding attempt consists of nest building, egg laying, incubation and offspring rearing, which spans the breeding season from April to July. During this time, nestboxes are visited regularly to record breeding attempts and identify adults (between days 6 and 14 of the nestling phase) and mark nestlings (on day 15) with a unique BTO (British Trust for Ornithology) metal leg ring and record standard morphometric information.

Throughout the winter season (September–March), great tits aggregate to form roving feeding flocks (Hinde 1952) that show considerable turn-over as different birds leave and join frequently, as flocks display high 'fission-fusion' dynamics (Farine *et al*. 2015). Since 2007, plastic leg rings containing unique RFID-microchips have been fitted to all great tits captured either during breeding or through winter mist-netting. This results in ~ 90% of the population being tagged (Aplin *et al*. 2013). The RFID tags allow detection of times and locations of individuals' occurrence at sunflower feeding stations equipped with two RFID-antennae (Dorset ID, Aalten, The Netherlands) placed in 65 locations in a stratified grid. In winters beginning 2011, 2012, and 2013, the feeders opened every weekend from December until the end of February (13 weekends), scanning for RFID tags from visiting birds from predawn to post-dusk.

Winter population social structure

The feeding stations' detections of RFID tagged birds generate a spatio-temporal data-stream consisting of bursts of activity as flocks arrive and feed. Each detection was then statistically assigned to the flock, or 'gathering event', it most likely belonged to using a machine-learning algorithm (Psorakis *et al*. 2012). This method is robust, effective for determining flock co-memberships, and performs significantly better than alternative methods such as using arbitrary time windows to define co-occurrence (Psorakis *et al*. 2015). From the flock co-memberships, social networks (association matrices) were constructed in R 3.2.2 (R Core Team 2015) using the Simple Ratio Index (Cairns & Schwager 1987) defined here as follows: $S_{AB} = \frac{x}{x+y_{AB}+y_A+y_B}$, where S_{AB} is the social association between bird A and B, x is the number of times they co-occurred in the same flock and y_{AB} is the number of times they were both detected at the same time but not together. y_A is the number of flocks that A occurred in without B over the time period both were known to be in the system, and y_B is the number of flocks that B occurred in without A over this period.

Social networks were created on a yearly (whole winter) basis, to measure the propensity of dyads to associate, as well as per weekend (i.e. per sampling period) to quantify co-occurrence during weekly intervals. We used non-directional weighted networks throughout our analyses that, along with the extensive sampling, reduces the limitations arising from employing a 'gambit of the group' approach (Franks *et al*. 2010). Social networks were built using all individuals, but in further analysis, we only considered breeding individuals. While mated pairs were included in the analysis, we excluded the dyadic association between partners, as these have strong social associations (Psorakis *et al*. 2012; Firth *et al*. 2015b) and share a breeding location. Due to high population turnover and individual movement, kin structure was very weak (< 1.5% of winter social connections were between first-order relatives); therefore, relatedness was not considered in any of the analysis.

Carry-over of winter social networks into breeding spatial proximity

We aimed to assess whether increased social associations between birds during the winter related to closer spatial proximity of their breeding positions in the subsequent spring. We assessed spatial proximity in two ways. First, we calculated Euclidean distance between each nestbox location and used the reciprocal of this as a measure of proximity. Second, we determined the ranked proximity between each box, including only nests containing eggs (i.e. occupied boxes), to establish the relative closeness of the surrounding individuals given the local breeding density. We then examined the ability of the winter social association matrix to predict the subsequent breeding proximity matrix.

As with any social network analysis, spatial and social effects are likely to be related. An individual's choice of winter spatial location will influence both which birds they associate with, as well as their subsequent breeding location. In order to separate social and spatial effects, following previous work (Shizuka *et al*. 2014; Firth & Sheldon 2015), we used two, complementary, approaches, namely (1) null models and (2) Multiple Regression Quadratic Assignment Procedure (MRQAP). In this way, we assess how dynamic winter social preferences *within* individuals' winter spatial locations predict subsequent spatial positioning of individuals' breeding decisions. Further, we also examined (3) how individuals' characteristics may influence this relationship. As social preferences themselves may potentially influence winter spatial decisions, both methods of controlling for winter spatial occurrence

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represent a conservative approach to examining the influence of social associations (Shizuka *et al*. 2014; Aplin *et al*. 2015).

Spatial null model. For each year separately, we used mantel tests (Smouse *et al*. 1986) to determine the correlation between the previous winter's social association matrix and the subsequent breeding proximity matrix. We then determined how this compared to that expected from individuals' winter spatial locations alone. Specifically, if individuals remain and breed at the same location as that they occupy at the end of the winter, this may cause them to breed close to others that also occurred there during the winter. Therefore, we used a null model that controlled for this winter spatial process (see Supplementary Information). In each permutation of the null model, each individual's social network position was randomly reassigned to another individual that had also been observed in the same final winter location as them (Fig. S1). Following this reassignment, the correlation between this permuted social network and the observed breeding proximity matrix was recalculated. Thus, each permutation maintained the overall social network structure and individuals' winter spatial locations but reassigned their dyadic social associations within this. We repeated the permutation procedure 1000 times, and hence derived the distribution of the correlation expected between winter social associations and breeding proximity given individuals' winter spatial locations alone. By comparing this empirically generated expected distribution to the observed correlation between the social network and breeding proximity matrix, we were able to infer the additional influence of dyadic social associations on breeding proximity, over and above that expected from winter spatial structure. Specifically, if the observed test statistic (in this case, Mantel test correlation) fell outside the 95% range of those generated from the permutations, this indicated a statistically significant effect.

Matrix regression models. We also used MRQAP (Dekker *et al*. 2007) to quantify how winter social associations related to subsequent breeding proximity given winter spatial factors. This approach has previously been used to separate the effects of winter social structure and winter spatial range overlap (Shizuka *et al*. 2014; Firth & Sheldon 2015), as it allows a single-dependent matrix to be regressed against multiple 'predictor' matrices. Therefore, we examined how subsequent breeding proximity was simultaneously predicted by the winter social association matrix and the winter spatial overlap matrix. The winter spatial overlap was based on the activity of each individual at each feeding station and ranged from 0 to 1, where dyads for which spatial activity patterns fully overlapped would score 1, whilst those that never occurred in the same place would score 0. Specifically, winter spatial overlap for each dyad was calculated as the sum, over all locations, of the minimum proportion of activity that either member spent at each location (see Supplementary Information for details).

Individual traits. We considered that the relationship between winter social associations and subsequent breeding proximity might differ depending on the type of individuals considered. In all cases, we used a general linear mixed model (GLMM) structure, which set the dependent variable as the subsequent breeding proximity between each dyad and fitted winter social association strength, year and other effects specific to the question of interest (see below) as predictor variables. Random effects of both individuals' identities and their nestboxes were also included. For each model, to determine the effect of winter association strength on subsequent breeding proximity in comparison to that expected from individuals' winter spatial locations, we carried out the GLMM 1000 times, but each time using a set of dyadic winter social association strength values generated from the spatial null model. The distribution of coefficients derived from these models illustrates that expected by individuals' winter spatial locations alone. Therefore, if the coefficient from the observed data fell outside the 95% range of this distribution, the effect was judged statistically significantly different to that expected from individuals' winter spatial locations. Three types of individual characteristic were considered.

First, as breeding proximity relates to mating opportunities (Patrick *et al*. 2012; Firth *et al*. 2015a), whether a dyad is of the same or opposite sex may influence how prior social association relates to subsequent breeding proximity. Therefore, we additionally included a factor indicating whether each dyad was same sex or opposite sex, along with its interaction with winter social association.

Second, adult birds' breeding proximity may be influenced by their breeding locations in the previous year, particularly if individuals remain in the same locations over years. Therefore, we assessed whether winter social associations remained an important predictor variable of subsequent breeding proximity, even given prior breeding positions, by including previous breeding proximity as a predictor variable in the model (which considered only adults that had bred the previous year).

Finally, individuals that were observed at only a single foraging location throughout the winter might be expected to hold strong social associations to others who remained there over winter, as well as to subsequently breed there. Therefore, we also carried out the GLMM but only including dyadic associations between individuals occurring at the same single location as one another all winter. This allowed us to directly assess whether individuals choose to breed closer to the ones those were most associated with even within a single winter location.

Carry-over of winter social networks into breeding spatial arrangements

The spatial arrangement of individuals' territories (i.e. which individuals share boundaries) has been shown to be important in this population (Wilkin *et al*. 2006, 2007; Grabowska-Zhang *et al*. 2012b; Hinks *et al*. 2015). Indeed, even given dyads of equal breeding proximity to one another, those that share territory boundaries (defined here as 'neighbours') may be more likely to encounter/interact with each other during the breeding season than those who do not (defined as 'non-neighbours'). Therefore, we tested whether, controlling for

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breeding proximity, breeding individuals were more likely to share territory boundaries with those that they had closely associated with in the preceding winter.

We created Thiessen polygons (voronoi diagrams) around each occupied nestbox that encompassed the area closer to it than to any other occupied box (Aurenhammer 1991). Territories created using this method correlate highly with mapped territory size and neighbours, and are known to be biologically meaningful in terms of local population density and breeding success (Adams 2001; Wilkin *et al*. 2006; Valcu & Kempenaers 2008; Grabowska-Zhang *et al*. 2012a; Schlicht *et al*. 2014). In this way, we defined which individuals were 'neighbours' (i.e. shared a territory boundary), and therefore may be more likely to interact with each other than indicated by proximity alone.

On average, however, neighbours are also more proximate than non-neighbours. Therefore, for each individual, we found all other individuals that fell within the boundaries of an annulus set by distances to their closest non-neighbour and their furthest neighbour (Fig. S2). This yields the set of individuals that were within a distance range to be potentially either neighbours or non-neighbours for each focal individual. Using only these dyads, we used a GLMM to determine whether individuals were more strongly associated in winter with their subsequent neighbours than with their non-neighbours, even after controlling for their breeding proximity. We set each individual's winter social associations to other individuals whose breeding locations fell within this annulus as the dependent variable and fitted fixed effects of breeding proximity, a binary indicator of whether or not the individuals were breeding neighbours, and year. Random effects of both individuals' identities and their nestboxes were also included. By including both of these breeding spatial terms within the model, we were able to examine whether neighbours had stronger prior winter social associations than non-neighbours of an equal breeding proximity. Again, we repeated this GLMM for each permuted data set, so in each case, the observed social associations between an individual and those that fell within the specified boundary were replaced with the winter social associations generated from the spatial null model. We then the compared the range of the resultant coefficients of the binary 'neighbour indicator' from these models to the coefficient calculated from the observed data.

Finally, we calculated individuals' mean social associations to their future breeding neighbours from each of the separate weekly social networks and examined whether individuals' social associations to their future breeding neighbours changed through the preceding winter. We then compared the observed value of individuals' social associations to their future neighbours to the values generated from the spatial null model for each weekly social network.

RESULTS

The winter social networks consisted of 1092, 721, and 809 individuals (in 2012, 2013, and 2014. respectively) observed over large numbers of flocks (2012 = 73 364; 2013 = 65 095; 2014 = 64 629). The majority of breeding birds had been observed in the previous winter network (~ 75%). Breeding individuals were recorded (on average: mean ± SE), on 10.5 ± 0.1 weekends at 3.5 ± 0.1 different feeding sites, with 13.9 ± 0.5 movements between sites over the 3-month winter period (December–February).

Winter social networks carry-over into breeding spatial proximity

Individuals generally bred closer to birds they had held stronger social associations with during the previous winter (Fig. 1a; Fig. S3). Indeed, across all years, winter social associations strongly predicted subsequent breeding proximity (Mantel r ~ 0.60; Fig. 1b). By carrying out permutations which re-assigned individuals' social network positions within their winter spatial locations (i.e. the spatial null model), we found that winter spatial structuring contributed to the correlation between winter social networks and subsequent breeding proximity (Mantel r 0.44–0.52; Fig. 1b). However, as predicted, this relationship was significantly weaker than the observed carry-over between prior social associations and future breeding positions (all years: $P < 0.001$, Fig. 1b). This demonstrates that the tightness of the social association between individuals related to how close their chosen breeding locations were to one another, over and above that expected from their winter spatial locations. This is particularly notable as the spatial null model was found to be highly conservative and generated social structure that was largely similar to the observed social networks (Fig. S4).

We found supporting results when the matrix denoting subsequent breeding proximity between individuals was regressed against matrices denoting (1) the winter social associations and (2) the winter dyadic spatial overlap, using MRQAP analysis. Individuals' winter spatial overlap significantly contributed to subsequent breeding proximity, yet even after accounting for this, the strength of fine-scale social associations between dyads was a highly significant predictor of their breeding proximity (Table 1).

We employed GLMMs to assess whether the positive relationship between winter social associations and subsequent breeding proximity may differ depending on the dyads considered. First, sex differences did not influence how winter social associations predicted breeding proximity, as there was no significant interaction between a factor indicating whether individuals were of the same or opposite sex and their winter social association strength on their subsequent breeding proximity (coefficient = − 0.001, $P_{null} = 0.237$ – Table S2a).

Second, we considered the influence of the previous year's breeding positions. In each breeding season, a small proportion of individuals had bred in the same location the previous year (~ 12%), and only ~ 0.5% of neighbours were neighbours the previous year due to remaining in the same locations. Nevertheless, in general, adult birds' breeding positions in the previous year were found to be related to the following winter's social associations and the subsequent year's breeding proximity (Table S3). However, when controlling for adults' breeding proximity to one another from the previous year, their social associations during the following winter remained a highly significant predictor of their subsequent breeding proximity (coefficient = 0.015, $P_{null} < 0.001$ – Table S2b).

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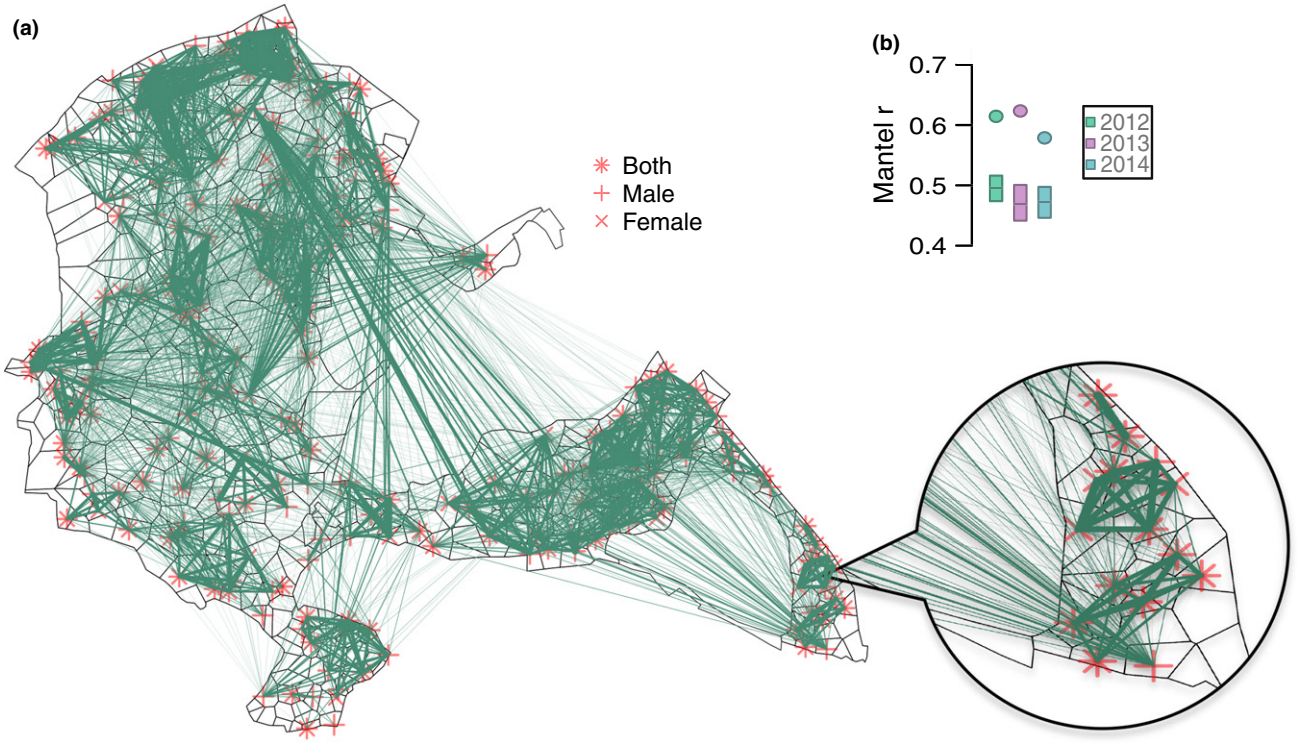


Figure 1 a) Illustrative breeding positions and winter social network of great tits from 1 year (2012) in Wytham Woods. Black dividing lines show the inferred territory boundaries around each individuals breeding location. Points show breeding sites of birds recorded in winter social network (star = both parents, cross = male, 'X' = female). Adjoining lines represent social associations recorded in the previous winter, and line thickness illustrates strength of association (mean strength is displayed for boxes where both parents were included). A section has been enlarged for clarity. b) Mantel r test statistic assessing the relationship between winter social networks and subsequent breeding proximity matrices. Circles show the observed statistic and boxes show the 95% range of statistics calculated from the spatial null model (mid-lines illustrate mean of these). Proximity is calculated from Euclidean distance. See Fig. S5 for ranked proximity and mantel tests for each class of individuals separately.

Similarly, for juvenile birds, the winter social associations formed in their first year predicted the proximity of their first breeding attempts (coefficient = 0.046, $P_{null} < 0.001$).

Finally, some individuals (~ 16%) foraged at a single feeding location all winter. By considering dyads that remained at the same, single, location as one another, we found that individuals subsequently bred closer to those they held stronger winter social associations to (coefficient = 0.033, $P_{null} < 0.001$ – Table S2c). Therefore, even within a single winter location, fine-scale winter social association strength between dyads increased their subsequent breeding proximity.

Regardless of the type of individuals or dyads considered or methods used, it was consistently found that individuals subsequently bred closer to those they were most socially associated with during the winter, over and above that expected from their winter spatial locations (Table S2; Fig. S5).

Table 1 Results of MRQAP tests. (a) Subsequent breeding season proximity (expressed as the reciprocal of Euclidean distance in metres) between individuals is significantly predicted by both their winter spatial overlap and their winter social associations prior to it. (b) Ranked version of proximity (to control for local breeding density) is also related to these two covariates

Response	Year	Covariate	Coefficient	*P*	Full R^2
(a) Euclidean distance	2012	Spatial overlap	0.0073	0.001	0.4310
		Social association	0.0106	0.001	
	2013	Spatial overlap	0.0062	0.001	0.4370
		Social association	0.0135	0.001	
	2014	Spatial overlap	0.0078	0.001	0.4126
		Social association	0.0037	0.001	
(b) Ranked proximity	2012	Spatial overlap	0.1203	0.001	0.3922
		Social association	0.3784	0.001	
	2013	Spatial overlap	0.1378	0.001	0.3971
		Social association	0.3340	0.001	
	2014	Spatial overlap	0.1727	0.001	0.3825
		Social association	0.2189	0.001	

Winter social networks shape breeding spatial arrangements

Along with subsequently breeding closer to their winter social associates, individuals could also arrange themselves so that they share breeding territory boundaries with those they had associated most with over the winter. Therefore, we tested whether individuals had held stronger winter social associations to birds they formed a breeding territory boundary with (i.e. their 'neighbours') than birds that bred the same distance away but with which they did not share a boundary (i.e. their 'non-neighbours').

We found that considering dyads that subsequently bred within the range to be neighbours or non-neighbours (Fig. S2), there were significantly stronger winter social associations between neighbours than between non-neighbours – even when controlling for the effect of winter social

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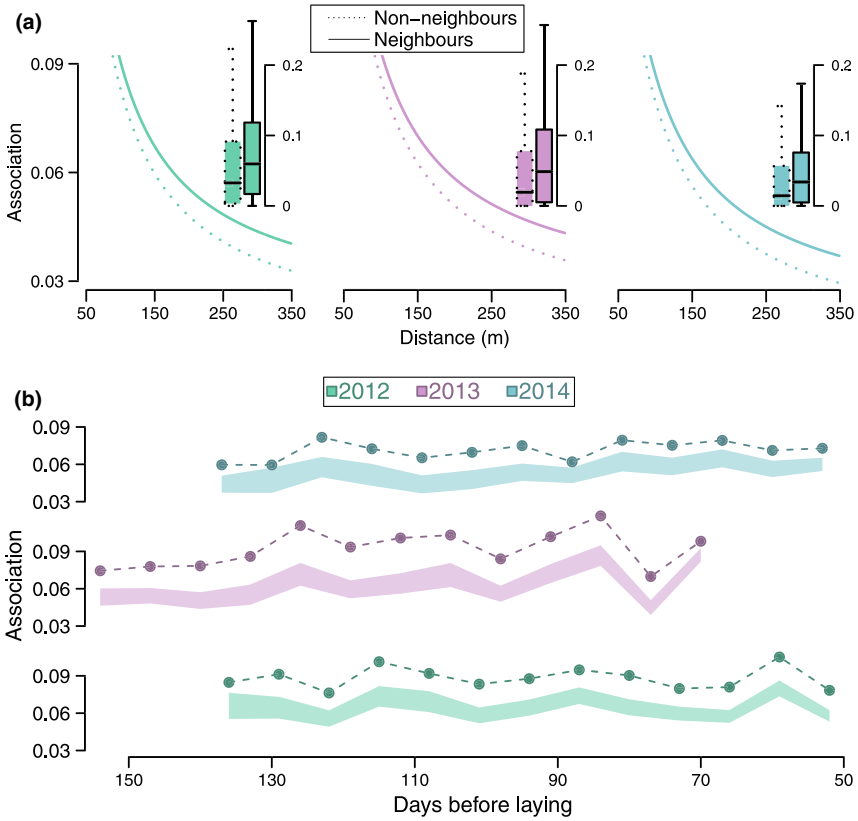


Figure 2 a) Relationship between winter social association strength and subsequent breeding distance for subsequent neighbours (solid lines) and non-neighbours (dotted lines). Lines are based on the GLMM (see Table S4 for details) and colour denotes year. Box plots show each individual's winter social association to subsequent non-neighbours (dotted – left) and neighbours (solid – right) within the range of their closest non-neighbour and furthest neighbour (Fig. S2). Mid-lines show median, box shows interquartile range (IQR), whiskers shows range (with values outside 1.5 times IQR excluded). b) The average winter social association strength individuals held to their subsequent neighbours at each sampling period (weekend) prior to it. Only social associations between subsequent neighbours are considered. *X*-axis shows the number of days before the mean lay date in the following breeding season. Circles show the observed average winter association strength, and polygons show the 95% range calculated from the spatial null model.

associations on breeding proximity (Fig. 2a). Thus, while individuals bred nearer to their closest winter associates, there was an additional effect of being more likely to share a territory boundary, and this was not driven by winter spatial locations (coefficient = 0.0075, SE = 0.002; $P_{null} > 0.01$; Fig. 2a; Table S4). Therefore, the boundary arrangements between territorial neighbours also reflected the prior winter social associations, more so than expected by breeding proximity or prior winter locations.

Indeed, winter social associations between subsequent breeding neighbours were particularly strong, and accounted for almost one-third of the sum of all social associations over the entire winter social networks (2012 = 28%, 2013 = 32%, 2014 = 30%). Winter social associations between neighbours were also significantly stronger than expected from individuals' winter spatial positions, with a 1.7-fold higher association strength than that generated by the spatial null model (Fig. 2b; Fig. S6). Strikingly, from early winter (even up to 150 days prior to the breeding season), individuals were more strongly socially associated to their subsequent breeding neighbours than expected under the spatial null model (Fig. 2b). This effect was maintained as the breeding season drew nearer, illustrating how temporally distant winter social association patterns can be important in predicting the subsequent spatial arrangement of individuals during breeding.

DISCUSSION

We demonstrate that prior social networks have trans-seasonal carry-over effects onto subsequent spatial structure within a wild bird population. Specifically, great tits' winter social associations, as they forage in freely moving flocks, are related to their long-term spatial decisions regarding who they breed next to in the subsequent spring. By carrying-over into future spatial structure, previous social structure may also be important to various processes that depend on individuals' locations and the environmental setting they experience. For instance in this study population, the relationship of winter social networks with subsequent breeding positions might have numerous consequences, as breeding structure is known to underpin both ecological (Garant *et al.* 2005; Cole *et al.* 2015; Hinks *et al.* 2015) and social processes (Grabowska-Zhang *et al.* 2012a; Patrick *et al.* 2012; Firth *et al.* 2015a).

Individuals' spatial positions determine not only the environmental conditions they experience but also their social setting. Therefore, when these choices are fixed over a period

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important to reproductive success, individuals may benefit from choosing locations based on their previous social associations. For instance, maintaining stable social associations can promote reciprocation of cooperative interactions (Croft *et al*. 2006; Carter & Wilkinson 2013). Indeed, within breeding great tits, familiar birds are more likely to cooperate in predator mobbing (Grabowska-Zhang *et al*. 2012a). Positioning oneself close to social associates may also reduce energy expenditure on competitive interactions, if individuals display less aggressive behaviours towards familiar neighbours (Temeles 1994). Breeding male birds, for example, appear to have more dissimilar song rates to surrounding individuals who they are more associated with (Foote *et al*. 2008; Snijders *et al*. 2015), potentially due to attempting to reduce competitive interference. Similarly, great tits may experience increased reproductive success under conditions of reduced competition with familiar neighbours (Grabowska-Zhang *et al*. 2012b). Therefore, the potential benefits between close social associates may cause individuals to subsequently breed closer to (Fig. 1, Table 1), and share a territory boundary with (Fig. 2), those they were more strongly associated to during the winter.

While previous research has demonstrated that mated partners shape each other's foraging locations (Firth *et al*. 2015b), here we show that a link between sociality and spatial structure can become fixed over a long period and be driven by more subtle social relationships, as social associations to other flock members, even from early in the winter (Fig. 2b), predicted subsequent long-term breeding locations. This finding may offer an explanation for why breeding location choices sometimes appear to be suboptimal in terms of the habitat (Chalfoun & Schmidt 2012), as such decisions may not be solely based on the features of the external environment, but also depend on the suitability of the fine-scale social landscape. Further work that assesses how individuals balance environmental and social factors when making spatial choices, along with quantifying the relative fitness benefits of positioning themselves around their previous social associates, would now be particularly informative.

Breeding near prior social associates may also potentially result in increased matings between neighbouring individuals, as prior social associations may increase attractiveness (Choudhury & Black 1994). But, the relationship between winter social associations and subsequent breeding positions was not related to sex differences (Table S2a) and also occurred between same-sex dyads (Fig. S5; Fig. S6). In fact, over all years and all classes of individuals (sex, age and movement patterns), winter social networks between individuals consistently predicted their subsequent breeding proximities and neighbours more than their winter spatial locations alone (Fig. S5; Fig. S6). For adult birds, winter social association predicted their future breeding proximity (Fig. S5; Fig. S6). This remained the case even when additionally controlling for their spatial positions in the previous breeding season (Table S2b), which can also influence winter social associations (Table S3). Similarly, birds that foraged in the same set location as one another all winter also subsequently bred closer to, and were more likely to form territory boundaries with, those they had held the strongest winter social connections with (Table S4; Fig. S5; Fig. S6). This suggests that the potential benefits of a trans-seasonal carry-over of previous social associations onto future spatial positioning are not only relatively broad but also strong enough that the effects are detected even after accounting for various individual and spatial factors.

Finding consistent and clear effects of winter social associations on subsequent breeding spatial arrangements after controlling for spatial factors is particularly striking when, as discussed in previous work (Shizuka *et al*. 2014; Aplin *et al*. 2015), an individuals' winter spatial location may also be driven by their social preferences. Disentangling social and spatial choices is challenging (Shizuka *et al*. 2014). However, we demonstrate a pronounced relationship between social associations and spatial decisions. Further, we provide this evidence in the particularly important context of spatial positioning of breeding attempts, where such decisions are fixed over a long and crucial time period, and the operation of various conspecific interactions, such as cooperation, competition and mating, depends on a single spatial choice.

In light of the evidence presented here, caution may be needed when accounting for spatial proximity in certain analyses. For example, if females of a certain type mate with males of a certain type, but also occur nearest to these individuals, controlling for distance might lead to a conclusion of no active mating choice, even if females' location choices are based on their preference for particular males. Through failing to recognise that observed spatial structure may itself be a product of individuals' social preferences, spatial terms fitted within a model may actually partly capture processes of interest.

Furthering the understanding of population spatial structure has various potential uses for conservation biology (Ferriere *et al*. 2004), and therefore, the findings of this study may have practical implications. For instance, playing conspecifics' calls is a conservation strategy used to attract target bird species to particular breeding sites when attempting to minimise adverse effects of anthropogenic activity (Ward & Schlossberg 2004; Ahlering & Faaborg 2006). However, if individuals choose to breed near their previous social associates, simulating conspecific calls that are likely to be familiar may further increase the effectiveness of this approach. Indeed, increasing knowledge of nesting-site decisions is beneficial for applied work aiming to improving avian species population viability (Chalfoun & Schmidt 2012).

To conclude, we demonstrate that spatial structure during breeding, when individuals make a fixed decision on a long-term location, is underpinned by prior social associations occurring as individuals take part in loose, freely moving, foraging flocks over winter. Prior social networks may also, therefore, carry-over into various population-level processes through shaping individuals' future environmental and social settings. Further research that directly manipulates social behaviour (Firth & Sheldon 2015) to assess the extent of the causal effect of social associations on subsequent breeding locations would be valuable. Indeed, revealing the long-term benefits and causal implications of holding social associations is of vital importance for elucidating the underlying drivers of social dynamics.

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AUTHORSHIP

JAF and BCS designed the study and contributed to data collection. JAF carried out the analysis and wrote the first draft and BCS contributed substantially to revisions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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SUPPLEMENTARY INFORMATION: Social carry-over effects underpin trans-seasonally linked structure in a wild bird population

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Supplementary Information – Additional Details:

(a) Spatial null model

As social data are inherently non-independent, null models are widely utilised in animal social network analysis (Whitehead 2008; Croft *et al.* 2011). In particularly, null models are often used for separating out the contribution of the social preferences and the spatial distribution of individuals (Whitehead 2008; Shizuka et al. 2014; Aplin et al. 2015; Farine et al. 2015).

We aimed to assess how individuals' winter social associations related to their subsequent breeding proximity to one another. However, as the study was carried out over a large spatial scale, it is likely that the spatial location of an individual during the winter will influence their winter social associations (as they form flocks with individuals in the same area) and their breeding position (as we would not expect a random redistributing of individuals after the winter). Specifically, if individuals remain in their same location at the end of the winter for breeding, this may cause them to breed close to others who also occurred there during the winter. In turn, this would result in individuals breeding near to those they were likely to have formed winter flocks with, and therefore a relationship between winter social associations and subsequent breeding positions would arise due to individuals' spatial locations/preferences.

Therefore, we used a null model to determine the extent of the relationship between winter social associations and subsequent breeding positions that may be expected under this spatial process alone (Fig. S1). If the observed relationship between winter social associations and subsequent breeding positions was significantly larger than the one generated by this spatial process alone, we can conclude that the relationship is not just driven by winter spatial distribution of individuals, and therefore this suggests that active social preferences are contributing to this relationship.

Each permutation of the null model began by assigning each individual to the winter location (feeding station) they were last observed before the breeding season began (89% of individuals were observed in the final sampling period, 98% in the final month). For individuals observed in multiple locations during their last period (45%), in each permutation, the probability of assignment to each location

was equal to their activity (proportion of flocks they were observed in) at each feeding station. Positions of individuals within the social network (which are equivalent to the node labels on the social association matrix) were then swapped so that each adopted the identity of another individual with their same assigned winter spatial location (Fig. S1b). A similar permutation process has been used in previous work in this study system (Aplin et al. 2015) to generate permutated social structure whilst controlling for individuals' spatial locations. An advantage of this method, over permuting the raw data, is that the network structure (i.e. actual dyadic values of social association between individuals) remains the same but the identity of individuals' is swapped within spatial locations. Thus, each permutation maintains the network structure and spatial location of individuals, but reassigns the dyadic social associations given these constraints (Fig. S1).

In this way, after we had calculated a statistic of interest assessing the relationship between the observed winter social associations with the subsequent breeding structure (whether this was a mantel test correlation, or a coefficient of a GLMM – see Main Text), we could then carry out the same statistical test 1000 times, but each time replacing the observed winter social associations with one of the 1000 versions of the permuted winter social associations. This generated the distribution of the statistic assessing the relationship between winter social associations and subsequent breeding structure expected under the spatial null model. If the statistic derived from using the observed winter social associations fell outside of the 95% range of the distribution of the null model, it can be inferred that there is a significant effect of fine-scale winter social associations patterns on subsequent breeding positioning, on top of that expected from winter spatial factors and general network structure alone.

As explained above, in each permutation of the null model, the individuals were reassigned to adopt the association patterns of others occurring the same final winter foraging locations as themselves *at random* (Fig. S1). However, some of our analysis specifically considered how the relationship between winter social associations and subsequent breeding positions may differ between individuals of different classes (sex, age, movement patterns). Therefore, in these analysis, in order to control for individual characteristics, we also carried out various versions of the same null model. Again, individuals could only be reassigned to the social association patterns of others in the same winter foraging locations, but with the added restriction that they could only be assigned to those of the same 'class' (i.e. whichever trait was considered) as themselves.

First, we only allowed reassignments within the same sex, thereby examining the males and females separately, as well as reducing any issues arising from non-independence of pair members. Second, swaps were restricted within age classes to enable first-year birds, with no associations from previous breeding seasons, to be assessed separately from adults. Third, to control for individual movement patterns, we carried out swaps between birds that remained at one feeder throughout the winter (termed 'set' birds, which may be expected to hold strong associations with others who remained there), and then between birds that moved locations (termed 'moving' birds).

Finally, as stated previously, the primary null model considers the final winter locations of where each individual was observed, as this is expected to be most strongly related to where they breed, and therefore more conservative method of controlling for spatial factors. However, as part of the supplementary analysis we also carried out the same null model but instead considering the entire winter range of each individual. The process was again the same, but in each permutation each individual was assigned to one of the locations where they were observed over the entire winter (rather than just during their final observation period). Again, the probability of assignment to each location was equal to their activity (proportion of flocks they were observed in) at each feeding station. In this way, in each permutation individuals were most likely to ultimately be reassigned the dyadic social associations of another individual who most often occurred in the same location as themselves (see Aplin et al. 2015). This, however, was shown to be similar to the primary null model considering the final winter locations of individuals (Fig. S4).

(b) Matrix Regression

Multiple Regression Quadratic Assignment Procedure (MRQAP) is a useful technique in network analysis as it allows multiple independent matrices (i.e. x_1 and x_2) to be simultaneously regressed against a single dependent matrix (y_1). In particular, an extension of MRQAP, termed MRQAP with double semi-partialing (MRQAPDSP), allows increased inference of the relationship that y_1 holds with both x_1 and x_2 separately, even when there is strong multicollinearity between the fixed effects (Dekker et al. 2007). For this reason, this is a useful approach for assessing the separate effect of winter social structure and winter spatial overlap (which are often highly correlated) on a single independent network (Shizuka et al. 2014; Firth & Sheldon 2015).

Therefore, in this work, we were able to assess how subsequent breeding proximity (i.e. 'y') was related to the prior winter social network ('x_1') given the effect of winter spatial overlap between individuals ('x_2'). To determine the 'winter spatial overlap' of between dyads, we took a conservative approach and aimed to consider both the amount of range overlap of each dyad, as well as the amount of activity across their range. Therefore, we first computed the proportion of activity each individual spent at each location. Then, the winter spatial overlap for each dyad was determined by calculating the minimum proportion of activity that either member spent at each location, and then taking the sum of these values over all locations. In this way, the value for each dyad shows both how much their spatial ranges overlapped, as well as how much their activity within their ranges overlapped. Indeed, the scale ranges from 0 to 1, where dyads with identical proportions of activity at each place to one another score 1, those that never overlapped score 0, and those that overall spent half of their activity in the same locations as one another would score 0.5. For instance, when using this method, birds (B_1 & B_2) who only occurred at the same two feeding stations (F_1 and F_2) as one another, with B_1 spending 90% of their time at F_1, and B_2 spending 90% of their time at F_2, would score 0.2 as their winter spatial overlap i.e. 0.1 (F1 minimum activity) + 0.1 (F2 minimum activity). On the other hand, if B_2 had also

spent 90% of their activity at F_1, they would score 1 i.e. 0.9 (F1 minimum activity) + 0.1 (F2 minimum activity).

Thus, using MRQAPDSP, we used i) this winter spatial overlap matrix, and ii) the winter social network, as predictor matrices and simultaneously regressed them over the breeding proximity matrix. This assessed whether the social network was a significant predictor of subsequent breeding proximity given individuals' winter spatial overlap. As this considers individuals' winter spatial overlap over the entire winter, it is distinctly different from the primary null model analysis that considers that individuals are likely to remain in the same area at the end of the winter to breed. However, we also ran a modified version of the null model aiming to consider individuals locations over the entire winter that produced the same patterns (see above and Fig. S4).

Supplementary Figures

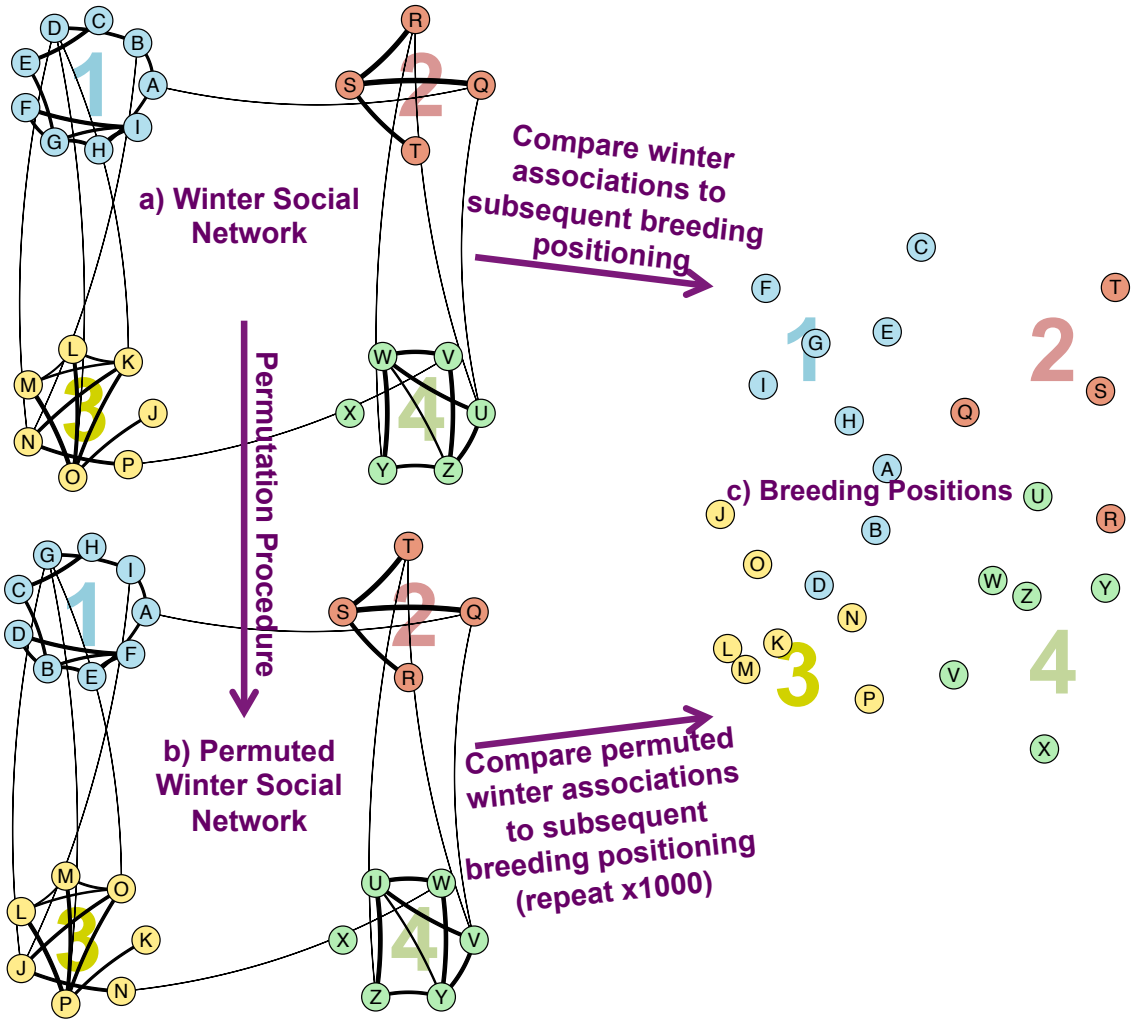


Figure S1. Graphical depiction of the analytical procedure using computer-generated example data. The large numbers show four different feeding stations, and surrounding circles (of the same colour) show the individuals who occurred there in the winter before the breeding season began. Letters indicates unique identification code of the individual, and connecting lines ('edges') show social associations occurring between them whilst the thickness of lines show the strength of the social association. a) The observed winter social network generated from the flocking co-occurrences between individuals over the winter. b) Example of one permuted social network after the null model has been carried out, whereby individuals at the same location are reassigned social network positions within this location whilst social network structure is held constant. c) The individuals' observed breeding positions, where individuals are generally likely to breed relatively close to their winter foraging location, but the proximity of individuals breeding attempts to one another appears more strongly related to their observed prior winter social associations (a), than to their permuted winter social associations (expected from their winter foraging locations alone) (b).

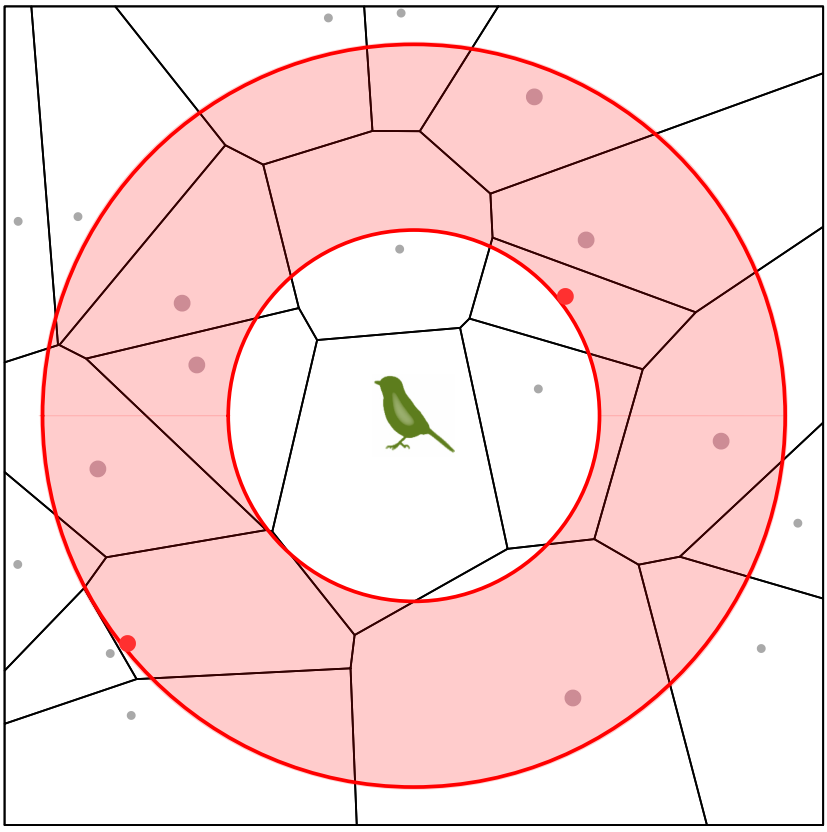


Figure S2. Example map showing territories around individuals' breeding locations. Bird icon shows the breeding location of the focal individual, and dots show other individuals' breeding locations. The black lines show the inferred territory boundaries around each individuals breeding location (derived using voronoi polygons – see Methods). Those who share a territory boundary are classified as neighbours, those who do not share a territory boundary are classed as non-neighbours. The focal individual's nearest non-neighbour and the furthest neighbour are shown in bright red. The boundary between the nearest non-neighbour and further neighbour is shown in red. Only individuals' social associations to those who subsequently fell within this boundary were considered when assessing whether individuals held stronger winter associations to their subsequent breeding neighbours than to their subsequent non-neighbours (see Methods, Fig. 2 & Table S4). Therefore, only dyadic links between those who subsequently bred within a given proximity to be either neighbours or non-neighbours was considered. In this way, it was not the case that proximity was strongly related to whether or not individuals shared a territory boundary. Indeed, this method meant that each individual's nearest individual considered was then a non-neighbour, and the furthest one was a neighbour. This also had the beneficial consequence of reducing multicollinearity for the model including fixed effects of breeding proximity as well as whether or not individuals were neighbours.

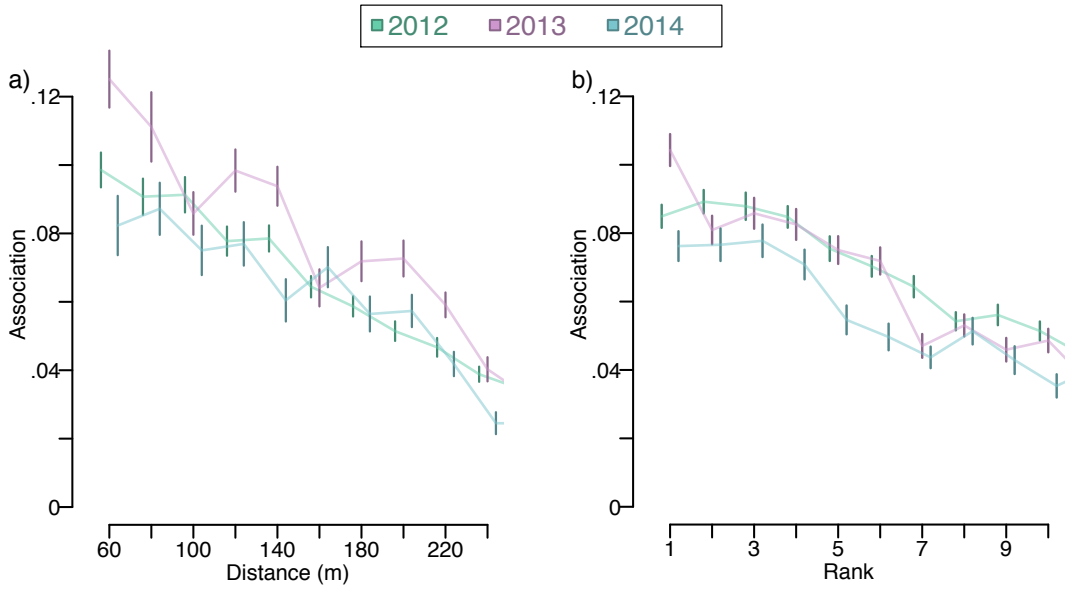


Figure S3. Summary figure showing the decline in dyadic winter social associations over subsequent breeding proximity when measured as a) distance in metres, beginning at 60m (average distance to nearest individual) at continuing in bins of 20m (average step distance to continuing next nearest individuals) and b) Ranked closest individuals. Vertical lines show standard error around mean. Colour indicates year. Even at relatively fine spatial resolutions, stronger winter social associations related to increased proximity in the subsequent breeding season

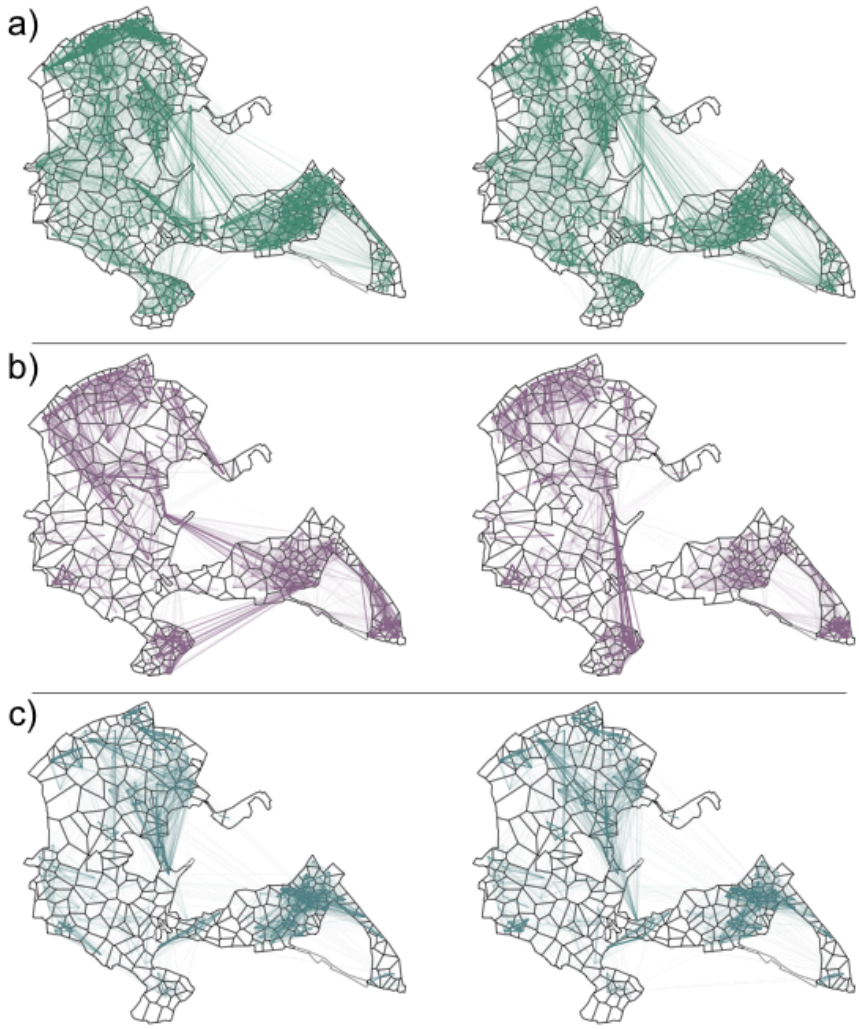


Figure S4. Comparison of the observed social networks (left hand side) with a social network generated from the null model permutations (right hand side). Winters ending in a) 2012, b) 2013 and c) 2014 are shown. Surrounding border shows Wytham woods, and each individual is in the location where they were observed breeding (points not plotted for clarity). Connecting lines show winter social associations (thickness represents strength). In cases where both the male and the female at a particular box where associated with another individual at another box, the mean strength is displayed. The observed networks were highly structurally similar to the networks generated from the permutation process: Mantel r (mean and 95% range) = 2011: 0.62 (0.59-0.66), 2012: 0.64 (0.60-0.70), 2013: 0.64 (0.59-0.70). Further, networks generated from the permutation process but using individuals' feeding locations over the entire year (instead of their final location) were also highly similar to observed networks: Mantel r (mean and 95% range) = 2011: 0.61 (0.56-0.66), 2012: 0.68 (0.63-0.73), 2013: 0.65 (0.59-0.71).



Figure S5. Mantel r test statistic assessing the relationship between winter social networks and subsequent breeding proximity matrix when links between dyads of particular classes are considered separately. Proximity was measured using a) Euclidean distance and b) ranked nearest individuals. Symbols show the observed statistic, and boxes show the 95% range of statistics calculated from the spatial null model that controlled for class-type. Mid-lines illustrate mean of the statistics from the null model. X axis shows denotes which dyadic links were considered. "M-F" = intersexual links only, "FY-Ad" = between age classes only, "Move-set" = between those that moved during the winter ("moving") and those that remained in the same location ("set"). The effect, in terms of the correlation between the observed winter social network and the breeding proximity compared to the correlation generated from using the permuted social networks, was similar across classes. The only exception was in 2013 when winter associations between first-year birds did not predict their breeding proximity more than expected from the null model. This is most likely to have been driven by the small sample size of first-year birds due to adverse weather conditions causing high mortality of nestlings in the previous year (only 17.4% of breeding individuals recorded in this winter were first-year birds – Table S1). Indeed, on a smaller scale, social associations between subsequent neighbours were found to be stronger than expected from their winter spatial distribution (see Fig. S6).

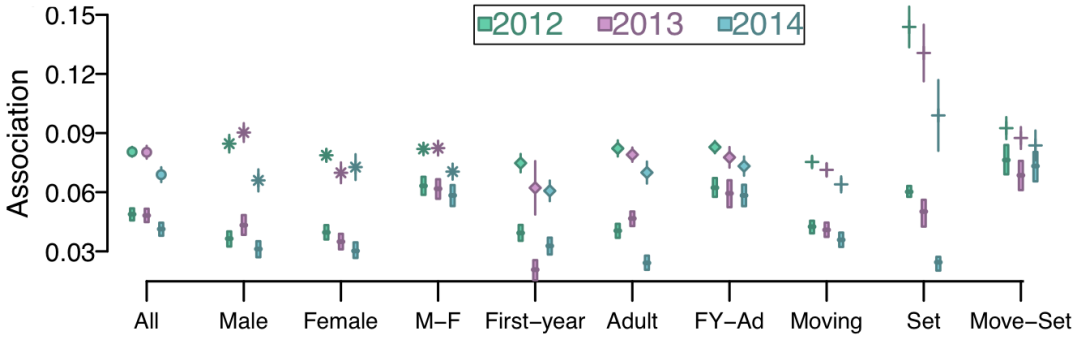


Figure S6. Individuals' average winter social association strength to their neighbours in the subsequent breeding season. Only social associations between neighbours are considered. Symbols show the observed mean with vertical lines showing standard error. Boxes show the 95% range of statistics calculated from the spatial null model which controlled for class-type. Mid-lines illustrate mean of the statistics from the null model. X axis shows denotes which dyadic links were considered. "M-F" = intersexual links only, "FY-Ad" = between age classes only, "Move-set" = between those that moved during the winter ("moving") and those that remained in the same location ("set"). Hence, even within sexes, within age classes, and within individuals that moved and did not, as well as between all these classes, individuals were more strongly associated in the winter with those they subsequently shared territory boundaries with than expected from their winter spatial locations.

Supplementary Tables

Table S1. Sample sizes and dyadic links between individuals who occurred in the social network and also were recorded in the subsequent breeding season. 'Individuals' columns show the counts of those in each demographic class each year, 'social network links' columns show the number of social network edges between those in that class that year, and 'neighbour links' columns show the number of breeding season neighbour boundaries shared. Hyphenated classes show 'between-class' counts.

Split	Class	Individuals			Social network links			Neighbour links		
		2011	**2012**	**2013**	**2011**	**2012**	**2013**	**2011**	**2012**	**2013**
-	All	396	272	247	7909	3085	2880	922	686	519
Sex	Male	163	137	119	1236	834	672	151	193	126
	Female	233	135	128	2902	727	761	323	156	136
	M-F	-	-	-	4138	1561	1433	474	349	262
Age	First-year	179	47	137	1797	97	900	179	24	171
	Adult	217	225	110	2102	2035	549	272	459	83
	FY-Ad	0	0	0	3899	2132	1449	451	483	254
Movement	Moving	342	214	212	6732	2216	2490	724	473	412
	Set	54	58	35	70	102	20	41	32	8
	Move-Set	-	-	-	6802	2318	2510	765	505	420

Table S2. Output of GLMMs assessing the relationship between winter social associations and subsequent breeding proximity for different classes of individuals. In all models, subsequent breeding proximity (reciprocal of Euclidean distance) between each dyad was the dependent variable. All models included winter social association strength and year as predictor variables. Random effects of both individuals' identities and their nest boxes were also included. Model a) included a factor indicating whether each dyad was same-sex (scored as 1) or opposite-sex (scored as 0), as an additional predictor variable, along with its interaction with winter social association. Model b) excluded all individuals except adults who bred the previous year, and included a predictor variable denoting the previous breeding proximity between these adults before the winter began. Model c) excluded all dyadic links except from those between individuals who remained in the same single location as one another over the winter. The $p\text{-value}_{null}$ shows the p-value for the coefficient generated from comparison to the coefficients from the permutations under the spatial null model.

Model	Covariate	Coefficient	SE	t -value	$p\text{-value}_{null}$
A	Association	0.05122	0.00024	209.46244	**0.001**
	Sex	0.0001	0.00001	8.71265	**0.015**
	Sex*Association	-0.00116	0.00035	-3.34968	0.237
	Year 2012	-0.00006	0.00002	-2.71562	0.741
	Year 2013	-0.00007	0.00005	-2.43136	0.326
B	Association	0.01537	0.0004	38.46216	**0.001**
	Prev. Proximity	0.63118	0.00466	135.35404	**0.001**
	Year 2012	-0.00002	0.00002	-0.8072	0.206
	Year 2013	0.00005	0.00005	0.48479	0.654
C	Association	0.03303	0.00944	3.50026	**0.001**
	Year 2012	-0.00092	0.00117	-0.78374	0.746
	Year 2013	-0.00299	0.00158	-1.88731	0.946

Table S3. Results of MRQAP tests assessing the relationship between adult birds' breeding proximities to one another in the previous year to the following year winter social network and the subsequent year's breeding proximity. Only birds that were recorded in all three periods were considered (n=125, 148 and 85 for 2012, 2013 and 2014 respectively).

Year	Covariate	Coeff.	P	Full R^2
2012	Subsequent Social Association	0.0111	0.001	0.6563
	Subsequent Breeding Proximity	0.7955	0.001	
2013	Subsequent Social Association	0.0222	0.001	0.6767
	Subsequent Breeding Proximity	0.6364	0.001	
2014	Subsequent Social Association	0.0113	0.001	0.7051
	Subsequent Breeding Proximity	0.9239	0.001	

Table S4. Output of GLMMs assessing the relationship of winter social associations with subsequent breeding proximity and subsequent breeding territory boundary sharing (whether individuals were breeding neighbours or not) (Fig. 2a). Only dyadic links that were within the range of their closest non-neighbour and furthest neighbour were considered (Fig. S2). Year was also included as fixed effect, whilst both individuals' identities and both their nest boxes were set as random effects. The $p\text{-value}_{null}$ shows the p-value for the coefficient generated from comparison to the coefficients from the permutations under the null model.

	Coefficient	SE	t -value	$p\text{-value}_{null}$
Intercept	0.013	0.004	3.2067	0.294
Proximity	7.0395	0.4723	14.9034	**0.01**
Neighbour	0.0075	0.002	3.6906	**0.01**
Year 2013	0.0029	0.0033	0.8644	0.626
Year 2014	-0.0034	0.0036	-0.946	0.558

Chapter 4

Wild songbirds modify their social behaviour in response to experimentally-imposed loss of their flock mates

Wild songbirds modify their social behaviour in response to experimentally-imposed loss of their flock mates

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ABSTRACT

There is often substantial variation between individuals within animal populations in how they interact with their conspecifics. Such interactions can have important consequences for both individual fitness as well as the social system itself. Yet, an individual's social behaviour is not only based on its own attributes, but also on those of the individuals it interacts with. While the loss of individuals from wild populations is known to have important repercussions for various ecological and evolutionary processes, how such loss influences the social behaviour of the remaining animals remains less well known. We used Radio-Frequency Identification (RFID) technology and machine-learning based analyses of social groups to quantify social associations occurring amongst over 500 wild great tits (*Parus major*) as they formed foraging flocks over the winter. Using social network analysis, we then quantified changes in individual social behaviour (or 'network positions') in response to experimental perturbations. The loss of an individual's associates had little influence on their activity and movement patterns, but it had significant consequences for their social behaviour. Those individuals that experienced the most social impact from the removals increased their number of flock mates, the tightness of their associations to their flock mates, and their overall connectedness within the network of remaining individuals. Furthermore, social changes were found to be in response to actual loss of their associates, rather than disturbance following their capture. Such adjustments in social behaviour may be due to

animals rapidly compensating for lost social connections through increasing their sociability with others. Interestingly, this indicates that the loss of social connectedness within populations brought about by removing individuals may be ameliorated by increased associations amongst remaining individuals. Therefore, the dynamic behavioural responses that animals are capable of should be considered when predicting outcomes of perturbations for social networks. Together, these findings provide experimental evidence of how individual wild animals react to social perturbations, and have implications for conservation efforts related to human-induced loss of individuals.

INTRODUCTION

The social structure amongst individuals within a population has long been acknowledged as related to a wide variety of ecological and evolutionary processes (Crook 1970; Alexander 1974). More recently, these patterns of associations have been quantified as 'social networks', a method of analysis which provides a framework that allows simultaneous assessment of both the direct associations between two individuals, as well as individuals' wider levels of connectedness within the society (Croft *et al.* 2008; Whitehead 2008; Sih *et al.* 2009; Brent 2015). Empirical studies have demonstrated that social networks can govern population-level processes that are dependent on interactions amongst individuals, such as patterns of mating (Oh & Badyaev 2010), the spread of disease (Godfrey *et al.* 2009; Weber *et al.* 2013; VanderWaal *et al.* 2014), the transmission of information (Aplin *et al.* 2012; Allen *et al.* 2013; Aplin *et al.* 2015a), as well as competition and subsequent selection pressures (Farine & Sheldon 2015). Therefore, individuals who are central in a network with high social connectedness differ from peripheral individuals both in terms of their extent of influence on the network, as well as their social experience and the pressures exerted upon them (Sih *et al.* 2009). Moreover, various lines of evidence support that individuals' positions within such networks are linked to a variety of fitness consequences. For instance, patterns of social associations have been linked to reproductive success and future survival probability in baboons (*Papio cynocephalus*) (Silk *et al.* 2003; Silk *et al.* 2009, 2010), feral horses (Cameron *et al.* 2009; Nunez *et al.* 2015), and macaques (*Macaca sp*.) (Schulke *et al.* 2010; Lehmann *et al.* 2016).

Previous studies have demonstrated that in various social systems, including fish, birds and mammals, individuals are repeatable and consistent across time in the social positions they hold within the network (Blumstein *et al.* 2013; Brent *et al.* 2013; Jacoby *et al.* 2014; Aplin *et al.* 2015b). This may partly be due to a genetic component of their social phenotype (Lea *et al.* 2010; Brent *et al.* 2013). Whilst an individual's network position may rely upon its own attributes and behaviour, it is also intrinsically dependent upon the social environment and which other individuals they interact with (Wey *et al.* 2008). However, there is little experimental evidence assessing the consequences of the loss of individuals from social networks amongst wild animals for those individuals that remain.

Understanding the repercussions of loss of individuals from wild populations has broad implications for conservation. This is in terms of both long term effects, such as human-induced selection pressures causing genetic changes (Allendorf *et al.* 2008) and immediate ones, such as the poaching of elephant matriarchs (*Loxodonta africana*) potentially reducing information availability to the rest of the group (McComb *et al.* 2001). Such social impacts of individual loss are likely to be rife. Indeed, computerized simulated removal of socially-central individuals from wild mammalian populations has shown to have the potential to cause social network fragmentation or increase the social distance between individuals (Lusseau 2003; Williams & Lusseau 2006; Manno 2008).

Although simulation studies may be necessary in wild populations for practical or ethical reasons (Lusseau *et al.* 2006), captive experiments have indicated that differences between simulations and actual removals can highlight important aspects of behavioural reconfiguration of sociality (Flack *et al.* 2006). For instance, if particular individuals promote cohesion; such as behavioural policing by high-ranking pigtailed macaques (*Macaca nemestrina*), the actual removal of such individuals can cause higher social breakdown than predicted by simulated node removal alone (Flack *et al.* 2006). Alternatively, simulated removals could also overestimate changes in network properties if remaining individuals increased their social associations in response to loss.

Whilst useful, experiments from non-wild groups do not allow full assessment of whether such findings are group/environment specific, or represent more general

phenomena (Kanngiesser *et al.* 2011). Further, laboratory studies have illustrated that the particular laboratory strain of the animals used may influence how groups respond to removals (Vital & Martins 2011), and that the rearing environment itself may perturb social traits of individuals (Jandt *et al.* 2015). Therefore, experimental removal of animals within wild social networks, and subsequent assessment of the social responses of the remaining individuals, is now needed.

In this study, we used the large-scale deployment of Radio-Frequency Identification (RFID) technology to monitor the flocking patterns of over 500 RFID-tagged wild great tits (*Parus major*), allowing us to quantify the social associations between these birds and infer social networks over an entire population. Whilst assessing individuals' position within the network at regular intervals, we used standard methods to capture and remove birds from the population, and were able to temporally and spatially replicate this experimentally imposed loss. Individuals within this population are known to be consistent in their social network position over short, and long, time periods (Aplin *et al.* 2015b). This allowed us to directly assess how birds that lost their flockmates subsequently altered their social behaviours as well as their individual activity patterns. Using data on the fine-scale associations amongst individuals, we examine how the social impact of the removals depended on the individual's prior social connection to the flock mates they lost.

METHODS

Study System

This study was conducted on a long-term study population of great tits in Wytham Woods, Oxford, UK (51°46'N, 1°20'W), which has been subject to standardised research protocols since the early 1960s (Perrins 1965). Around 1020 nestboxes in fixed positions and known GPS co-ordinates are visited regularly through-out the breeding season to record breeding attempts and performance, and capture adults (between days 6-14 of nestling phase) and nestlings (after day 15) to mark with a unique BTO (British Trust for Ornithology) metal leg ring and record standard morphometric information. Throughout the winter, great tits aggregate in large, mixed species foraging flocks (Hinde 1952), within which they interact with con- and heterospecifics (Aplin *et al.*

2012). Since 2007, plastic leg rings containing individual passive integrated transponder (PIT) tags have been fitted to great tits captured during breeding (both adults as well as nestlings), along with extensive mist netting being carried out from September to February to enable the marking of immigrants.

These PIT tags allowed the detection of the time, date and location of each individual's feeding attempts at sunflower feeding stations equipped with RFID antennae attached to two opposing access holes (Dorset ID, Aalten, Netherlands). These were placed in a stratified grid at 65 fixed locations, ~250m apart, throughout Wytham Woods, from August to February. Feeders opened automatically every weekend for both days, scanning for PIT tags 16 times per second from pre-dawn until after dusk. The system provides a 'snapshot' of social structure, enabling the monitoring of social composition throughout the winter.

Experimental Procedure

At the start of September 2013, four weeks into standard non-breeding season data collection (during which periodic winter mist-netting was taking place on appropriate weekdays, and RFID loggers running over weekends), the experimental procedure began. The experiment consisted of four replicates (run on a weekly basis), each following the same standard protocol. Each of the four trials involved using previous logging data to select two areas (with each area consisting of two neighbouring RFID feeders) that were known to have a similar number of birds but with minimal exchange of individuals between them (Figure S1). We chose areas with relatively high levels of activity to ensure that experiments were feasible. In each replica, one of the areas was then randomly designated as the 'removal' site whilst the other area was assigned to the standard capture, process and release procedure – i.e. to ensure some individuals were a suitable control for the effect of disturbance due to capture (Figure S1). In this way, the experiment consisted of four pairs of areas (eight separate areas in total), and was ran over four weeks (four replicas/trials), where on each week one of the pairs of matched areas was used. Thus, on the Wednesday of each week (or Thursday if weather conditions were unsuitable), one of the pairs of matched areas was selected, and a catching session was undertaken at each of the areas (i.e. the one selected for the "removal" treatment, and the one selected for the "capture and release" treatment) by

mist netting at both of the feeding stations. Over the four weeks, we alternated whether catching took place first in the removal area or in the standard capture area, and attempted to carry out sessions of similar intensity (~3.5hrs) over the replicates and treatment conditions. Entirely standardized effort under the field conditions was impossible due to variation in weather conditions and environmental surroundings changing the ease of catching individuals.

In the standard capture areas, all captured individuals were simply subjected to the usual identification and/or ringing procedure and then released. The same standard protocol was applied to individuals captured in the area selected for the removals, but we aimed to capture and remove 6 RFID-tagged great tits. On one occasion, twelve birds were caught so 6 were randomly selected, whilst in another replicate only 5 were caught and removed. By carrying out the non-removal capture in a matched area, this ensured we would be subsequently able to compare the effects of the actual removal of individuals to any underlying effects produced simply by the procedure involved in mist netting (but without any loss of individuals). Upon removal from Wytham Woods, the birds were held in captivity until their release the following Monday (See Ethical Note). During all four trials of the removal experiment, and afterwards, the standard data collection continued as usual.

Ethical Note

All work, including capturing birds by mist netting, ringing, and temporary keeping in captivity, was carried out under British Trust for Ornithology (BTO) licence (A5435, C6030) and Natural England licence (20131205 & 20123075), and adhered to U.K. standard requirements. Birds held in captivity were transported to the University of Oxford's John Krebs Field station in standard BTO cloth bags within 1.5hours of capture, and monitored throughout the first day of captivity. They were kept indoors at ambient temperate and under a natural light regime. Individuals were housed in separate but neighbouring wire-mesh cages (45cm x 45cm and 68cm high), equipped with roost boxes and provided with water and food (sunflower seed & live mealworm) daily. Individuals were released at the site of capture following four full days in captivity, and checks were carried out to ensure body mass changes between capture and release were within natural range of diurnal mass fluctuations (Haftorn 1992). Out of the 23 removed

individuals, all but three (i.e. 87%) of the removed individuals were resighted at some point.

Data Analysis

Social Network Analysis

Data collected from the automated recording of individuals' RFID tags over the grid of antenna-equipped feeding stations provides a fine-scale temporal datastream at each feeder. This is made up of bursts of activity as flocks of birds arrive and feed (Psorakis *et al.* 2012; Psorakis *et al.* 2015). These 'flocks' (or 'flocking events') can be identified using a machine learning algorithm which employs a gaussian mixture model to assign each individual detection to the event it most likely occurred in (Psorakis *et al.* 2012). This technique has been shown to be a robust method of identifying flocks for further use in social network analysis, and preferable to applying techniques requiring the specification of arbitrary parameters, such as using set time windows to define co-occurrences (Psorakis *et al.* 2015).

By calculating the flock memberships amongst all individuals, we created a 'group-by-individual' matrix (Whitehead 2008) specifying the co-occurrences of all birds with one another. We used R 3.2.2 (R Core Team 2015) for all network analyses, and applied the Simple Ratio Index (SRI) (Cairns & Schwager 1987) to calculate weighted social associations amongst each dyad and to create social networks. In this way, the 'nodes' of the network represent the individuals, whilst the 'edges' linking the nodes show the social association between each dyad. We created these weighted networks for each weekend separately (four prior to the experiment, and four during). For each weekend we also calculated cumulative networks; this was carried out by considering all flocking events recorded from the beginning of the season and up to the end of the focal weekend, therefore creating a social network from all possible data available at that point in time.

Identifying focal individuals

For each trial, we identified all individuals that were recorded in both the weekend directly before and following the mid-week trial, and classified these as the focal individuals for that trial. Using these individuals enabled us to assess their change in

behaviour following the trial. We excluded the small number of birds who were captured throughout the mid-week catching efforts from further analysis (so as to exclude the effect of direct capture on behaviour). Any focal individuals that were recorded in the same flock (or "gathering event") in the previous weekend as an individual that was captured during the trial was categorised as having their 'flock mate/s captured'. This included the flock mates of those caught at removal sites and those at the matched capture sites (Figure S1), as well as those caught elsewhere during the week in order to simultaneously account for this and increase sample size. Within the set of birds that had one or more flock mates captured, those who were identified as a previous flock member of removed birds were subcategorised as having their "flock mate/s removed", whilst those whose flock mates were subject to standard capture procedure were categorised as having their "flock mate/s released". No birds fell into both categories during a single replicate. All birds identified as focal individuals within the trial but not associated in the previous sampling period with any captured bird were categorised as "non-affected".

Estimating social impact

The categorisation of focal individuals simply identified which birds were potentially affected by the removals. However, the social impact an individual experienced can be expected to be related to the number and strength of associations towards the removed birds. For example, those birds that experienced the removal of a single prior flock mate with which they were weakly associated, should be affected less than those who lost six flock members with which they held strong social associations. Therefore, for each individual categorised as having their 'flock mates captured', we calculated the proportion of their total social associations in the previous week that was directed towards captured individuals. This was done for both those subcategorised as having their flock mates removed, and those having their flock mates released. We used this as the primary measure of how much social impact the treatment had on each individual. However, we also carried out a supplementary analysis using the "proportion of flock mates captured" as an alternative measure of social impact. This is equivalent to the proportion of their total binary connections in the previous week directed towards captured individuals, and represents the unweighted version of the primary analysis.

Measuring changes in behaviour

We chose to assess four metrics of social behaviour that are known to be repeatable within individual great tits, even when accounting for individual patterns of space use, both over short (weeks) and long time frames (years) (Aplin *et al.* 2015a). These metrics are the (i) average flock size an individual occurs in, (ii) unweighted degree, which gives the number of edges an individual holds in the binary network and represents their general gregariousness as it is equivalent to the number of unique individuals it co-occurs with, (iii) total association strength i.e. the sum of all an individual's edges within the weighted network, thus measuring their general centrality and sociability, and (iv) betweenness, calculated as the number of shortest paths between all other individuals in the network that pass through the individual, which measures the extent to which an individual may act as a bridge for transmission of information and disease (Croft *et al.* 2008). Following previous work (Aplin *et al.* 2015b), betweenness was measured on a log scale in order to reduce skew. We also assessed an additional social network metric (v) average edge weight, which measures the average score of their dyadic social associations to each of their flock mates, and gives an indication of the tightness of social bonds held.

For each metric, we aimed to determine how each focal individual changed their behaviour following the experimental trial (i.e. immediately 'post-trial') given their social behaviour before it took place (i.e. 'pre-trial'). As pooling data over longer time periods appears to provide a more accurate depiction of individuals' social phenotypes than single sample periods (Aplin *et al.* 2015b), we used the cumulative networks, which included all of the data before the trial took place, to calculate pre-trial measures of average flock size, strength, betweenness, and edge weight. As unweighted degree is intuitively expected to be significantly larger in cumulative networks than any stand-alone sampling period (as individuals would be recorded with a large number of binary edges with increased sampling), we set pre-trial degree as their average degree score over the networks created for each pre-trial sampling period separately.

To calculate the change in each individual's metrics, we compared their recorded behaviour directly post-trial to their pre-trial behaviour score. We express this change as relative to the average observed change over all individuals over this time-frame, as network parameters are likely to change even over short periods due to the dynamic nature of the fission-fusion system (Farine *et al.* 2015). In a supplementary analysis, we

measured pre-trial flock size, strength, betweenness, and edge weight as their average score over previous weekly networks (i.e. applying the same methodology used to calculate changes in degree) rather than using cumulative networks. The same procedure was also applied to assess changes in other behaviours that were not directly related to social network position (but potentially related to it). These additional metrics comprised i) an individual's average number of records at the feeders, as a basic measure of their total activity, ii) the average number of flocking events they were recorded in, to assess propensity to occur in the feeding flocks and iii) the average number of feeding sites visited, which gives an indication of their transience and mobility.

Assessing the relationship between social impact and change in behaviour

We assessed whether the measured changes in social phenotypes of the focal individuals in each trial were related to the extent of removal of their flock mates. For each metric we firstly compared the relative change displayed by focal individuals belonging to the different categories (flock mates removed, flock mates released, or non-affected). Due to the implicit non-independence of network data (Whitehead 2008; Croft *et al.* 2011), we established baseline rates using permutation procedures for each trial in which the pre-trial and post-trial network positions of focal individuals were randomly swapped with another focal individual in the pre-trial and post-trial networks. During the permutation, the swaps did not have to be reciprocal and it was possible for an individual to be assigned to their own network position. This is equivalent to resampling (without replacement) the relative changes in network positions amongst the focal individuals within each trial and keeping the new identities constant across metrics. Therefore, this maintained the same network structure and distribution of changes in metrics, but randomised the category that each within-individual change was assigned to within each trial. We carried out 10000 permutations for each trial, and compared the average observed differences between the three categories to the differences calculated from the permutations. Observed differences between any two categories of focal individuals in relative change of a metric were classified as significant at $p<0.05$ if they fell outside the 95% range of the permutations.

The primary aim of the analysis, however, was to assess whether the estimated social impact of the removals on an individual influenced their subsequent social behaviour.

Thus, for all individuals that had a flock mate captured in a trial, we assessed how their subsequent change in behaviour metrics given their pre-trial score was predicted by (i) the proportion of their social associations to captured flock mates, (ii) whether their flock mates were subjected to removal or release and, importantly, (iii) the interaction of these two predictors – which allows us to separate whether behaviour changes are due to increasing exposure to the loss of flock mates or simply due to exposure to the procedure in which flock mates are captured. Therefore, we ran linear mixed models (LMM) for each metric, setting the post-trial change in metric as the response variable. The predictor variables were accordingly set as the measure of social impact (proportion of the strength to captured flock mates), the treatment class (whether flock mate/s were subject to removal or release), and the interaction between these. We included trial week as a fixed effect to account for changes across time, and set individual identity as a random effect. Whilst we report the significance levels calculated using standard methods (Pinheiro *et al.* 2016), we also calculated significance by comparing the t-value of each coefficient to the distribution of the t-values generated from carrying out the same models on each of the 10000 data sets generated from the permutations (described above). The models were also carried out on the two forms of supplementary variations of the analysis described earlier. In the first instance, this was done by replacing the fixed effect quantifying social impact with simply "the proportion of flock mates captured" as a basic measure assessing the extent individuals were potentially socially impacted by the removal or capture and released of their flock mates. Secondly, for models evaluating relative changes in flock size, strength, betweenness and edge weight, we set the response variable as the change calculated from using the average score over separate weekly networks as a measure the pre-trial behaviour (as opposed to using cumulative networks). In all cases, we again repeated the models on the permuted data and calculated significance given the value of the observed test statistics in relation to the distribution of those generated from the models carried out on the randomisations.

RESULTS

Over the 8-week study period, 395,113 records of 542 unique great tits making up 18,388 flocks were recorded. The flock size experienced by the average individual, i.e. 'typical' group size (Jarman 1974), was 4.86±0.02 (mean ± SE), whilst each flock consisted of 2.94±0.02 great tits on average. Over the four trials, the number of focal

individuals (i.e. those that were observed in both sampling periods directly before and after the trial but were not captured themselves) ranged from 15 – 49 for those having a flock mate removed (120 instances in total), 7 – 46 for those who had a flock mate captured and released (92 instances), and 152 – 192 for those whose flock mates were unaffected between the two sampling periods (680 instances). The average network for each sampling period during the experiment consisted of 307 individuals (range: 287 – 352) with an edge (social connection) density of 3.86% (range: 3.5 – 4.2%).

Effect of removals on foraging behaviour of flock mates

In order to assess whether any changes in social network metrics were due to changing individuals foraging behaviour in other ways, we examined the influence of the flock mate capture treatments on relative changes in individuals' raw activity on feeders, number of flocks they occurred in, and number of sites visited.

When considering the average relative changes for each these measures of foraging behaviour, there were no significant differences between that experienced removal of a flock mate, those whose flock mates were captured but released immediately, and those whose flock mates weren't captured at all (Figure S2a-c). Thus, simply whether or not an individual actually experienced flock mate removal, flock mate release, or no treatment at all, had no influence on basic measures of their foraging behaviour. We also considered whether the strength of their bonds to their flock mates who were removed, or just captured and released, influenced their foraging behaviour. Again, for all three measures of individual foraging behaviour, treatment class (i.e. whether an individual experienced flock mate loss, or flock mate release) and proportion of association strength towards captured flock mates did not interact to affect any of the behaviours (Table 1a-c). Therefore, the loss of flock mates had no influence on these behaviours above that expected by the capture procedure alone. Furthermore, whilst there was also no statistically significant effect of previous social association towards captured flock mates regardless of treatment type, there was a general, but weak, trend for those with stronger associations to captured flock mates to show a relative increase in their activity both in terms of their number of feeding records and the number of flocks they engaged in (Figure S2a-b).

Effect of removals on social behaviour of flock mates

In general, in comparison to the permutations, there were no significant differences between the average relative changes in the social metrics of the focal individuals that experienced flock mate removal, those whose flock mates were released upon capture, and those who were unaffected as their flock mates weren't captured (Figure 1a-e). Thus, simply which category of treatment each individual experienced had little influence on their change in social network metrics (Figure 1a-e). The only exception was the relative change in network strength individuals displayed. Here, there was a significant difference in the observed average increase in the network strength of those experiencing flock mate removal compared to those whose flock mates were released immediately (Figure 1c; randomisations mean difference = 0.02, observed mean difference = 0.41, $p < 0.01$), as well as compared to those who were unaffected (Figure 1c; randomisations mean difference = 0.01, observed mean difference = 0.36, $p < 0.01$).

For individuals affected by the experimental treatment, through having their flock mates captured and either removed or released, we considered how the proportion of their social associations directed towards the captured flock mates (i.e. the estimated social 'impact' or 'loss') influenced their social behaviour. Relative changes in both average flock size and betweenness centrality were not significantly related to the extent of association an individual held to captured individuals, regardless of the treatment class i.e. whether they were removed or released (Figure 1f;1i; Table 1d;1g).

However, the interaction between treatment class and proportional association strength to captured flock mates significantly predicted changes in average unweighted degree and strength (Figure 1g;1h; Table 1e;1f). Flock mates of immediately released birds did not change their behaviour with increased association to these birds, but those birds that lost flock mates due to the removals showed increases in degree and strength with increasing previous levels of proportional association strength to the removed birds (Figure 1g;1h). Therefore, birds that suffered the most social impact in terms of removing their previous flock mates also showed the greatest increases in degree and strength. For instance, around one third of birds who experienced the loss of at least one flock mate only had a small proportion (>10%) of their network connection strength directed towards the removed birds, and these generally showed no change in number of flock mates (Figure 1g). One the other hand, for around 16% of birds who experienced

flock mate removal, more than half of all the previous social connections they held were with the removed birds, so these individuals experienced a large 'social impact' and generally increased their number of flock mates by five in comparison to the average change that trial (Figure 1g). Those suffering such loss also increased overall network strength by ~1 (Figure 1h). This roughly equates to occurring 20% of their time with five new associates who also occur 20% of the time with them, or could alternatively be driven by occurring more often with the same number of flock mates.

The general relative increase in network strength was not entirely due to increasing their number of flock mates, as individuals suffering the most loss from removals also showed a relative increase in the tightness of their connections (average edge weight) to their associates (Figure 1j). Again, the interaction between treatment type and association to captured individuals was present, and had a significant effect on relative change in average edge weight (Table 1h - although note marginally non-significant when not accounting for non-independence of network structure). Greater previous social association with removed individuals caused an increase in average edge weight whilst higher association scores to captured and released individuals did not (Figure 1j).

Due to the nature of social network metrics derived from co-occurrence data, the predictor variable of interest (proportion of association to captured birds – 'social impact') and the response variables (relative change in social network metrics) can potentially be scored in various ways (see methods). Supplementary analysis demonstrated that the effects were also present when (i) the 'proportion of flock mates captured' was set as the social impact predictor variable i.e. using the unweighted version of the primary analysis (Figure S3a-S3e), as well as when (ii) pre-trial metrics were calculated as the average scores over networks built separately for each pre-trial sampling period, as opposed to using cumulative networks in the primary analysis (Figure S3f-S3j).

DISCUSSION

Through experimentally removing individuals whilst monitoring the social network of a wild bird population, we demonstrate that loss of individual great tits has significant social ramifications for remaining individuals. There was a significant relationship

between the amount of social loss an individual experiences and their change in social behaviour: higher levels of loss relate to subsequent increases in the number of flock mates, the general strength of their connectedness within the network, as well as the tightness of their associations to their flock mates (Figure 1g;1h;1j; Table 1e;1f;1h).

These changes were particularly striking as individuals' basic measures of foraging behaviour, such as activity, number of flocks, as well as size of the flocks their engaged in, were not affected by the removal of their flock mates. Therefore, the apparent changes in social network positions appear to be due to fine-scale modifications of social association patterns between the remaining individuals. Due to the bi-directional nature of social associations, changes in social behaviour of these individuals may also in turn influence those who they are associated with (Sih *et al.* 2009; Brent 2015). Further, as social associations during foraging can carry over into different aspects of sociality, perturbations causing individuals to change their behaviour in a social foraging context may also influence other situations as well (Firth & Sheldon 2015).

As individuals appear to increase their general sociability upon external factors removing their previous associations, this may represent a rapid behavioural response to compensate for the loss of connectedness. Social associations are known to be valuable to individuals (Krause & Ruxton 2002). For instance, within our study population, the most central individuals are known to benefit from increased access to information regarding new food sources (Aplin *et al.* 2012). Thus whilst the loss of flock mates may reduce an individual's access to information, rapidly acting to increase their centrality in relation to their associations to others may mitigate this.

Similarly, maintaining high numbers of flock members may also help protect against predation (Krause & Ruxton 2002), and previous work has illustrated that simulated predation risk increases flock turnover within this study system, potentially causing individuals to form associations with a higher number of flock mates *(*Voelkl *et al. In Revision*). Therefore, it could be hypothesized that, the finding that individuals increase their social centrality as they experience increasing amounts of flock mate removal (but not simply with increasing exposure to the capture procedure), is due to birds recognizing the actual loss of their associates, and interpreting this as a cue of high predation conditions (thus causing them to favour central network positions). However,

if this were the case, we may also expect changes in other foraging behaviours that may be linked to anti-predator responses, such as activity and movement patterns. Yet, none of these foraging behaviours appeared to be directly related to experiencing loss of flock mates (Table 1a-c; Figure S2). Indeed, as well as short term benefits (such as predation avoidance), there may also be future benefits of sustaining associations to flock mates. For instance, pair members remain strongly associated through the winter and base their behaviour around one another (Firth *et al.* 2015). Birds also appear to shape their breeding positions and territories around their close winter associates (Firth & Sheldon *In review*).

Rather than a compensatory response to losing social associations, the increase in centrality measures may instead potentially be driven by competitive replacement. Early, seminal, studies of great tits found that breeding territories and locations where limited, and removing breeding individuals from their territory during the spring resulted in rapid replacement as close neighbours from non-optimal territories took on their positions (Krebs 1970).Whilst it is still unclear whether or not positions within winter social networks are 'limited', such limitations on social positions could occur if, for example, social centrality was a desired attribute, and individuals generally aimed to associate with the most 'attractive' individuals. In this way, 'attractive' individuals would be able to hold the most social connections (as others are attracted to associating with them), and therefore the removal of individuals may 'free up' connections to be adopted by those socially closest to them, and result in the pattern of increased centrality with increased social loss (Figure 1g;1h;1j).

Regardless of the mechanisms causing individuals to increase their social associations upon experiencing flock mate loss, the occurrence of this alone signifies that any loss of connectedness amongst the network itself through node removal may by ameliorated by increases in the edges amongst others previously linked to them. Thus, if individuals change their social behaviour in response to associate removal, studies simulating node loss in animal networks (Lusseau 2003; Williams & Lusseau 2006; Manno 2008) may fail to properly account for this, and potentially incorrectly estimate the impact of individual elimination on social processes, such as information spread (Aplin *et al.* 2012; Allen *et al.* 2013; Aplin *et al.* 2015a).

Significant network resilience has recently been detected in wild African elephant (*Loxodonta africana*) populations, which maintain the same structure despite ivory poaching eliminating the highly connected nodes (i.e. older elephants) (Goldenberg *et al.* 2016). This robustness to perturbation is achieved through daughters replicating the social positions of their mothers, thus generating social redundancy and allowing structural maintenance (Goldenberg *et al.* 2016). Similarly, analyses tracing the changes in path length and connectivity in experimental colonies of the social wasp (*Ropalidia marginata*) following removal of individuals demonstrated that the redundancy within the original network provides substantial resilience to any future losses (Naug 2009).

Advancing knowledge surrounding the repercussions of individual loss is also likely to have important implications for predicting infectious disease spread (Weber *et al.* 2013). For instance, culling Tasmanian devils (*Sarcophilus harrisii*) known to be carriers of an infective facial tumour disease did not reduce its spread, as the highly connected social system lead to rapid transmission regardless of relatively small-scale losses (Hamede *et al.* 2009; Lachish *et al.* 2010). Similarly, attempts to control rabies within vampire bats (*Desmodus rotundus*) through removing adults was found to be ineffective as younger individuals were the primary transmitters (Streicker *et al.* 2012).

We suggest that future work involving varying both the quantity and centrality-type of experimentally removed individuals, along with extensive replication to provide sufficient sample sizes of networks, would be timely. Furthermore, whilst the loss of individuals is intuitively disruptive, the effect of introducing individuals in less considered. Experiments on captive female shark groups demonstrated that whilst addition of novel females generally increases association between all group members, male introduction disrupted weakly bonded groups whilst networks with strong ties remained unperturbed (Jacoby *et al.* 2010). In another study, the social structure of guppy shoals showed resilience to the reintroduction of individuals following their removal during a cooperative task (Thomas *et al.* 2008), suggesting maintenance of associations despite this inference. Thus, further examination of the consequences of the addition of individuals for other individuals' social behaviour would be a useful avenue of research.

Finally, the loss of individuals from a social network may also be important in terms of Allee effects, which occur when individual fitness is reduced via a reduction in group size or density (Stephens & Sutherland 1999; Stephens *et al.* 1999). For example, if individual predation risk is a function of group size or density, the loss or removal of individuals from a network (or group) may increase individual predation risk (Berec *et al.* 2007; McLellan *et al.* 2010). Further, when individuals rely upon others for information, associating with fewer conspecifics can lead to decreased foraging efficiency (Grunbaum & Veit 2003). Indeed, the loss of individuals can also generate social Allee effects (Kokko & Sutherland 2001). For instance, if cues from conspecifics are used for breeding habitat selection (Doligez *et al.* 2002), a reduction in this information may cause an Allee effect, which subsequently affects population extinction risk (Schmidt *et al.* 2015). A social network framework may therefore offer new insights into the mechanisms underpinning the operation of Allee effects (Krause *et al.* 2015), which has yet to be fully explored (Courchamp *et al.* 2008).

In summary, our study provides experimental evidence that the removal of individuals from wild populations has a range of social implications for the remaining animals. We demonstrated that heightened exposure to social loss leads to general increases in individual sociability, which may be driven via rapid compensatory responses or competitive replacement of social network positions. Such findings have implications for predicting how individual loss may alter population-level processes important to conservation efforts, as well as generally for the application of network theory and simulation studies to animal social systems.

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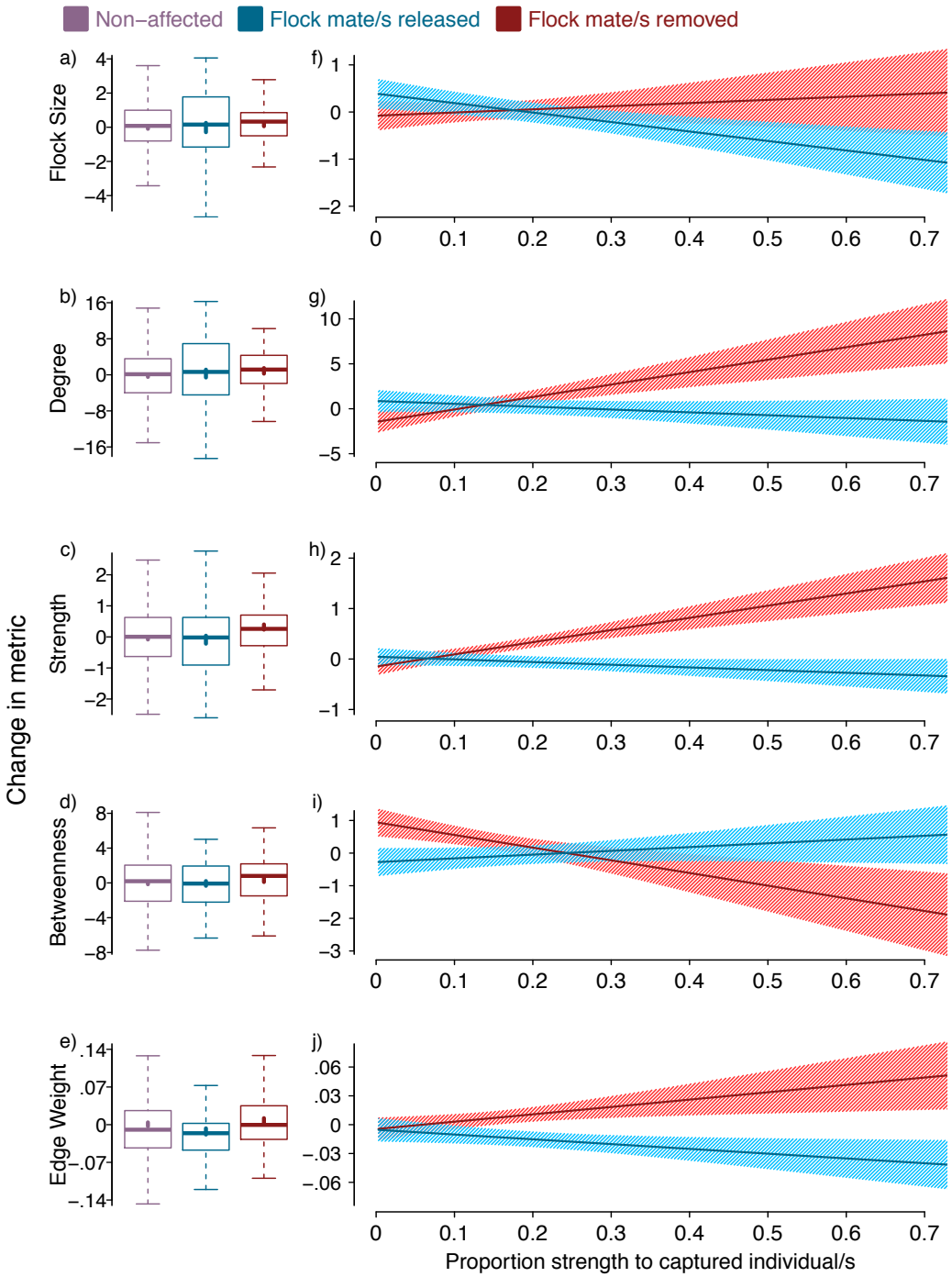


Figure 1. Change in metrics of social behaviour given treatment condition (not affected, flock mate/s release, or flock mate/s removed). Parts a-e show boxplots of change in metrics for those who fall into each category. Thick vertical lines show mean±SE, mid horizontal lines show median, box shows interquartile range (IQR), whiskers shows range (with values outside 1.5 times IQR excluded). Parts f-j shows individuals change in social metrics over the proportion of their social association strength directed towards captured individuals, with blue denoting those who had their captured flock mates released and red denoting those who had their flock mates removed. Lines and surrounding polygons show LMM fit and standard error over all replicates (see Table 1d-h for full model details).

Table 1. Results of Linear Mixed Models (LMM), all including individual identity as random effects and assessing the effect on the response variable of the change in the social metric by the fixed effects of (i) 'Prop. assoc', which is the proportion of an individuals association held to captured individuals (ii) 'Treatment" i.e. whether the individuals captured flock mates were released or removed, (iii) the factor denoting the week which the replica took place and (iv) the interaction between 'Prop. assoc' and 'Treatment'. The coefficient, standard error, T value and the standard p value are provided, along with the p value calculated from the randomisations (P_{rand}).

		Coeff.	SE	T value	P	P_{rand}
a) Change in N. Records	Intercept	-11.496	22.234	-0.517	0.606	0.584
	Prop. assoc	55.479	63.729	0.871	0.39	0.411
	Treatment	6.363	23.915	0.266	0.792	0.806
	Week	3.162	6.673	0.474	0.639	0.576
	Interaction	65.683	111.49	0.589	0.559	0.535
b) Change in N. Flocks	Intercept	-2.304	2.686	-0.858	0.392	0.352
	Prop. assoc	8.084	7.797	1.037	0.307	0.283
	Treatment	0.808	2.819	0.287	0.776	0.787
	Week	0.497	0.801	0.621	0.539	0.462
	Interaction	5.544	12.922	0.429	0.67	0.652
c) Change in N. Sites visited	Intercept	-0.03	0.096	-0.31	0.757	0.751
	Prop. assoc	-0.224	0.279	-0.803	0.427	0.493
	Treatment	-0.148	0.1	-1.485	0.146	0.141
	Week	0.042	0.029	1.48	0.148	0.121
	Interaction	0.339	0.453	0.75	0.458	0.467
d) Change in Flock size	Intercept	-0.108	0.421	-0.257	0.798	0.794
	Prop. assoc	-1.497	1.224	-1.223	0.229	0.226
	Treatment	-0.591	0.445	-1.326	0.193	0.187
	Week	0.22	0.126	1.748	0.089	0.036
	Interaction	2.771	2.053	1.35	0.185	0.171
e) Change in Degree	Intercept	-1.479	1.603	-0.923	0.357	0.326
	Prop. assoc	-0.14	4.675	-0.03	0.976	0.953
	Treatment	-2.785	1.678	-1.66	0.106	0.097
	Week	1.006	0.48	2.096	0.043	0.014
	Interaction	15.233	7.652	1.991	0.054	0.051
f) Change in Strength	Intercept	-0.169	0.222	-0.762	0.447	0.411
	Prop. assoc	-0.339	0.643	-0.527	0.602	0.56
	Treatment	-0.244	0.237	-1.029	0.31	0.318
	Week	0.094	0.067	1.411	0.167	0.099
	Interaction	2.999	1.098	2.732	0.01	0.009
g) Change in Between-ness	Intercept	-0.596	0.572	-1.043	0.298	0.284
	Prop. assoc	1.539	1.659	0.927	0.36	0.402
	Treatment	1.156	0.607	1.903	0.065	0.059
	Week	0.141	0.171	0.822	0.417	0.34
	Interaction	-5.412	2.808	-1.928	0.062	0.062
h) Change in Average Strength	Intercept	0.014	0.013	1.06	0.291	0.267
	Prop. assoc	-0.061	0.039	-1.589	0.121	0.08
	Treatment	0.005	0.014	0.355	0.725	0.716
	Week	-0.008	0.004	-2.063	0.046	0.036
	Interaction	0.123	0.063	1.968	0.057	0.043

SUPPLEMENTARY INFORMATION: Wild songbirds modify their social behaviour in response to experimentally-imposed loss of their flock mates

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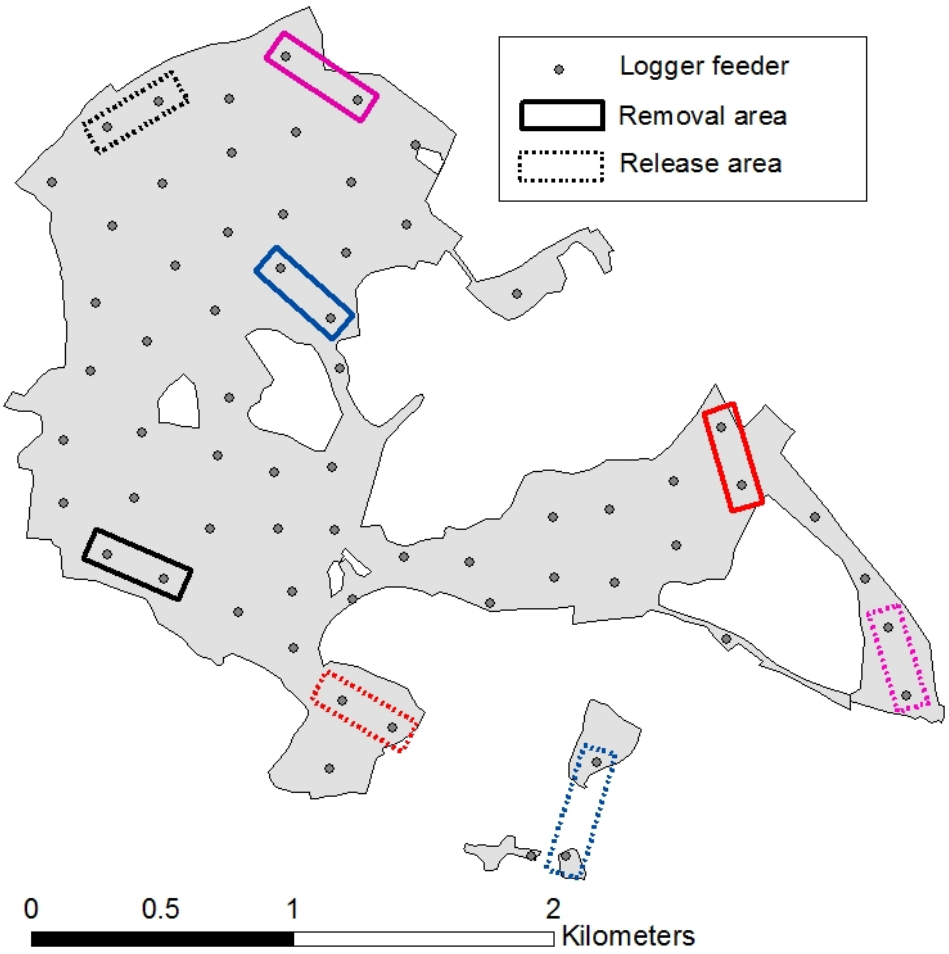


Figure S1. Wytham Woods with feeding stations shown as grey points. Rectangles show areas where the catching was carried out, where same colours represent the same replicate, and took place in order of Red, Black, Blue, Orange. Areas where birds where captured and released (control areas) are boxed in dotted lines and areas where birds where captured then removed (removal areas) are in solid. These areas where chosen based on suitability of catching conditions, matched into pairs based on similarity of activity levels, and within each pair the sites were randomly assigned to either the 'removal' treatment or the 'capture and release' treatment. From the onset of data collection to the end of the experiment (but excluding the experimental weekends at each site), there was a similar number of birds each weekend in the removal (24.38±2.04), and capture and release (22.84±1.77) areas, with no significant difference based on treatment assignment (linear model controlling for time and replica: $t = 0.59$, $p = 0.57$). Further, the turnover of birds each weekend, defined as the number of birds that remained in that area divided by the total number of birds recorded over both weekends, was also not significantly related to treatment assignment (removal = 0.54±0.03, capture and release = 0.57±0.04, linear model controlling for time and replica: $t = -0.69$, $p = 0.49$).

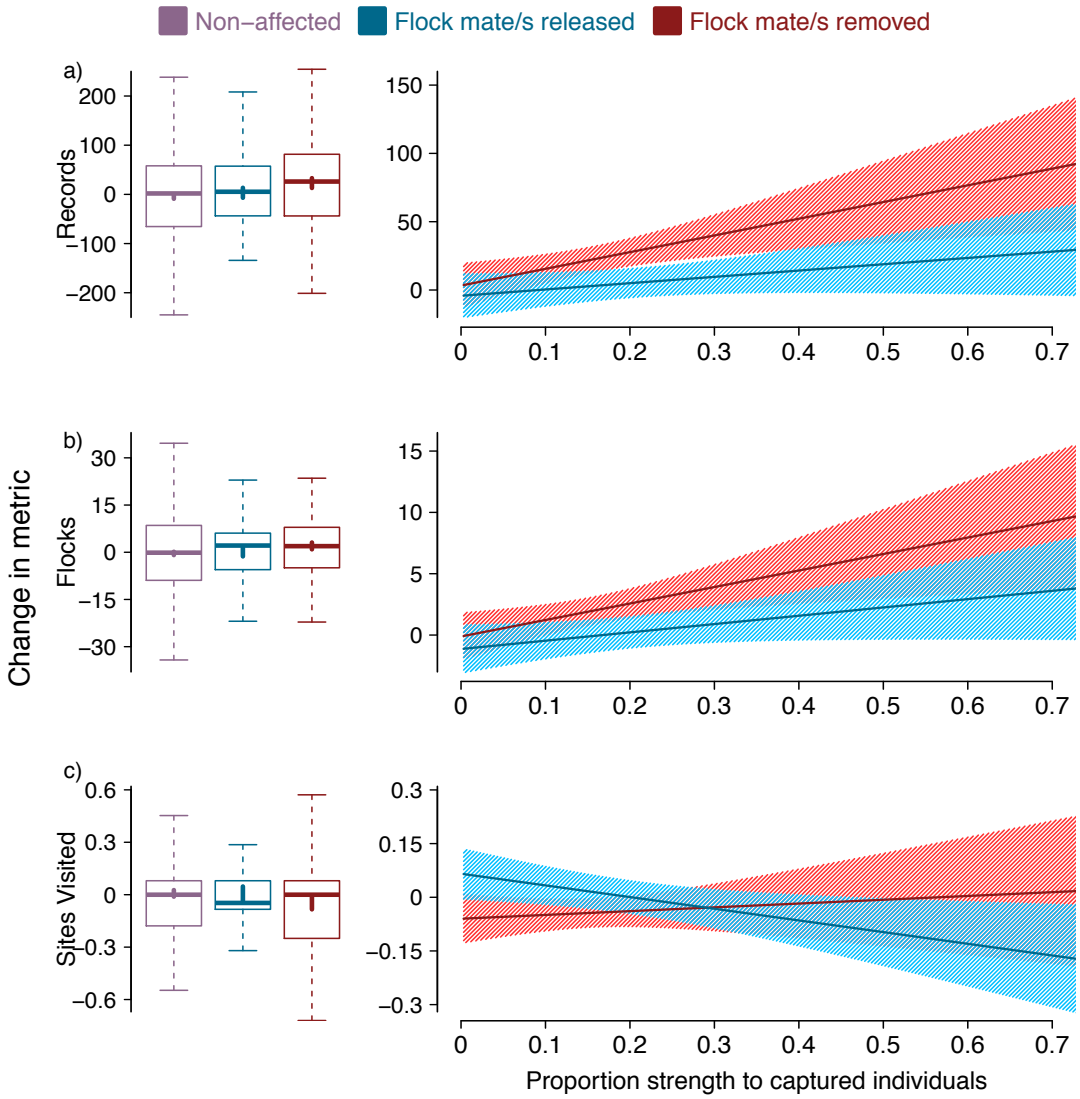


Figure S2. Change in metrics of non-social behaviour given treatment condition (not affected, flock mate/s release, or flock mate/s removed). Parts a-c show boxplots of change in metrics for those who fall into each category. Thick vertical lines show mean±SE, mid horizontal lines show median, box shows interquartile range (IQR), whiskers shows range (with values outside 1.5 times IQR excluded). Parts d-f shows individuals change in non-social metrics over the proportion of their social association strength directed towards captured individuals, with blue denoting those who had their captured flock mates released and red denoting those who had their flock mates removed. Lines and surrounding polygons show LMM fit and standard error over all replicates (see Table 1a-c for full model details).

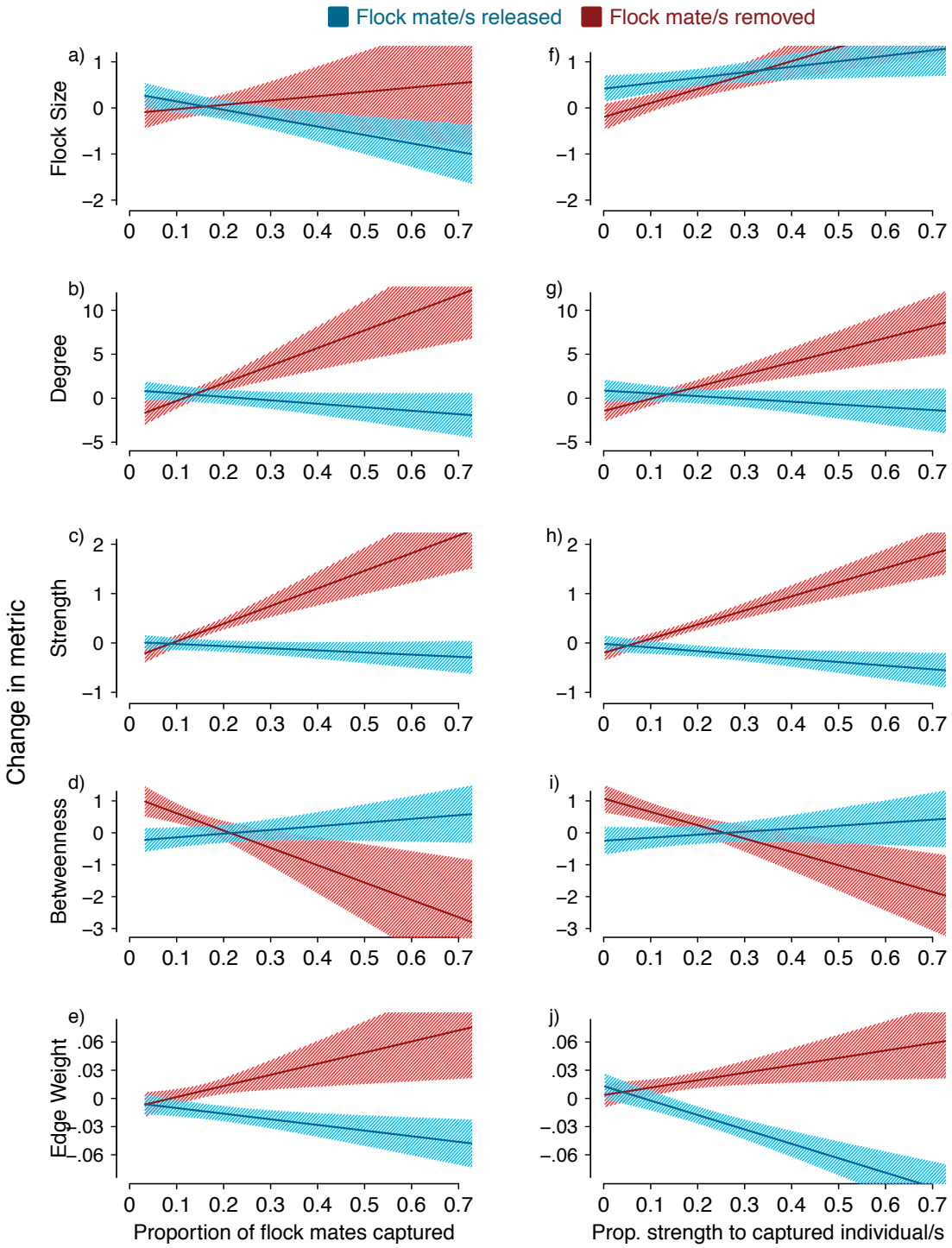


Figure S3. Change in social behaviour given treatment condition (flock mate release, or flock mate removed). Follows Figure 1 in main text, but presents results when proportion of flock mates captured is used for the primary predictor variable (a-e) and when change in weekly average of each metric is used as the response variable (f-j). Sections show individuals change in that social metrics over the proportion of their social associations directed towards captured individuals (see above). Blue denotes those who had their captured flock mates released and red denotes those who had their flock mates removed. Lines and surrounding polygons show LMM fit and standard error over all replicates (see Table S1 full model details).

Table S1. Results of full model corresponding to Figure S3. The table follows Table 1 in main text, but presents results when a) proportion of flock mates captured is used for the primary predictor variable ("proportion of degree to captured") and when b) change in weekly average of each metric is used as the response variable ("change in weekly average metric"). Results of Linear Mixed Models (LMM), all including individual identity as random effects and assessing the effect on the response variable of the change in the social metric by the fixed effects of (i) 'Prop. affect', which is the proportion of individuals associations held to captured individuals (see above) (ii) 'Treatment" i.e. whether the individuals captured flock mates were released or removed, (iii) the factor denoting the week which the replica took place and (iv) the interaction between 'Prop. assoc' and 'Treatment'. The coefficient, standard error, T value and the standard p value are provided, along with the p value calculated from the randomisations (P_{rand}).

		a) Proportion of degree to captured					b) Change in weekly average metric				
		Coeff.	SE	T value	P	P_{rand}	Coeff.	SE	T value	P	P_{rand}
Change in Flock size	Intercept	-0.185	0.405	-0.457	0.648	0.607	-0.108	0.421	-0.257	0.798	0.784
	Prop. affect	-1.271	1.189	-1.069	0.292	0.289	-1.497	1.224	-1.223	0.229	0.231
	Treatment	-0.632	0.523	-1.209	0.235	0.209	-0.591	0.445	-1.326	0.193	0.172
	Week	0.227	0.127	1.781	0.083	0.028	0.22	0.126	1.748	0.089	0.031
	Interaction	3.22	2.784	1.157	0.255	0.214	2.771	2.053	1.35	0.185	0.16
Change in Degree	Intercept	-1.612	1.544	-1.044	0.298	0.241	-1.479	1.603	-0.923	0.357	0.307
	Prop. affect	-0.554	4.545	-0.122	0.904	0.891	-0.14	4.675	-0.03	0.976	0.971
	Treatment	-4.225	1.949	-2.168	0.037	0.028	-2.785	1.678	-1.66	0.106	0.107
	Week	1.122	0.484	2.318	0.026	0.004	1.006	0.48	2.096	0.043	0.01
	Interaction	24.702	10.284	2.402	0.022	0.014	15.233	7.652	1.991	0.054	0.051
Change in Strength	Intercept	-0.205	0.213	-0.963	0.337	0.277	-0.29	0.217	-1.337	0.183	0.15
	Prop. affect	-0.203	0.618	-0.329	0.744	0.735	-0.479	0.633	-0.757	0.454	0.447
	Treatment	-0.414	0.28	-1.479	0.148	0.136	-0.258	0.226	-1.14	0.262	0.266
	Week	0.1	0.067	1.483	0.147	0.078	0.124	0.065	1.901	0.065	0.021
	Interaction	4.127	1.504	2.744	0.009	0.007	3.572	1.028	3.474	0.001	0.001
Change in Between-ness	Intercept	-0.535	0.551	-0.971	0.333	0.315	-0.872	0.575	-1.517	0.131	0.111
	Prop. affect	1.49	1.619	0.92	0.363	0.399	1.704	1.655	1.029	0.31	0.328
	Treatment	1.317	0.709	1.857	0.072	0.044	1.189	0.616	1.929	0.062	0.052
	Week	0.124	0.173	0.718	0.477	0.427	0.277	0.172	1.608	0.117	0.073
	Interaction	-6.683	3.777	-1.769	0.085	0.064	-5.825	2.867	-2.032	0.05	0.041
Change in Average Strength	Intercept	0.015	0.013	1.151	0.251	0.226	0.026	0.015	1.738	0.084	0.065
	Prop. affect	-0.07	0.037	-1.871	0.07	0.028	-0.144	0.044	-3.309	0.002	0.001
	Treatment	0.002	0.016	0.11	0.913	0.909	-0.004	0.016	-0.28	0.781	0.789
	Week	-0.008	0.004	-2.053	0.047	0.035	-0.007	0.004	-1.495	0.144	0.122
	Interaction	0.151	0.084	1.791	0.082	0.073	0.208	0.071	2.946	0.006	0.002

Chapter 5

Experimental manipulation of avian social structure reveals segregation is carried over across contexts

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Experimental manipulation of avian social structure reveals segregation is carried over across contexts

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Our current understanding of animal social networks is largely based on observations or experiments that do not directly manipulate associations between individuals. Consequently, evidence relating to the causal processes underlying such networks is limited. By imposing specified rules controlling individual access to feeding stations, we directly manipulated the foraging social network of a wild bird community, thus demonstrating how external factors can shape social structure. We show that experimentally imposed constraints were carried over into patterns of association at unrestricted, ephemeral food patches, as well as at nesting sites during breeding territory prospecting. Hence, different social contexts can be causally linked, and constraints at one level may have consequences that extend into other aspects of sociality. Finally, the imposed assortment was lost following the cessation of the experimental manipulation, indicating the potential for previously perturbed social networks of wild animals to recover from segregation driven by external constraints.

1. Introduction

Network approaches have long been acknowledged as an effective tool for studying animal sociality [1], and social interaction patterns recognized as imperative for understanding how selection acts upon individuals [2–4]. However, only recently have the necessary advances been made to allow large-scale tracking of individual associations and subsequent quantification of social structure [5,6]. Application of these approaches has discovered non-random social associations in numerous systems, and shown that these may be driven by a range of factors, including demographic classes [7], size [8], relatedness [9] or behavioural types [10,11]. Furthermore, social structure can show stability through time [12] and display consistency across different contexts [13–15].

Observed network structures also appear to be related to emergent processes, such as sexual selection [16] and inbreeding avoidance [17], and the spread of information [18,19] and disease [20–22]. Therefore, it is important to determine the drivers of network structure, as well as to characterize the flexibility of social networks and the relationships with population-level processes. Furthermore, the response of social networks to external perturbations or imposed constraints remains of much importance to advancing understanding of social systems and potentially animal conservation [23–25]. However, the difficulty of experimentally manipulating social associations has limited our understanding of the causes, and thus arguably the consequences, of network structure. Indeed, the lack of experiments in this area may somewhat reduce our confidence in the findings of network studies generally [26].

Fortunately, the monitoring of wild animals whose social structure is perturbed by single, incidental events has demonstrated that such factors may contribute to social segregation arising, yet this imposed assortment can dissipate as the effect of the perturbation is reduced [25,27,28]. Nevertheless, it remains unclear if the eventual loss of segregation is due to network resilience,

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Figure 1. Aerial photo of study area, marked to indicate key features. Numbers indicate original selective feeder site locations. 'E' shows where feeders which fed only even tagged individuals were positioned during the experimental manipulation, and '0' shows where feeders only allowing odd tagged individuals were located.

or simply restructuring. Further, owing to the uncontrolled nature of such rare, natural experiments, it is uncertain whether such environmental perturbations cause separation or exaggerate an underlying assortment, and whether perturbed social networks change permanently or tend to return to their earlier state.

Controlled experimental approaches aimed at directly manipulating social structure have so far been limited to removal and addition of individuals. For instance, manipulations using captive fish have found social ties can be maintained despite experimentally reduced cooperation via removal [29], and that the strength of a network's links influence whether or not it is disrupted by the introduction of novel individuals [30]. Similarly, social connectivity within wasp colonies (*Ropalidia marginata*) appears resilient to substantial loss of individuals, owing to the initial redundancy within the network [31]. Yet Flack *et al.* [32] demonstrated that temporary removal of key individuals can cause multiple changes to social structure in captive pigtailed macaque (*Macaca nemestrina*) societies.

Nevertheless, in addition to logistical and ethical challenges [23], simple addition or subtraction of individuals inevitably changes both population density and composition, which may have numerous effects independent of changes in social structure [31,32]. Further, networks considering the same individuals but different kinds of interactions or associations show correlations in overall structure and dyadic relationships [13–15,33], yet removal of individuals does not allow investigation of this. However, these cross-context correlations may have practical implications for animal welfare and conservation, particularly in predicting how disturbance to one social dimension may have implications for another [33], as well as being of interest for our understanding of sociality and general network theory [15].

In this study, we use a novel experimental method to enable fine-scale manipulation, and subsequent assessment, of a wild passerine bird social system. By controlling which birds were allowed to forage together at different electronically controlled feeding stations, we imposed social assortment and segregation between spatially affiliated and previously associated individuals. Assessing the social associations at these sites before, during and after manipulation enabled us to explicitly determine the flexibility and recovery of the social structure subject to external constraints. Finally, through independently monitoring associations at unrestricted ephemeral food patches, as well as at nest-boxes as individuals prospected for breeding territories, we determine whether a causal relationship exists between these different contexts, and how influences at one level may have carry-over effects into other components of sociality.

2. Material and methods

(a) Study system

This work took place as part of larger study examining the social ecology of wild birds in Wytham Woods, Oxford, UK (51°46′ N, 1°20′ W) [e.g. 11]. Great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*) and Eurasian nuthatches (*Sitta europaea*) were caught either at nest-boxes during the breeding season, or by mist-netting through the winter to include immigrants as well. Upon capture, birds were fitted with a standard metal British Trust for Ornithology (BTO) ring as well as a unique passive integrated transponder (PIT) contained in a plastic leg ring. As part of the core work, sunflower seed feeding stations equipped with radio-frequency identification (RFID) antennae (Dorset ID, Aalten, The Netherlands) were deployed in a stratified grid at 65 fixed locations throughout Wytham Woods; these were opened from pre-dawn until after dusk each weekend from September to February, and allowed detection of the time and location of individual's feeding attempts upon reading their PIT tag [11].

(b) Selective feeder sites

The current experiment was conducted between November 2013 and April 2014 in neighbouring areas of broadleaf deciduous woodland on the southern edge of the main study site (figure 1), partially separated from it by an area of scrub and arable land. These form part of the long-term study system described above and contain six of the 65 feeder stations. In November 2013, the six standard feeders were replaced with experimental feeder stations ('selective feeders'). Selective feeders followed the same design as the standard feeders but had a clear flap locked in position over the feeding hole. The unlocking

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mechanism, which would allow a bird access, was controlled by a programmable circuit board (Stickman Technologies, Southampton, UK) and was only activated when the antenna registered a PIT tag number specified to be granted access (specified prior to the experiment—see the electronic supplementary material). By this means, rules controlling which individuals had access to a feeding station could be imposed automatically. During the course of this study, these automated feeders were open every day, from pre-dawn until after dusk. Initially, all tagged individuals were granted access to all the feeders; this period is referred to as 'pre-manipulation'. After 40 days' acclimation, the experimental treatment was applied by introducing a selective regime, controlling individual access to feeders. Two selective feeders replaced each of the initial feeders, both placed approximately 50 m from the initial location (figure 1). In each case, the antenna on the feeder recorded all visits to the feeder, but one feeder within each pair was programmed to grant access only to individuals with a PIT tag ending in an odd digit, while the other would only allow access to even-digit PIT tags. This treatment enabled us to split the population into two randomly selected, equally sized groups. This time period is referred to as 'during manipulation'. After 90 days' exposure to this condition, these 12 feeders were reset to allow access to all tagged individuals, which are referred to as the 'post-manipulation' period. This final period was limited to 6 days in order to minimize the impact of supplementary feeding on breeding performance and behaviour.

(c) Ephemeral food patches

We aimed to test whether the constraints imposed at the selective feeder sites were reflected in the association patterns at unrestricted, ephemeral food patches. These were created by putting four small sunflower seed feeders [18], equipped with RFID-reading antennae (Francis Instruments Ltd., Cambridge) in randomly selected positions throughout the study area (with the constraint that they were at least 50 m from a selective feeder site). These collected data on all birds visiting and were removed after 4 days. This was carried out once during the pre-experimental period and four times during the experimental treatment, with a 10-day interval between trials. It was not repeated in the post-manipulation period as we aimed to limit interference during this shorter time period.

(d) Nest-box recording

We also examined whether the manipulation of individual access to feeding sites also influenced which individuals would be likely to encounter one another during breeding site prospecting. We fitted nest-box RFID recorders (Dorset ID, Aalten, The Netherlands) to a randomly selected one-third (44/133) of the nest-boxes located in the largest continuous area of woodland (figure 1). These scanned for PIT tags three times per second and recorded any individuals that landed on the entrance hole while prospecting for breeding territories. This began before any nesting attempts were recorded, 12 days before the removal of the selective feeder sites (in March 2014), and continued for 24 days in total to April 2014. We did not monitor nest-boxes in the pre-manipulation period as territory prospecting only begins in late winter/early spring.

(e) Social network construction

PIT tag detections from both types of feeder provide a spatio-temporal data stream, which shows intermittent bursts of activity as flocks of individuals come in to feed. Foraging flocks (groups) were detected using a Gaussian mixture model. This model exploits the non-homogeneous profile to statistically assign each visit to the group for which it has the highest probability of belonging to [34]. We also aimed to infer associations taking place while individuals prospected for breeding territories. Typically, only a small number of individuals visit each nest-box each day (mean = 1.7), and preliminary analysis of a larger dataset (B. Verhelst & B. C. Sheldon 2012, unpublished data) found individuals land on the entrance numerous times, usually spanning over 4 h on average, with this peaking between 8.00 and 12.00. Also, birds landing on the entrance hole of a nest-box typically engaged in activity in the surrounding vegetation (J. A. Firth 2014, personal observation). Thus, groups were defined simply as individuals detected on the same nest-box during the same day, and co-memberships represent individuals that overlapped in nest-box exploration patterns during the same day. Although this is a longer temporal period than for groups defined from foraging flocks, the spatial scale (44 boxes within one area of woodland) is of much higher resolution. Networks were calculated from these group-by-individual matrices using the half-weight index [35]. While our approach essentially relies on the gambit of the group for inferring associations [36], the extensive sampling employed and use of weighted networks in further analysis reduces the limitations of this approach [37–39].

(f) Network assortativity

We predicted that the experimental manipulation would impose assortment by tag type (i.e. birds with even pit tag numbers would be likely to be associated with other individuals with even tags, and odd-tagged individuals with other odd-tagged individuals) within the network. The degree of such homophily within the network was measured using the widely used assortativity coefficient [40,41] that has recently been extended to incorporate weighted associations using the R package *assortnet* [42,43]. Positive values demonstrate assortativity, with perfectly segregated networks scoring 1, and negative values represent disassortment. Perfectly integrated networks do not always score −1 as the minimum value depends on the number of node types and relative number of ties within each group [41]. The associated standard error was calculated using jackknifing [41,43]. However, to account for the non-independence of network data, the assortment coefficients were compared with results calculated from 10 000 randomized networks generated via node permutation (i.e. maintaining the node labels while shuffling the rows and columns) of the considered network, which allows permutation of individuals' tag types while maintaining the observed association patterns, levels of gregariousness and distribution of types [44,45].

(g) Network consistency

As well as assessing levels of imposed assortment by tag type, we examined network consistency. First, we used Mantel tests [46,47] using the R package *ecodist* [48] to compare the pre-manipulation social network with the entire networks created both during and after the manipulation. As the post-manipulation network was derived from a smaller sampling period than the during-manipulation network and was more temporally separated from the pre-manipulation period, we constructed networks for each consecutive 6-day time window, and compared each of these with the final 6 days of the pre-manipulation network and with the 6 days of the post-manipulation network. Second, Mantel tests were used to examine the relationship between the association patterns at the selective feeder sites and those at the ephemeral food patches and nest-boxes. We compared networks derived from each 4-day deployment of ephemeral food patches with the networks at the selective feeder sites 4 days before the food patches were deployed (to avoid any interference that the food patches may have had). We also compared the nest-box network with the selective feeder networks. To do this, we used the final 6 days of the manipulation period and the 6-day post-manipulation period. We split both of these periods into two 3-day networks,

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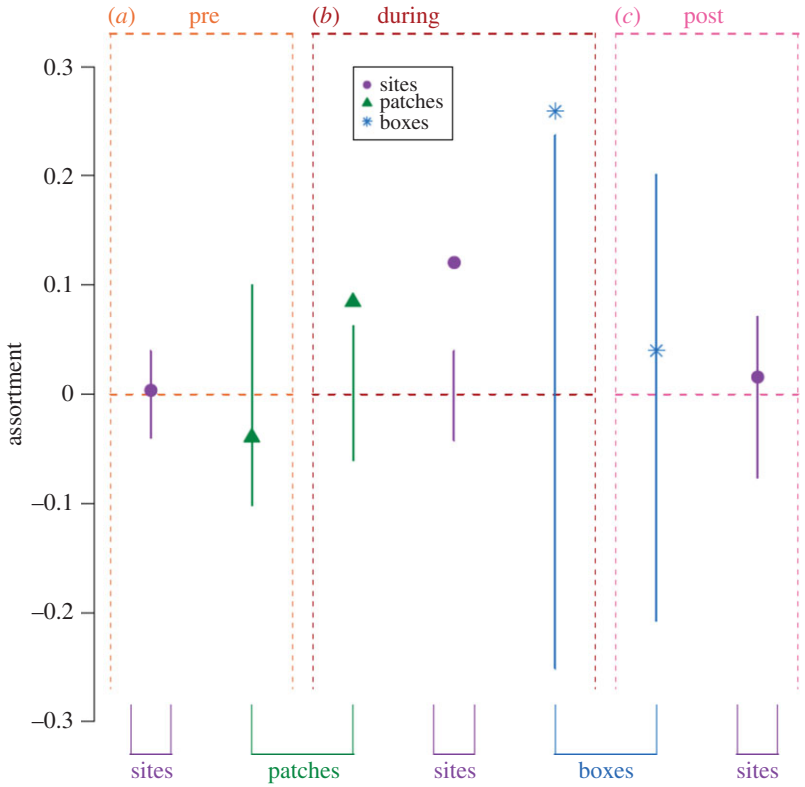


Figure 2. The observed level of assortment by PIT tag type in the system over the different periods and social contexts. Vertical lines show the 95% range of the assortment coefficients calculated from permuted data. Dots indicate the observed assortment coefficient. Colours of lines and point types illustrate data from different contexts (purple circle, selective feeder sites; green triangle, ephemeral patches; blue star, nest-boxes; base × axis). (*a*) 'Pre-manipulation' period. (*b*) 'During-manipulation' period. (*c*) 'Post-manipulation' period.

and comparisons were drawn between the selective feeder site networks and the nest-box networks simultaneously in time. In all cases, Mantel tests were run including only individuals observed in both of the matrices that were being compared.

A relationship between the social associations at the selective feeder sites with either of the other two social contexts might simply be driven by the spatial distribution of individuals, where those sharing the same home range could be more likely to encounter one another over all dimensions [12]. Therefore, we employed a multiple regression quadratic assignment procedure with double semi-partialing (MRQAPDSP) [49] using the R package *asnipe* [50], which allows a single dependent matrix to be regressed against multiple independent matrices. The dependent matrix was set as the social association matrix of the context of interest, while the independent matrices were (i) a binary spatial range overlap matrix, where only dyads occurring at the same selective feeder site (figure 1) over the considered time period (i.e. 4 days for when comparing to ephemeral patches, 3 days for nest-boxes) were scored 1, and (ii) a social association matrix at the selective feeders. This allowed us to determine the relative contribution of both the fine-scale social associations at the selective feeder sites the spatial range overlap of individuals to the associations within the other contexts.

3. Results

Over the entire study period the selective feeder sites collected 3.06 million records of visits from 376 individuals. From this, 67 027 groups were detected using the Gaussian mixture model (see Material and methods) with a mean size of 3.8 ± 0.01 while the typical flock size (i.e. group size experienced by the average individual) was 5.8, and these gathering events lasted an average of 191 ± 0.6 s. 339 birds were detected during the experimental manipulation period; these individuals contributed 3.04 million (more than 99%) of the total records, and included all the study species and showed frequent movements around the sites (electronic supplementary material, tables S1 and S2). Since these individuals were subject to the treatment, they were included in all further analyses. However, we also ran the analysis considering (i) only the primary Wytham study species, *Parus major* (1.48 million records, 136 individuals), and (ii) only those individuals that were detected on the selective feeders before, after and during the manipulation, therefore indicating they were using the study area over the entire period (2.51 million records, 109 individuals). The results using these subsamples demonstrated similar effects as those discussed below, but differed in levels of statistical significance, probably due to the reduced sample size (electronic supplementary material, figure S2).

(a) Experimentally imposed social assortment

No assortment by tag type was detected at the selective feeders in the period before the experimental treatment began (weighted assortativity coefficient: $r = 0.003 \pm 0.007$, $n = 204$) and this did not differ significantly from the assortment values generated from the permuted networks (figure 2*a*). A similar pattern was also found at the ephemeral food patches ($r = -0.039 \pm 0.031$, $n = 53$; figure 2*a*). Therefore, the assumption that associations are random with regard to tag type prior to the experimental manipulation, and that any changes are the result of the treatment, appears valid.

During the manipulation period, relatively strong assortment by tag type was observed at the selective feeders ($r =$

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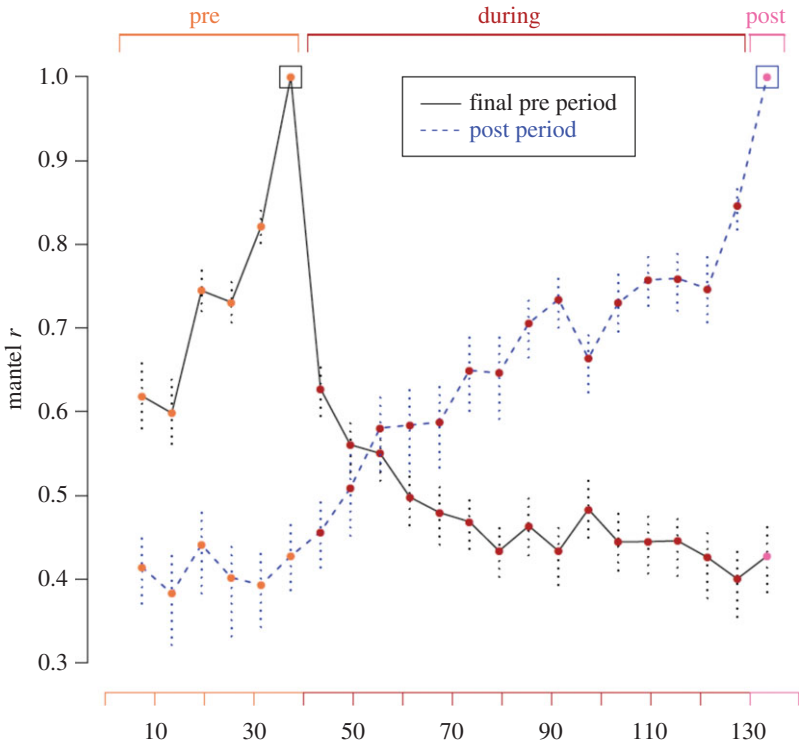


Figure 3. Mantel test results comparing each 6-day network to the final 6-day network of the pre-experimental period (solid black line) and to the 6-day post-experimental network (dashed blue line). Point colour denotes experimental period. Boxes show point of comparison. Vertical dotted lines indicate 95% range of Mantel test statistic.

0.121 ± 0.005, $n = 339$), which was also significantly higher than the assortment observed in the randomized data (figure 2*b*). Therefore, the experimental treatment successfully imposed assortativity by tag type, so that birds of the same type became more strongly associated with each other than with individuals of the opposite type.

Over the experimental manipulation period, 141 out of 147 (96%) individuals using the ephemeral patches and 54 out of 64 (84%) individuals recorded prospecting at the sampled nest-boxes were also detected at the selective feeder sites. This allowed us to assess whether the segregation imposed at the selective feeder sites was carried over into other aspects of sociality. Indeed, assortment by tag type was observed in both of these independently measured contexts (patches: $r = 0.084 \pm 0.01$, $n = 141$; boxes: $r = 0.259 \pm 0.014$, $n = 54$) and this was also significantly higher than in the permuted data (figure 2*b*). Therefore, we found clear evidence of carry-over of the experimentally imposed effect onto the associations occurring in non-manipulated social contexts.

Following the cessation of the manipulation, the assortment observed in the associations at the selective feeders returned to its initial low value and was once again not significantly different from zero ($r = 0.016 \pm 0.010$, $n = 124$) or the randomized networks (figure 2*c*), therefore demonstrating a recovery from the imposed segregation. This was also mirrored in the associations at the nest-boxes after the manipulation period ($r = 0.040 \pm 0.021$, $n = 74$; figure 2*c*).

This apparent recovery (i.e. loss of the experimental condition) was not due to a lack of power to detect assortment at the selective feeder sites over the shorter 6 days of the post-experimental period, as assortment during the experimental period was detected in all but one case when split into 6-day periods (electronic supplementary material, figure S3). Moreover, the post-experimental period had lower assortment than any of the 6-day experimental period sections (electronic supplementary material, figure S3).

(b) Network consistency

There was no evidence that this loss of the experimentally induced assortment at the selective feeders was driven by a reversion to the same social network structure as that prior to the manipulation, as the Mantel correlation between the pre-manipulation network and the post-manipulation network was not higher than the correlation between the pre-manipulation network and the during-manipulation network (Mantel test—pre versus during: $r = 0.55$, lower $= 0.45$, upper $= 0.67$; pre versus post: $r = 0.49$, lower $= 0.19$, upper $= 0.63$). This remained true when networks were created from 6-day periods to assess consistency over more equal sampling periods and time scales. Here, the final 6 days of the pre-manipulation period did not predict the post-manipulation network more strongly than it predicted 6-day 'during-manipulation' networks (figure 3). Therefore, no evidence of a 'reset' to previous specific dyadic associations was evident following the experiment. Similarly, the post-manipulation network was not more strongly related to the 6-day pre-manipulation networks than it was to the 6-day during-manipulation networks (figure 3). Beginning the manipulation immediately and strongly affected the network, but it monotonically and gradually approached its post-treatment structure, just as the pre-treatment networks approached the final pre-treatment structure (figure 3). These patterns remained even when only considering individuals that appeared in every 6-day period (electronic supplementary material, figure S4).

Associations at the set selective feeder sites were highly consistent with those at ephemeral food patches and during nest-box prospecting (table 1). Further, consistency levels between the social network at the set selective feeder sites

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Table 1. Mantel (column 4) and MRQAPDSP (columns 5 onwards) results of the relationship between the set selective feeder site social network and ephemeral patches and nest-boxes networks over the different periods (in relation to when the manipulation was applied). Mantel *R* gives 95% range, and test statistic in bold. MRQAPDSP results show estimate and *p*-value for (i) social networks and (ii) spatial co-occurrences, along with full model statistics.

context	period	days	Mantel *R*	social coeff.	social *p*.	spatial coeff.	spatial *p*.	full F.	full R^2
patches	pre	34–37	0.24–**0.33**–0.40	0.45	<0.001	0.012	0.36	46	0.108
	during	75–78	0.35–**0.40**–0.45	0.306	<0.001	0.11	<0.001	460	0.334
		89–92	0.38–**0.46**–0.51	0.393	<0.001	0.037	<0.001	147	0.228
		103–106	0.28–**0.37**–0.43	0.367	<0.001	0.063	<0.001	149	0.195
		117–120	0.35–**0.40**–0.45	0.338	<0.001	0.031	<0.001	141	0.18
		124–126	0.36–**0.48**–0.56	0.783	<0.001	0.008	0.718	55	0.222
		127–129	0.31–**0.38**–0.43	0.559	<0.001	0.021	0.338	21	0.138
boxes	post	130–132	0.39–**0.47**–0.55	0.745	<0.001	0.002	0.863	85	0.221
		133–135	0.31–**0.41**–0.51	0.665	<0.001	−0.012	0.322	53	0.166

with the other contexts showed no large differences between when the experimental manipulation was applied and in its absence (table 1). MRQAPDSP models showed that the social association matrix at the selective feeders had a large significant effect on the social association network created from the nest-boxes (table 1). Yet a matrix simply measuring range overlaps between individuals (spatial range overlap matrix) yielded no significant relationship (table 1). Therefore, the consistency of the selective feeder site network with the nest-box network was driven primarily by fine-scale social associations, rather than simply the spatial distribution of individuals. Similarly, although spatial range overlap had a significant effect on associations at ephemeral food patches, the selective feeder social network had between 3- and 10-fold greater effect (table 1). It should be noted that the spatial location of individuals may also be related to social choices at a coarser scale, as individuals moved freely around the selective feeder sites (electronic supplementary material, table S1) and may occur in particular areas due to the other individuals that are there. Over the 6-day periods considered for social network consistency at the selective feeder sites (figure 3), spatial range overlap between individuals remained highly consistent (approx. 0.65 Mantel *R*; electronic supplementary material, figure S5), and the manipulation did not influence this (electronic supplementary material, figure S5).

4. Discussion

Using a novel social network experiment, we demonstrated how external factors can govern associations between individuals. The effect of altering the distribution of resources available to different individuals within the same community was carried over into other aspects of social structure, yet the imposed segregation was lost following removal of the treatment. These findings were obtained by imposing rules about which individuals could forage together at different feeding sites, within a large community of wild birds fitted with RFID tags.

Monitoring wild animals subject to particular perturbations has already been extremely valuable in understanding how external factors may shape social structure, such as the observation of two distinct groups existing within a single population of bottlenose dolphins (one that fed from prawn trawlers and another that did not) [25,27]. Yet individuals may respond differently to such environmental effects based on individual differences (e.g. cognition or learning strategies), and separate groups may exist even before the perturbation. Therefore, by using a controlled experiment that determines individuals' resource access entirely randomly with respect to innate differences and prior social ties (figure 2*a*), we demonstrate that external factors alone are indeed capable of manipulating social structure. Furthermore, this imposed segregation is maintained despite continued spatial range overlap between individuals and is transferred to non-manipulated social contexts (figure 2*b*).

This flexibility provides insight into how systems with high fission–fusion dynamics, such as these birds [51], can respond to perturbations, and may differ from that, for example, of dolphin societies, where numerous strong relationships may be present [25,27]. However, even within this system, previous work has indeed revealed non-random social network structure, as well as relationships to individual traits, such as sex and personality [11]. Also, while numerous relatively weak bonds exist, such as

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interspecific associations [43,52], even these are known to be important (for example, to information flow [18]), and strong, non-random bonds, such as mated pairs also occur [34,51]. Further research is now needed to clarify how the strength or type of association determines their vulnerability to perturbation, the consequences of this, and how mechanisms of decision-making at the individual level relate to higher-order network structure.

We found that the experimentally driven partitioning of birds according to tag type was lost upon removing the treatment (figure 2*c*; electronic supplementary material, figure S3). We demonstrated that this recovery from the imposed segregation did not comprise a return to a social structure identical to that prior to the manipulation (figure 3), but rather simply allowed free mixing of individuals once again. This also may be expected from the system's fission–fusion dynamics, as the stability of such groups is thought to be reasonably low [51]. Hence, the social network may rapidly return to expressing non-manipulated properties following the loss of previous constraints. This is in line with the findings among bottlenose dolphins that removing the external factor resulted in the loss of segregation [25].

Finally, although the network recovered from the segregation once it was no longer imposed, association patterns during the treatment phase were maintained across different contexts. The social network at the selective feeder sites closely matched those at ephemeral, non-restricted food patches and at nesting sites during breeding territory prospecting (table 1). Although there seems little previous work in birds, research on mammals has suggested relationships between associations within different contexts may be driven by the spatial distribution of individuals [13,14,33]. Here, by considering spatially affiliated individuals, and subsequently separating the effects of spatial range overlaps and social association, we showed that the experimentally imposed associations at the selective feeder sites were a much stronger predictor of the associations within the other contexts than the simple range overlaps of individuals (table 1). Previous studies of mammals have suggested that changes or perturbations to interactions within one context may influence associations within another [33,53,54]. Yet experimental manipulations influencing associations within one context alone were needed to assess whether these can directly influence associations in another, and indicate whether perturbations or constraints within single contexts may carry over. Here, we show that the arbitrary imposed constraints on social associations at the selective feeder sites carry over to the networks in open ephemeral food patches and during territory acquisition (figure 2), thus clearly demonstrating the causal relationship between social contexts, and the potential for external factors which influence associations within one dimension to impact upon other aspects of sociality.

Along with testing the causes of social network structure, experiments directly manipulating social structure will also enable the causal links to be established between social networks and emergent processes, such as mating decisions and the transmission of disease and information [16–22]. As an example, Aplin *et al.* [18] showed that in mixed flocks of tit species (Paridae; as studied here) discovery of novel food patches increased with the centrality of an individual, and appeared to transfer between social companions. This suggests a relationship between social structure and information transfer. However, further work by Aplin *et al.* [11] has shown that the network of one of the study species (*Parus major*) is significantly assorted by standardized measures of exploration behaviour, a trait that is also known to be linked to foraging behaviour [55], and also that relatively fast explorers occupy more central network positions [11]. Therefore, rather than social structure being instrumental in determining resource discovery, it is possible that the association is founded on an underlying trait correlated with both. Thus, while correlational evidence indicates social networks may affect emergent processes [16,18–22], experiments directly manipulating associations are needed to establish how causal these links are, and at what scale they operate.

In this study, we have demonstrated that these direct fine-scale manipulations of social structure are indeed possible. This revealed that social networks are flexible, and external factors can impose social segregation between spatially affiliated individuals. Furthermore, this assortment is also manifested within social contexts where the constraint is not enforced, thus demonstrating the potential for external factors to have knock-on effects into multiple aspects of sociality. Nevertheless, recovery from the externally imposed segregation is achieved rapidly in this fission–fusion system. Future experiments directly manipulating various social networks will enable explicit assessment of other properties of social structure, as well as links to wider processes.

Data accessibility. Data are available on Dryad (doi:10.5061/dryad.dh777).

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Author contributions. J.A.F. collected and analysed the data. J.A.F. and B.C.S. designed the research and wrote the manuscript.

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Conflict of interests. We have no competing interests.

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SUPPLEMENTARY INFORMATION: Experimental manipulation of avian social structure reveals segregation is carried over across contexts

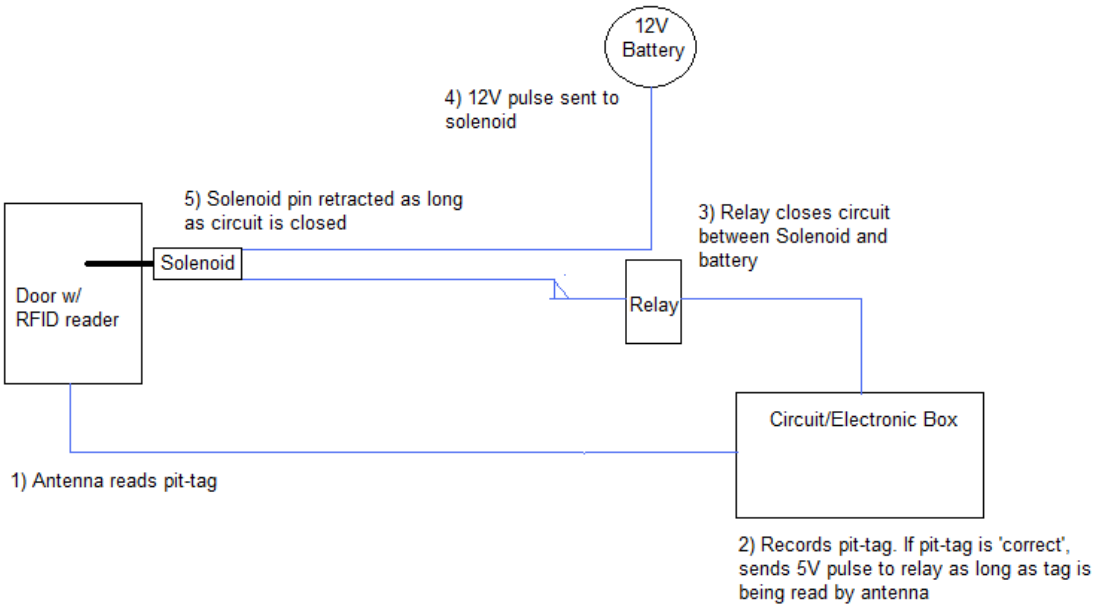


Figure SI 1. Logic flow of selective feeder. A hinged, clear, door/flap over the feeding hole is held shut by a vertical solenoid pin. Upon the antenna reading a PIT-tag, the printed circuit board (PCB) (Stickman Technologies Inc. Southampton, U.K.) determines whether this is specific tag is allowed access, and if so it activates the relay that closes the circuit between the 12V battery and the solenoid, causing the pin to be retracted. Upon the bird leaving, the door/flap closes. The relay breaks once the tag is no longer being read by the antenna and the solenoid pin is reset to its original position, holding the door shut.

Table SI 1. The number of 339 considered individuals recorded at each site (diagonal) (See Figure 2; where 'E' and 'O' at single sites are grouped together) and the number of individuals shared between each pair of sites (Off-diagonals).

	1	2	3	4	5	6
1	73					
2	48	71				
3	16	17	57			
4	32	30	13	217		
5	16	18	7	109	133	
6	12	13	7	63	44	84

Table SI 2. The species composition of the 339 considered individuals at each site. Final column shows number of individuals detected over all sites

	1	2	3	4	5	6	All
Blue tit	37	30	30	121	60	40	178
Great tit	32	36	23	81	59	36	136
Marsh tit	3	4	2	7	8	5	12
Nuthatch	1	1	2	4	2	0	7
Coal tit	0	0	0	4	4	3	6

Table SI 3. Sample size information for Figure 3. The total number of individuals within each of the 22 6-day periods (First row), along with the number shared with the 'final pre experiment' period (Second row) and the 'post experiment' period (Third row). Colours denote the experimental period as in Figure 3 i.e. orange = pre-experiment, red = during experiment, pink = post-experiment

PRE						DURING														POST
131	135	126	135	145	149	165	174	152	164	160	172	154	164	152	143	145	151	139	124	125	122
103	109	113	116	124	149	130	126	117	118	118	120	112	112	106	106	103	106	99	93	93	92
82	88	82	85	94	92	101	101	95	102	109	108	105	108	109	108	110	108	112	109	111	122

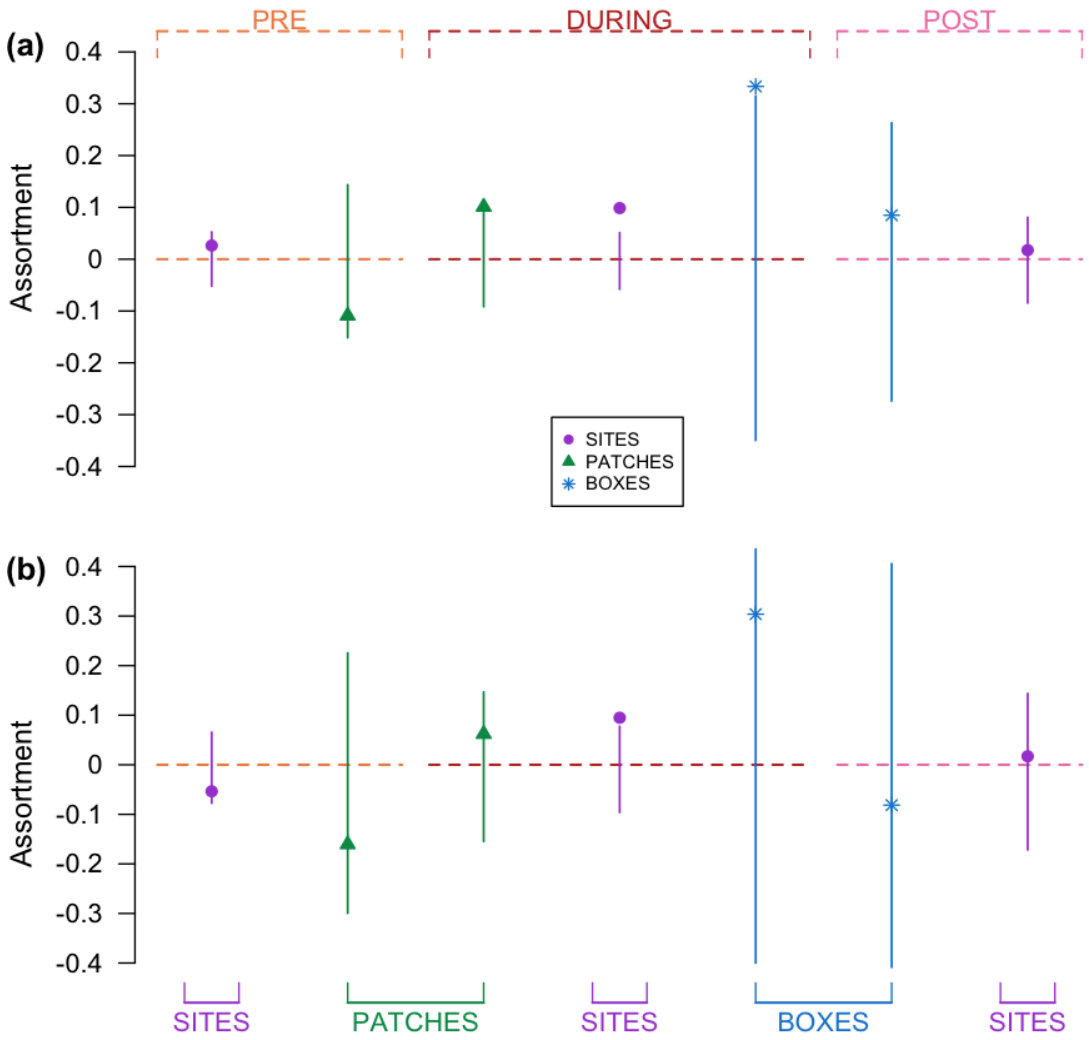


Figure SI 2. Results of supplementary analysis considering subsamples of individuals (See Figure 2 for all individuals, and Methods for description). The observed level of assortment by tag type in the system over the different periods and social contexts. Vertical lines show the 95% range of the assortment coefficients calculated from permuted data. Dots indicate the observed assortment coefficient. Colours of lines and point types illustrate data from different contexts (Purple circle = selective feeder sites, Green triangle = ephemeral patches, blue star = nest boxes; base x axis). A) Only individuals detected at the selective feeders before, during, and after the experimental manipulation. B) Only great tits (*Parus major*).

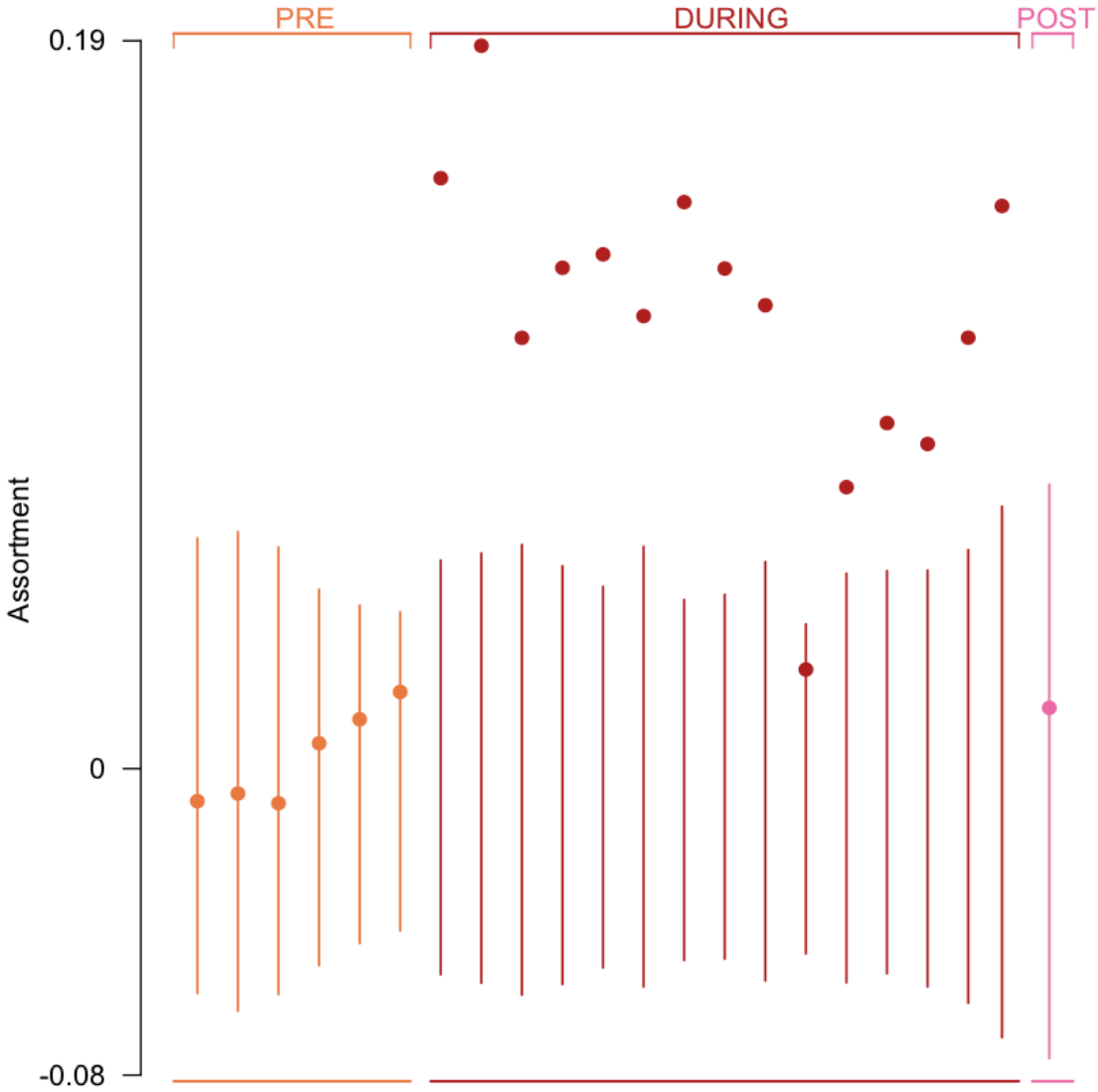


Figure SI 3. Assortment by tag type at the selective feeder sites analyzed in 6 day periods over the three measures. Vertical lines show the 95% range of the statistics derived from permuted data. Dots indicate observed value. Where the vertical lines overlap the stars there is no significant difference between the observed statistic and the null models. Colours illustrate different periods (x axis).

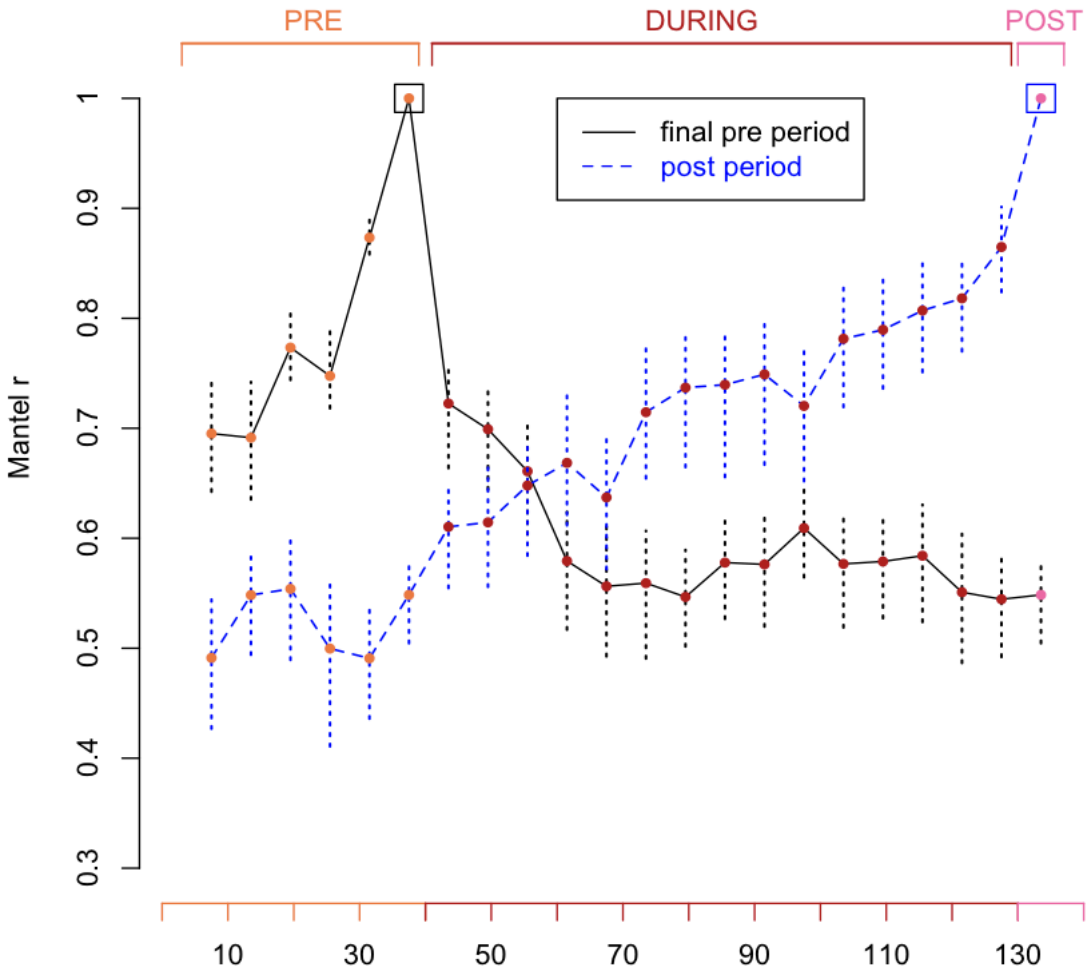


Figure SI 4. Mantel test results comparing each 6 day network to the final 6 day network of the pre-experimental period (solid black line) and to the 6 day post experimental network (dashed blue line), but only considering the 54 individuals that were observed in all 6-day periods (in comparison to Figure 3, which includes all individuals). Point colour denotes experimental period. Boxes show point of comparison. Vertical dotted lines indicate 95% range of Mantel test statistic.

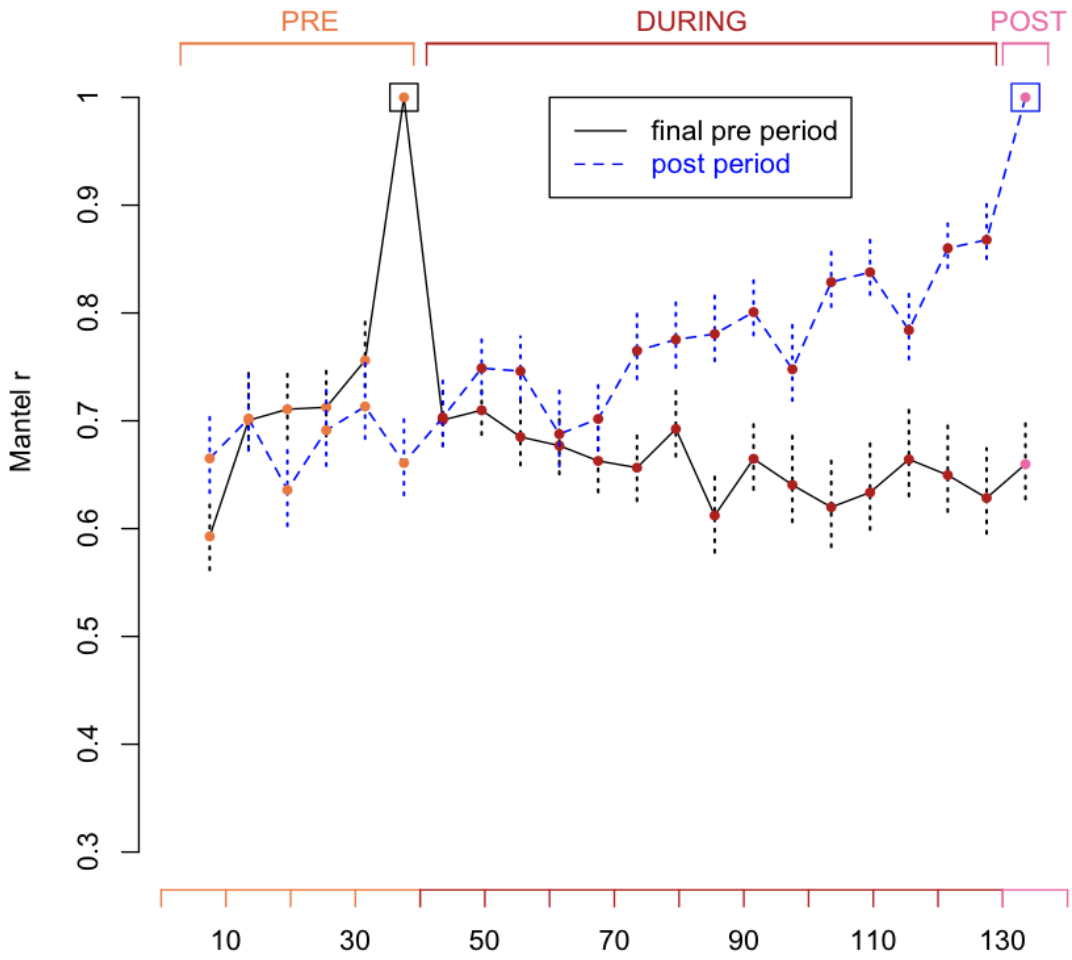


Figure SI 5. Mantel test results comparing each 6 day spatial range overlap matrix to the final 6 day spatial range overlaps of the pre-experimental period (solid black line) and to the 6 day post experimental spatial range overlaps (dashed blue line). Point colour denotes experimental period. Boxes show point of comparison. Vertical dotted lines indicate 95% range of Mantel test statistic.

Chapter 6

Pathways of information transmission amongst wild songbirds follow experimentally imposed changes to social foraging structure

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Animal behaviour

Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure

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Animals regularly use information from others to shape their decisions. Yet, determining how changes in social structure affect information flow and social learning strategies has remained challenging. We manipulated the social structure of a large community of wild songbirds by controlling which individuals could feed together at automated feeding stations (selective feeders). We then provided novel ephemeral food patches freely accessible to all birds and recorded the spread of this new information. We demonstrate that the discovery of new food patches followed the experimentally imposed social structure and that birds disproportionately learnt from those whom they could forage with at the selective feeders. The selective feeders reduced the number of conspecific information sources available and birds subsequently increased their use of information provided by heterospecifics. Our study demonstrates that changes to social systems carry over into pathways of information transfer and that individuals learn from tutors that provide relevant information in other contexts.

1. Introduction

Many animals use social information when making decisions related to fitness, such as for breeding and foraging [1–5]. Recent studies show that information transmission follows social network structure [2–5]. However, it has remained challenging to assess how changes to social structure directly influence information flow [6] or whether social information use itself—owing to its importance—can drive individuals' social associations [7,8]. If the social information produced by certain associates becomes irrelevant, individuals might modify which of their existing associates they learn from [9] or change associates altogether.

Through experimentally manipulating the social foraging associations occurring among wild songbirds, we test how social information transmission is dependent upon social structure. First, as individuals are predicted to gain new information from those they are in contact with, we test whether birds learnt about new ephemeral food sources predominantly from individuals they were experimentally induced to associate with. Second, while changes in information pathways may reflect changes in contact patterns, this could be exaggerated if individuals adaptably direct their learning towards those that provide relevant information. To test whether birds used this social learning strategy, we quantified whether birds disproportionately acquired

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information from individuals that could regularly access the same resources as themselves.

2. Material and methods

(a) Study system

The experiment took place in three plots at Wytham Woods, Oxfordshire, UK between September 2013 and March 2014 (see [10] for details). Great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*) and Eurasian nuthatches (*Sitta europaea*) were fitted with unique but randomly numbered radio frequent identification (RFID)-transponders when caught during the breeding season or by winter mist-netting [4].

RFID antenna-equipped sunflower seed feeding stations continuously recorded the times of individuals' feeding visits at six locations for 40 days. We then replaced each feeder with two 'selective' feeders (placed approx. 100 m apart). Selective feeders had clear flaps locked over the feeding hole, which could be unlocked based on a bird's identity (see the electronic supplementary material, videos). At each site, one selective feeder was programmed to allow access only to birds with even-numbered RFID-tags and the other only allowed odd-numbered birds (but both recorded all visits, irrespective of tag-type). Birds of the same tag-type could access the same feeding stations as one another (termed 'matched' dyads), while those of the opposite tag-type could only access different feeding stations from one another (termed 'mismatched' dyads). We ran this manipulation for 90 days, during which time birds with odd and even tags remained spatially overlapping but became socially segregated [10], as they quickly learnt which feeders they could access [11].

We constructed one social network from the data before the experimental manipulation (40 days) and one during (90 days). We used machine-learning algorithms to identify distinct flocks visiting each feeder [12,13] and constructed social networks given individuals' co-occurrences in flocks using the simple ratio index [14] defined as $S_{AB} = x/(x + R_A + R_B + R_{AB})$, where S_{AB} is the social association between birds A and B; x is the number of observations of A and B co-occurring together; R_A and R_B are the number of times A was recorded without B or B without A and R_{AB} is the number of times both birds were simultaneously observed apart.

(b) Information transfer

To assess information flow [2,5], we used small RFID antenna-equipped feeders to create ephemeral food patches that were freely accessible to all birds and automatically recorded the time when each individual discovered them. Each trial consisted of leaving four such feeders out in random locations (at least 50 m from selective feeders) for four days. We conducted one trial prior to, and four trials during, the manipulation period (leaving 10 or more days between each).

We applied a recent variant [5] of network-based diffusion analysis (NBDA). NBDA estimates the rate, s, that individuals learn from knowledgeable tutors (social information transmission) compared to gaining the new information by themselves independently of others (asocial learning [15,16]; see the electronic supplementary material). The multi-network approach [5] estimates different s parameters for different types of social associations and hence allows inference about the relative importance of different information transmission pathways.

We first fitted individuals' discovery times of the novel food patches during the pre-manipulation period to the pre-manipulation (baseline) social network. We partitioned the network into four components: (i) matched conspecifics, (ii) matched heterospecifics, (iii) mismatched conspecifics, and (iv) mismatched heterospecifics. We expected to see greater information transfer (i.e. higher s) for social associations between conspecifics than between heterospecifics [5], but no difference in s values between those of matched and mismatched tag-types (as all individuals could access all pre-manipulation feeding stations).

Next, we fitted patch discovery times during the manipulation period to the pre-manipulation network. Once the manipulation was introduced, individuals become more strongly associated with matched birds (those that could access the same feeding stations as them [10]). Thus, if individuals gain information from those they continually associate with, we expected that mismatched individuals who were previously connected (in the baseline network) would no longer transmit information to one another (lower s), and matched individuals would learn from one another faster (higher s).

Finally, we fitted patch discovery times to the manipulated network to determine whether individuals also demonstrated a social learning strategy. If the s parameter is higher in matched dyads, it suggests that individuals disproportionately copied individuals who would access the same feeding stations as themselves over those they are equally associated with but could only access different feeding stations, i.e. the mismatched individuals they continued to co-occur with during the manipulation (see the electronic supplementary material). This inference is possible because the s parameter quantifies the increase in the rate of information transfer *per unit* of social association to knowledgeable individuals [16].

We used an information-theoretic approach when fitting parameters [16], summing Akaike weights to calculate the support for hypotheses regarding information transfer between (i) conspecifics, (ii) heterospecifics, (iii) matched dyads, (iv) mismatched dyads, and combinations of these. Following previous work [2,5], we took a conservative approach to inferring rates of social information use by removing discoveries between individuals that were within 10 min of each other to discard any occasions of birds discovering food together.

3. Results

(a) Data summary

The pre-manipulation social network comprised 10 954 flocking events, with 50 201 co-occurrences among 240 unique individuals. The network during the manipulation comprises 52 483 flocks, with a total of 187 232 co-occurrences among 339 individuals. Novel ephemeral food patches logged 275 discoveries, with 98% of the 148 birds discovering one or more novel patch also occurring at the selective feeders (electronic supplementary material, table S1). Discovering food patches was unbiased relative to tag-type; the distribution of odd-tagged and even-tagged birds among food patches was not significantly different from that expected given the ratio of tag-types (multiple-binomial test $\chi^2 = 25.11$, $p = 0.07$).

(b) Information transfer

Before the manipulation began, the rates of information transmission (model-averaged estimates of s) following the baseline network were equal between matched and mismatched dyads (figure 1*a*). However, when fitting the baseline network to patch discovery times during the manipulation, pathways of information transmission were notably different (figure 1*b*). While information was still transmitted within the original conspecific and heterospecific networks, including among mismatched dyads, we found strong support for differing rates of information transfer among networks (98% support; see the electronic supplementary material, table S2 for full hypothesis testing). Matched dyads were much more likely to transfer

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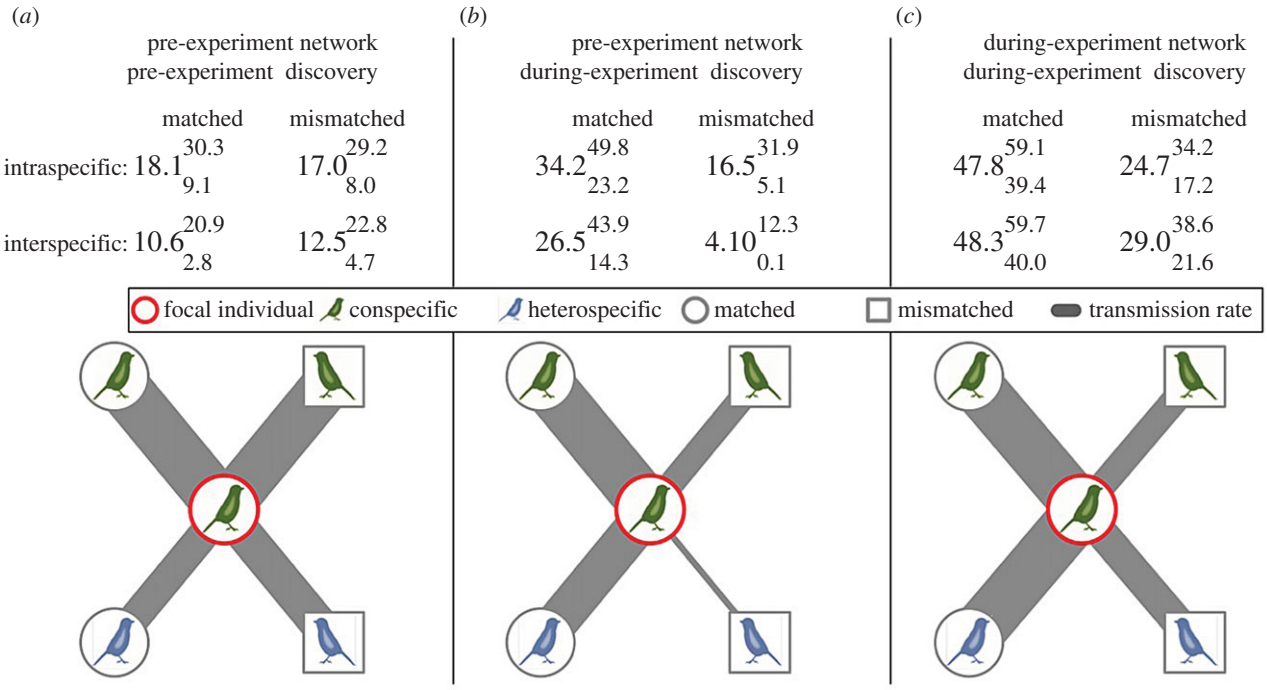


Figure 1. Results of network-based diffusion analysis using: (*a*) pre-experimental network to predict patch discoveries pre-experiment, (*b*) pre-experimental network to predict patch discoveries during experiment and (*c*) network during experiment to predict patch discoveries during the experiment. Grids show model-averaged estimates of *s* for each network type (upper and lower 95% intervals as superscript and subscript, respectively). Diagrams illustrate information transfer between a focal individual (centre) and different types of individual with which they hold equal social associations to within the network (types correspond to grid values). 'Matched' refers to individuals who could access the same selective feeder stations as the focal and 'mismatched' refers to those who could only access different stations from them. Line thickness shows relative value of *s* within each panel (scaled by maximum *s* estimate); direct comparisons across panels are difficult as parameter estimates also depend on the accuracy and density of the social network.

information than mismatched dyads (figure 1*b*). Therefore, individuals acquired information regarding new food sources from those they were experimentally induced to associate with. This effect was particularly evident for heterospecific associations.

Using the experimentally manipulated networks from the selective feeders, we again found support for information transmission across all types of social associations. However, some components of the network were more important for information transfer (electronic supplementary material, table S2). Although *s* values give the rate of information transfer per unit of social association, a significant difference in *s* values between tag-types remained. Information was twice as likely to transfer between matched individuals than between mismatched individuals (figure 1*c*). Yet, while individuals learnt about novel food patches from those that could access the same selective feeding stations as themselves (figure 1*c*), the social associations inferred from flocking co-occurrences at the new food patches after individuals discovered them were equally related to those inferred from the selective feeders for both matched and mismatched dyads (see the electronic supplementary material). Thus, despite the fact that all individuals could access the ephemeral food patches equally, individuals disproportionately learnt from others who could access the same selective feeding sites as themselves, even when controlling for association strength. Additionally, transmission rates within and between species became more similar.

4. Discussion

We demonstrate that experimentally manipulating social structure in a wild animal community changes pathways of information transmission. Individuals acquired information about novel food patches from those they were experimentally induced to forage with. Furthermore, over and above the changes to foraging associations, we show preferential use of information provided by birds that produced relevant information in other contexts (i.e. those that could access the same selective feeding stations), despite the fact that the information about freely accessible food was equally valid from all individuals.

A recent laboratory study found that increasing environmental complexity modified social structure, which consequentially increased social transmission [6]. Our study demonstrates that externally driven social segregation linked to an arbitrary phenotype is reflected in patterns of information spread. This could have important implications. For example, cultural divergence can occur when information is transferred primarily within groups [8], which may subsequently restrict gene flow and encourage genetic divergence, thus influencing biological evolution [17].

The types of relationships individuals share are also likely to influence social learning [5]. We found that interspecific social associations that formed before the experiment between birds that subsequently could not feed together (mismatched dyads) were disproportionately less important in predicting information transfer than intraspecific ones (figure 1*b*). This could be owing to some mismatched associations being retained among conspecifics, for example, mated pairs prioritize maintaining their relationship over food access [11]. Nevertheless, birds were more likely to learn from individuals that could access the same feeding stations as themselves than mismatched birds with whom they were equally socially associated (figure 1*c*). This illustrates preferential learning from those that regularly provide relevant information. Individuals also

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increased their use of information from heterospecifics during the manipulation, potentially to compensate for the decrease in available social information provided by conspecifics (manipulations resulted in a two-thirds decrease in network density). Together, our findings expand the currently limited pool of knowledge regarding how social learning strategies influence information flow in wild populations [4,9].

Ethics. This work was approved by the local ethical review committee (Department of Zoology, University of Oxford, UK) and adhered to UK licensing requirements (BTO license: A5435, C6030).

Data accessibility. Data are available on dryad: http://dx.doi.org/10.5061/dryad.6h4t2.

Authors' contributions. All authors devised the study; J.A.F. collected the data; J.A.F. and D.R.F. analysed the data and wrote the first draft and B.C.S. contributed substantially to revisions. All authors approved of, and agreed to be held accountable for, the final manuscript.

Competing interests. We have no competing interests.

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SUPPLEMENTARY INFORMATION: Pathways of information transmission amongst wild songbirds follow experimentally imposed changes in social foraging structure

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Supplementary Material - Supplementary Methods

Network-based diffusion analysis

Network-based diffusion analysis (NBDA) [1, 2] has two key parameters. The first, λ, represents the baseline rate of learning – how fast individuals acquire the trait in the absence of social information. The second, *s*, is the main parameter of interest as it quantifies the increase in the rate of learning for every unit of connection to a knowledgeable tutor. For example, when $s = 2$, an increase of 1 in an individuals social association (or "edge weight") to knowledgeable individuals means that the individual will learn twice at twice the baseline rate (i.e. twice as fast).

In the multi-network NBDA model, different values of *s* can be inferred for different parts of the network [3]. For example, if a network comprises of two species, then a value of *s* can be inferred for all edges occurring between individuals of the same species, and a value of *s* can be inferred for all edges occurring between individuals from different species. Thus, the same network is now partitioned into two components. If the within-species $s = 10$, then for every increase in edge weight of 1 to knowledgeable conspecifics, an individual is expected to learn at 10 times the baseline rate. If the between-species $s = 5$, then an increase in edge weight of 1 to knowledgeable heterospecifics in the same network will increase the rate of learning by 5 times the baseline rate.

Inferring experimentally-induced changes in information transfer

The primary hypothesis we test is whether changing who associates with whom changes the pathways of information transfer. However, there are two potential mechanisms underpinning how pathways of information transfer could change. The first is that the network reconfigures itself because individuals only associate with those they can feed with. If these flocks also search for food together, then information transmission will follow this new pattern of social associations. Previous work suggests that the structure of the social network does change to reflect who can forage with whom [4] (see also next section). Here, we tested if the discovery of novel, freely-accessible, food resources was also more strongly predicted by birds with whom individuals could forage. To do this, we tested which social connections in the pre-manipulated network were inferred to have a higher increase in the rate of learning during the experiment i.e. whether the connections between those who could subsequently access the same feeding stations as one another became more important to information transfer once the experiment began.

Unfortunately, it was not possible to simply test whether the manipulated network was a better predictor of the discoveries than the pre-manipulated network, as other variable may also influence the relationship between an inferred social network and the parameter estimates of information transfer. Notably, the manipulated network was measured temporally closer to the discoveries during the experiment than the pre-manipulated network, and therefore may differ in predictive power for this reason alone. Similarly, the

density and accuracy of the inferred social network may also relate to differences in the results of NBDA analysis. Therefore, we base our hypothesis testing exclusively on comparing the relative values of *s* within a network rather than comparing networks or values between different social networks.

Inferring the presence of a social learning strategy

An alternative, or potentially contributing, mechanism for observing changes in pathways of information transfer is if individuals pay more attention to those who provide valid information on a regular basis – i.e. if individuals demonstrate a social learning strategy. Note that the two mechanisms are not mutually exclusive, but that this potentially contributing mechanism can be tested independently. As mentioned above, NBDA infers the increase in the rate of information transfer for every unit of connection that an individual has to knowledgeable individuals. Because *s* is a unit-based measure, then differences in rates of learning are estimated independently from differences in the relative strengths of the different social networks. For example, an individual might have a total edge weight of 3 to knowledgeable tutors with the same tag, and a total edge weight of 1 to knowledgeable tutors with an opposing tag type. Given the first mechanism (previous paragraph), we would expect that this individual should learn 3 times faster from matched individuals than mismatched individuals. If that is the case, then the *s* value for these two networks will be the same. By contrast, if the individual learns 9 times faster from matched-access individuals, then *s* for that network will be 3 times higher than *s* for the mismatched dyads' network. Thus, by applying NBDA to the during-manipulation social network, we can infer how much individuals have changed their behaviour in relation to whom they learn from over and above whom they simply associate with. If we observe similar values of *s* across all networks, then this suggests that the social network manipulation changed patterns of association (individuals associated less with opposing-access individuals), but that individuals did not weigh information from opposing-access associates differently.

Assessing ability to infer the social learning strategy

The results of the NBDA analysis, presented in the main body of this paper, used the during-manipulation network to show that individuals were more likely to gain this information from matched associates than mismatched associates. This suggests that birds are more likely to learn from another individual with which they can access the same food on a day-to-day basis in comparison to another individual with which they are equally socially associated to, but that cannot access the same resources as themselves.

However, as with any study of a wild population, the analysis relies on inferred, rather than perfectly known, social associations. Although the robustness of this inference is likely to be relatively high (due to the large amounts of information gathered on the flocking patterns amongst individuals – see *Results*), this may require additional consideration. Specifically, if the inferred social associations between mismatched dyads were underestimated in comparison to the inferred

social associations between those of matching dyads, this could confound the conclusions drawn from it.

Therefore, we test if, given the social associations inferred at the selective feeders, considering whether dyads were matched or mismatched would improve the ability to predict social associations in another context. Previous work has shown that the experimental manipulation (selective feeding by tag-type) caused birds to become socially assorted to individuals of the same tag-type (matched) as themselves at the selective feeder sites [4]. It also demonstrated that the social associations at the selective feeders significantly predicted the social associations inferred from the flocking co-occurrences at the food patches ("discovery feeders" – where all individuals could access the food). Consequently, social segregation between those of mismatched tag-types was also present within the social network inferred from the flocks observed at the food patches [4]. Whilst these patterns are known to exist, we had not tested whether social associations inferred from the selective feeders between those matched dyads and mismatched dyads differ in their ability to predict social associations at the discovery feeders.

To do so, we used multiple regression quadratic assignment procedure with double semi partitioning (MRQAP.DSP) [5, 6] which allows a dependent matrix to be regressed over multiple independent matrices, and estimates the effect of each of these. Using this technique, we set the dependent matrix as the social network inferred from the discovery feeders, and the independent matrices as (i) the social network inferred from the selective feeders and (ii) a binary matrix denoting whether dyads were matched or mismatched. We found that, as expected, the selective-feeder social network was a strong predictor of the social associations at the discovery feeders, since the values of the social associations at the selective feeder sites showed a positive relationship with the values inferred from the discovery sites (mrqap.dsp; coeff = 0.394, $p<0.001$). However, the matrix denoting whether dyads were matched or mismatched showed no significant relationship to the dyadic associations at the discovery sites (mrqap.dsp; coeff = -0.001, $p=0.179$). Therefore, this illustrates that social associations occurring at the discovery feeders are (i) strongly related to the social associations inferred from the selective feeders, but – when controlling for this – (ii) not related to whether or not individuals could access to same selective feeder sites or not. Hence, accounting for whether or not dyads were matched or mismatched has no significant effect when assessing the relationship between the selective feeder social network and the discovery feeder social network. Therefore, when comparing the social associations inferred from the selective feeders to those in the context of the discovery feeders, social associations between mismatching dyads are not significantly underestimated in comparison to those of matched dyads.

Supplementary Material – Supplementary Tables

Table S1. Details of sample sizes by species for the pre-experimental period, during the experiment, and the total over the entire study period.

	No. birds in network at set feeders			No. birds discovering ephemeral patches			No. of discoveries of ephemeral patches		
Species	Pre	During	Total	Pre	During	Total	Pre	During	Total
Blue tit	119	178	200	31	64	76	31	109	140
Coal tit	4	6	7	1	3	3	1	9	10
Great tit	102	136	150	18	67	69	18	127	145
Marsh tit	9	12	13	4	7	7	4	15	19
Nuthatch	6	7	7	2	7	7	2	15	17
Total	240	339	377	56	148	162	56	275	331

Table S2. Model support (weights) for various hypotheses of social transmission when using i) The pre-experimental network to predict pre-experimental patch discoveries ('pre-pre'), ii) The pre-experimental network to predict patch discoveries during the experiment ('pre-during'), iii) The during experiment network to predict patch discoveries during the experiment. The support for opposing hypotheses was examined in different tests. A) Support for the various model forms of Non-constant (social transmission) vs. Constant (asocial transmission), and Additive (no interaction between social and asocial acquisition) vs. Multiplicative (interaction present between social and asocial acquisition) (see Hoppitt et al. 2010). B) Support for whether to include each component of the full social network in the model. C) Support for allowing different *s* values (rate of transmission) when considering the associations between matched dyads vs. the associations between mismatched dyads. See Figure 1 for *s* value estimates.

Test	Hypothesis	i) Pre-Pre	ii) Pre-During	iii) During-During
A) Model types	Non-constant	>0.99	>0.99	>0.99
	Constant	<0.01	<0.01	<0.01
	Additive	>0.99	>0.99	>0.99
	Multiplicative	<0.01	<0.01	<0.01
B) Networks to include	Intraspecific only	0.13	<0.01	<0.01
	Interspecific only	0.01	<0.01	<0.01
	Both intra & inter	0.87	>0.99	>0.99
	Within tag-types only	0.04	0.02	<0.01
	Between tag-types only	0.10	<0.01	<0.01
	Both within & between tag-types	0.86	0.98	>0.99
C) S parameters to include	Different for within/between tag-types	0.41	0.98	0.84
	Not different for within/between	0.59	0.02	0.16

Supplementary Material – Supporting Video Material

Two compilations are provided. Video 1 shows some examples of when birds use a selective feeder that they are allowed to feed at. In this case, they are of the correct RFID-tag type i.e. they have an odd-numbered RFID tag and the feeder is programmed to allow birds with an odd-numbered RFID tags to feed there. Video 2 shows examples of when birds attempt to access food at a selective feeder they are not allowed to feed at. Here, they are of the wrong RFID-tag type i.e. they have an even-numbered RFID tag and the feeder is programmed to only allow birds with odd-numbered RFID tags to feed there

Descriptions of the video footage at the 'selective' feeding stations:

Video 1:
Accessible at link: https://youtu.be/DOXTM4Blfuc
Also provided in Supplementary material as "selective_feeder_access.mp4"
Video showing a selective feeder allowing access to birds. The following process is taking place: i) the bird lands, ii) the RFID antennae reads the unique RFID tag on the birds leg, iii) the RFID tag is recognised as one which is allowed to access the feeder, iv) the solenoid holding the clear flap in front of the feeding hole is activated and the 'door' is now unlocked, v) the bird can now push the flap open and access the seed inside, vi) the bird leaves, and the door is relocked as the solenoid is deactivated.

Description of Video 2:
Accessible at link: https://youtu.be/Ldt38f3Q9Ik
Also provided in Supplementary material as "selective_feeder_denied.mp4"
Video showing a selective feeder denying access to birds. The following process is taking place: i) the bird lands, ii) the RFID antennae reads the unique RFID tag on the birds leg, iii) the RFID tag is not recognised as one which is allowed to access the feeder, iv) the solenoid holding the clear flap in front of the feeding hole remains deactivated and the 'door' remains locked, v) the bird cannot push the flap open and therefore cannot access the seed inside, vi) the bird leaves, and the door is remains locked as the solenoid is still deactivated.

Supplementary Information – Supplementary References

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Chapter 7

Experimental evidence that social relationships determine individual foraging behaviour

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Current Biology

Experimental Evidence that Social Relationships Determine Individual Foraging Behavior

Highlights

- Wild birds traded off foraging opportunities in order to stay with their partner
- By altering spatial choices, key relationships also influenced wider social structure
- Birds learned to scrounge to reduce conflict between sustaining bonds and food access
- Social bonds shape behavioral variation and, consequently, population processes

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In Brief

Firth et al. show that wild birds forgo access to food to sustain their pair bond. This causes them to flock with others that they would not otherwise associate with and to learn a flexible scrounging strategy. In this way, key relationships influence individual behavior and strategies, consequently shaping population spatial and social structure.

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Current Biology
Report

Experimental Evidence that Social Relationships Determine Individual Foraging Behavior

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SUMMARY

Social relationships are fundamental to animals living in complex societies [1–3]. The extent to which individuals base their decisions around their key social relationships, and the consequences this has on their behavior and broader population level processes, remains unknown. Using a novel experiment that controlled where individual wild birds (great tits, *Parus major*) could access food, we restricted mated pairs from being allowed to forage at the same locations. This introduced a conflict for pair members between maintaining social relationships and accessing resources. We show that individuals reduce their own access to food in order to sustain their relationships and that individual foraging activity was strongly influenced by their key social counterparts. By affecting where individuals go, social relationships determined which conspecifics they encountered and consequently shaped their other social associations. Hence, while resource distribution can determine individuals' spatial and social environment [4–8], we illustrate how key social relationships themselves can govern broader social structure. Finally, social relationships also influenced the development of social foraging strategies. In response to forgoing access to resources, maintaining pair bonds led individuals to develop a flexible "scrounging" strategy, particularly by scrounging from their pair mate. This suggests that behavioral plasticity can develop to ameliorate conflicts between social relationships and other demands. Together, these results illustrate the importance of considering social relationships for explaining behavioral variation due to their significant impact on individual behavior and demonstrate the consequences of key relationships for wider processes.

RESULTS AND DISCUSSION

Social relationships generate fitness benefits for social animals [1–3]. Indeed, a wide range of specialized social behaviors, ranging from acoustic signals to courtship displays and mate guarding, have evolved to facilitate their maintenance [9, 10]. Yet, behaviors related to other key activities, such as foraging, may also be influenced by the necessity to maintain important social relationships. The extent of this effect remains unknown, despite its potentially important role in explaining behavioral variation and its consequences for other processes.

During late winter, when great tits attempt to increase their body condition in preparation for breeding [11] and socially monogamous mated pairs forage together [12], we experimentally introduced conflicts between accessing resources and maintaining social relationships. We deployed radio frequency identification (RFID)-controlled feeding stations that responded to individuals differently depending on their unique RFID tag code. This novel approach allows the creation and enforcement of experimental treatment groups between individuals within free-ranging populations and offers the potential for wide-ranging applications, from changing population structure to manipulating the stimuli each individual perceives, or even performing controlled access to different drugs, nutrients, or food types. For this experiment, however, we controlled the spatial locations at which each individual could access food [13]. We programmed half of the feeding stations to only allow access to birds with odd-numbered RFID tags and the others to only allow birds with even-numbered RFID tags. As RFID tag codes were assigned randomly when fitted, the population was split with equal probability into two classes. Some mated pairs had "compatible" tag types (i.e., both had odd-numbered tags or both had even-numbered tags) and therefore were allowed to access the same feeders as each other. The remaining mated pairs had "conflicting" tag types (i.e., one had an odd-numbered tag, whereas the other had an even-numbered tag) and therefore were only allowed access to different feeders (see the Experimental Procedures). These were termed "conflicted" pairs. We assessed how social relationships influenced individual foraging activity, wider social structure, and the development and plasticity of individuals' foraging strategies.

Social Relationships Determine Spatial Foraging Activity

Individuals are expected to prioritize foraging at locations where they can maximize their reward [14–16]. Indeed, great tits as a whole strongly preferred to forage at locations where they could access food ("allowed" locations), over locations where they could not ("prohibited" locations): the activity at feeders was primarily by individuals who were allowed access there (Figure 1;

CrossMark



Figure 1. Map of Great Tit Feeding Activity during the 90-Day Experimental Period

Circles show separate feeder sites. Border colors show which type of tag the feeder allowed access to (black, birds with even-numbered tags; white, birds with odd-numbered tags). Inner colors show the proportion of activity by each tag type (dark gray, activity by birds with even-numbered tags; light gray, activity by birds with odd-numbered tags). The diameter of the circle is proportional to the square root of the total amount of activity recorded.

χ^2 = 315,750, $p < 0.001$). However, 60% of the activity by birds at feeders at which they were prohibited was by birds in conflicted pairs. As conflicted pair members only made up 12% of individuals at these locations, their frequency of activity at prohibited feeders was much higher than expected (χ^2 = 598,746, $p < 0.001$). Indeed, there were no differences between individuals from compatible and conflicted pairs in overall activity levels (Figure S1A), but birds from conflicted pairs, on average, spent 3.8 times more of their activity at prohibited sites compared to birds from compatible pairs (Figure 2A; Mann-Whitney U = 78, p = 0.030). This suggests that mated partners influenced individuals' foraging decisions, even if these decisions appear to be sub-optimal. Thus, although it is known that individuals may accept costs in order to gain potential benefits of foraging with others, such as predator defense and vigilance, discovery of new resources, and cooperation [17–21], birds in our experiment did so to maintain a single relationship. In the case of great tits, this relationship was the pair bond with their mate, yet this principle can apply to any type of social relationship. Furthermore, relatively low inter-annual fidelity rates (~18%–30%) due to high mortality and divorce within great tits [22] suggests that mated pair bonds may be even more important in other species. Recognizing that key social relationships are prioritized over resource access not only helps in explaining variation in foraging patterns, but also sheds a new light on the notion of optimality in social species.

Consequences of Key Relationships for Wider Social Structure

A classic view of sociality [4–8] is that resources underpin the spatial distribution of individuals, which in turn determines social structure. However, as certain social bonds provide various long-term benefits [1–3], they can also be considered a resource [6, 23, 24]. A feedback between social relationships and social structure can then arise, as maintaining important relationships may influence an individual's spatial location, and in turn their social environment and weaker social links to others.

Considering individuals' social associations to all its conspecifics except their own partner (see the Experimental Procedures), we find, as expected, that birds in compatible pairs mainly foraged with others who had access to the same feeding stations as themselves: 72% of their associations were to individuals of the same tag type (Figure 2B; median average). Because birds from conflicted pairs spent more time at locations preferred by their partners, they had significantly more associations with individuals of the opposite tag type (only 49% to same tag type; Figure 2B; Mann-Whitney U = 199, p = 0.039, permutation test p = 0.026).

These findings illustrate how an individual's key social relationships can influence their spatial occurrence and thus influence which other individuals they encounter. This may have widespread implications, particularly as changes in foraging associations carry over into other social contexts [13], and many

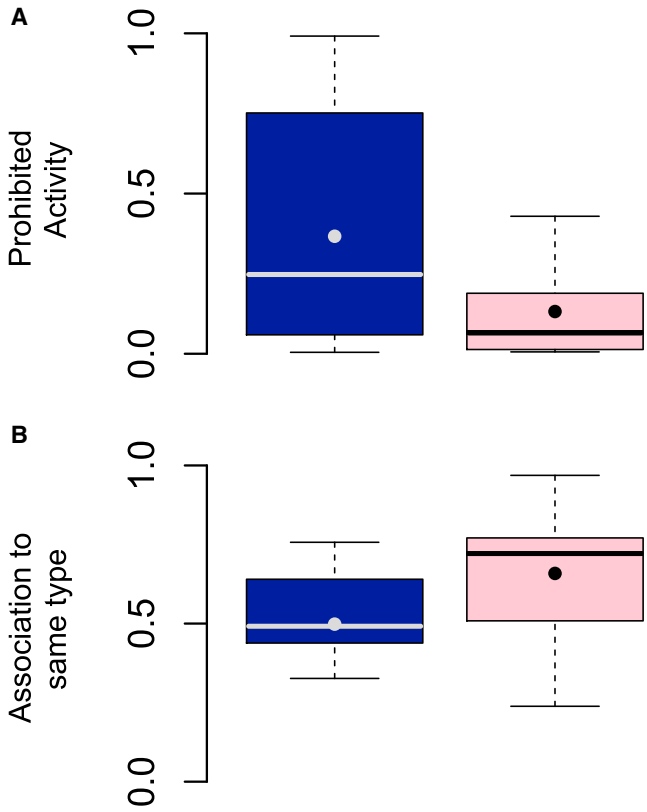


Figure 2. Activity and Social Assortment of Compatible and Conflicting Pairs

Birds from conflicted pairs (left, blue boxes; n = 14) and compatible pairs (right, pink boxes; n = 20) differed in their proportion of (A) activity at feeders prohibited to them and (B) association with others of the same tag type (excluding associations between pair members). Dots show the mean, midlines show the median, boxes shows the interquartile range (IQR), and whiskers shows the range (with values outside 1.5 times IQR excluded).

processes are linked to social structure, such as the acquisition of information and disease transmission [25–30]. Although demonstrated here through the influence on an individual's spatial foraging activity, we suggest that, in general, maintaining key relationships through continued association with another individual (e.g., their mating partner) may force individuals to adopt the particular social position and associates of their preferred companion. This can occur even if the resulting social environment is sub-optimal. In this way, the operation of social selection could be directly influenced [31, 32].

Social Relationships Influence Social Foraging Strategies

The social strategy an individual employs, such as scrounging or following, may depend not just on its own characteristics, but also on the characteristics of its social counterparts [33–36]. In our experiment, although birds could not independently access food at locations they were prohibited from, the locking mechanism re-engaged only 2 s after the detection of an allowed RFID tag number. Therefore, individuals could scrounge by rapidly "following" (defined here as landing on a feeder within 2 s of another individual) another bird. We examined the consequences of social relationships for the development of this strategy (see the Experimental Procedures).

Individuals from conflicted pairs adopted this following strategy to scrounge from prohibited feeders (i.e., their partner's permitted location), as a higher proportion of their visits than expected (64.4%) came within 2 s of another individual leaving [other flock members: 54.1%; null model (i): $p < 0.001$; Figure S2A]. They were also more likely to scrounge by following their partner [null model (ii): $p < 0.001$; Figure S2B]: 19.8% of scrounging events involved following their partner, whereas only 9.8% of scrounging by other birds was achieved through following birds from conflicted pairs. Similarly, birds from conflicted pairs were also significantly more successful at scrounging from their partner than when attempting to do so from another flock member [null model (iii): $p < 0.001$; Figure S2C] as more of their visits were within 2 s (81.2%) when arriving after their partner than when arriving after another flock member (65.1%).

Individuals from conflicted pairs scrounged at a significantly higher rate than expected. This increase was partly driven by following their partner more frequently and quickly than following other flock members. This could represent a cooperative strategy (i.e., facilitated scrounging) that enables birds to reduce the costs arising from differences in preferred foraging locations. In contrast, individuals from conflicted pairs at their allowed locations, and individuals from compatible pairs at any locations, did not follow others at a higher frequency than expected, nor did they follow their partners more often or successfully (Figure S2). Hence, individuals clearly adopted this scrounging strategy at sites they could not exploit themselves by increasing their following frequency, and birds from conflicted pairs exhibit a larger increase than compatible pair members (Figure 3A; Mann-Whitney $U = 197$, $p = 0.01$). This suggests that behavioral flexibility was driven by the necessity to adapt to the ecological conditions individuals experience arising from maintaining a social relationship.

Individuals using prohibited feeders increased their following behavior with experience, and conflicted pair members adopted this strategy at a faster rate (Figure 3B and Table S1A; generalized linear mixed model [GLMM] interaction coefficient = −0.005, $p = 0.001$; see the Experimental Procedures). Birds also remembered which locations they were prohibited from over days, but this was not significantly related to the type of relationship they held (Figure 3C and Table S1B). Finally, birds reduced their following behavior at sites at which they were allowed access to over time, and this also occurred faster in birds from conflicted pairs (Figure S3A and Table S2A; interaction coefficient = 0.004, $p = 0.001$).

While an individual's phenotype and environment are known to influence the expression of social strategies [36, 37], we show that key social bonds alter the expression of behavioral plasticity. This also provides another route for important social relationships to influence wider social structure, as the social strategies employed by individuals within a population directly affect their interactions [18, 33, 38]. Further, such principles may extend to numerous behaviors, such as dietary preferences, risk-taking, or social position, all which can influence the associations among individuals [39–44] and also could conceivably be shaped around key social relationships.

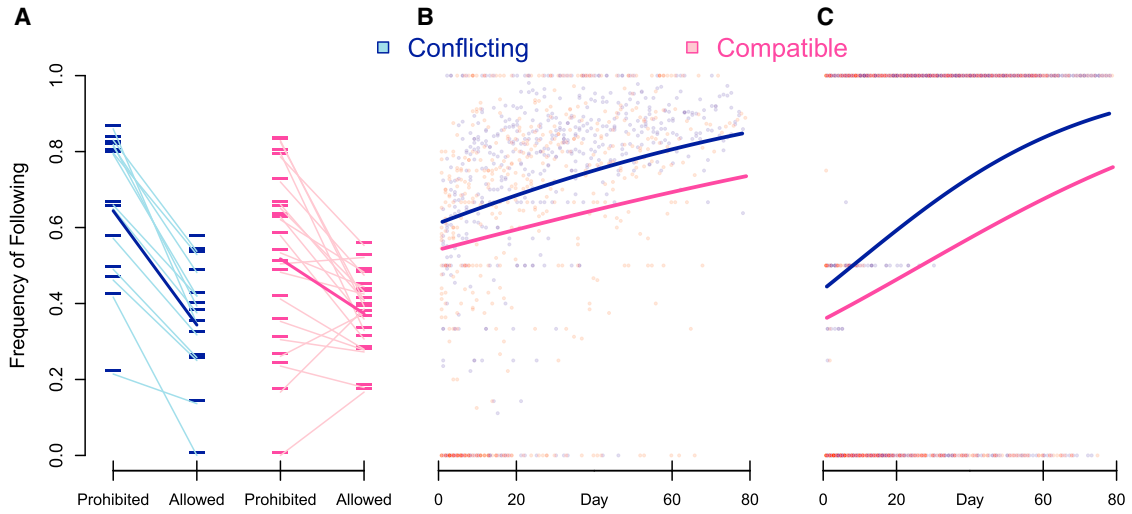


Figure 3. Following Behavior of Compatible and Conflicting Pairs

The frequency of following (i.e., the proportion of visits that come within two seconds of another individual) by individuals from conflicted pairs (blue) and compatible pairs (pink).

(A) Individuals' following frequency when at feeders prohibited to them compared to that at feeders they were allowed access to. Blocks show the mean proportion of visits that were "follows" for each individual at the different feeder types (x axis). Thin adjoining diagonal lines indicate each separate individual. Thick lines show the mean over all individuals.

(B) The change in the propensity for individuals to follow others (at a feeder that they were prohibited from) over the number of days the individual had been observed at that feeder (x axis). Translucent points indicate the mean proportion of follows for an individual at a prohibited feeder site, and lines show GLMM fit (see Table S1 for the full model and details).

(C) The change in the propensity for individuals to follow others on their first visit of each day to a feeder at which they were prohibited as a function of the number of days that the individual has been observed at that feeder (x axis). Points and lines are analogous to (B).

Conclusions

Wild great tits shape their foraging activity around their mated partner and prioritize maintaining this relationship over their access to food. This key relationship also influenced their wider social associations by altering who else they foraged with, illustrating an important feedback between social structure itself and its suggested drivers. Additionally, maintaining these relationships had consequences for the expression of behavioral plasticity, which can develop to mitigate the trade-off between social relationships and other demands. Overall, these results demonstrate the importance of social relationships for the expression, and consequences, of individual behavior. Such principles may extend to individuals accommodating their social partners in many ways. Therefore, social relationships may be important drivers of variation in numerous behaviors and have far-reaching implications across a range of population-level processes.

EXPERIMENTAL PROCEDURES

Study System

Wytham Woods, Oxford, UK (51°46′ N, 1°20′ W) hosts a long-term study population of great tits [45]. During spring, these birds breed as pairs in nestboxes and are captured between 6 and 14 days of nestling phase and marked with a unique BTO (British Trust for Ornithology) metal leg ring; the same procedure is carried out for nestlings at 15 days old. Immigrant great tits, along with other species that participate in winter flocks, are also caught using mist netting throughout the winter [46]. Since 2007, all captured birds have been fitted with RFID tag leg rings, and it is estimated over 90% of great tits are tagged [47]. Birds were ringed and tagged under BTO licenses C6030 and A5435. On November 9, 2013, within four areas that form part of the main woodland, we deployed "selective feeders" that had a clear flap blocking the feeding hole that was only unlocked when a bird carrying a specified RFID tag was read by the feeding station [13]. Initially, all individuals could access all feeders. After 40 days' acclimation, the experimental treatment was applied for 90 days. Here, two selective feeders replaced each of the six original feeders, both placed ~50 m (in opposite directions) from the initial location (Figure 1). In each case, one allowed the food flap to be opened upon reading an odd-numbered RFID tag, whereas the other only allowed assess to even-numbered RFID tags. Through successful feeding at allowed sites and failure to access prohibited sites, birds generally quickly developed spatial preferences for sites they could access (Figure 1) [13]. However, birds from conflicted pairs only slowly expressed this preference for their allowed locations, potentially as the demand for energy became more prominent (Figure S3C and Table S2).

Social Associations

These birds feed in flocks throughout the winter period [48, 49], and we applied machine-learning algorithms to the spatiotemporal data stream from the feeders to identify flocking events (i.e., groups) of birds [12, 50]. Association matrices (social networks) based on flocking event co-memberships were calculated using the simple ratio index [51]. A permutation test controlling for individual gregariousness and spatiotemporal occurrence [52, 53] (see the Supplemental Experimental Procedures) revealed 17 great tit pairs (34 individuals) recorded breeding in the study area (May 2014) with strong, non-random, associations to one another throughout the experimental period, in line with previous findings that pair bonds exist throughout the winter period [12]. Ten pairs (20 individuals) were allowed access to the same feeding stations as each other (compatible pairs), whereas seven pairs (14 individuals) only had access to different feeding stations to each other (conflicted pairs). During the 90-day experimental period, 66,184 detections of the 34 paired individuals were recorded at the selective feeders, which occurred within 21,885 flocking events.

Excluding associations between mated pairs, we calculated the proportion of each individual's total associations to others who were allowed access to the same locations as themselves. We compared individuals from conflicted pairs to those from compatible pairs using the Mann-Whitney U test, as well

as using a node permutation test [53], to determine significance given the non-independence of network data (see the Supplemental Experimental Procedures). Before the experiment began, all pairs showed equal association to birds of the same and opposite tag type (Figure S1B).

Following Behavior

We assessed following behavior by comparing the observed statistic of interest to those generated from 10,000 runs of a specific null model (see the Supplemental Experimental Procedures). Null model (i) examined whether the proportion of a bird's visits that came within 2 s of another individual leaving the feeder (i.e., follows) was more than expected. Within each flocking event, each individual was randomly assigned the visitation pattern of another individual also observed within that flocking event. Null model (ii) considered of the proportion of each individual's follows that came after their pair member was larger than expected by adding the restriction that individuals were only swapped with another individual of the same tag type. Finally, success at arriving within 2 s after their pair member was compared to null model (iii), which swapped the time gaps that occurred between individuals arriving after one another and applied the restriction that time gaps were only swapped with another instance of a bird of the same tag type leaving the feeder.

To examine whether following behavior increased with previous experience (the number of days that an individual had been recorded at that feeder site) and whether this rate depended on their social relationship (whether they were from a conflicted or compatible pair), we employed GLMMs with binomial error structure and logit link function. In the first model, the binary response variable was whether each visit was a follow (i.e., within 2 s of another bird leaving) or not. Previous experience and pair type were fitted as fixed effects, along with the interaction between them, and individual and unique pair number were included as random effects. For examination of learning over days, a second model's response variable only included the first visit by each individual to each feeder on each day.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.09.075.

AUTHOR CONTRIBUTIONS

J.A.F. and B.C.S. designed the experiment. J.A.F. collected the data. J.A.F. and B.V. analyzed the data. D.R.F. programmed the selective feeders. All authors wrote the manuscript.

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SUPPLEMENTAL INFORMATION: Experimental Evidence that Social Relationships Determine Individual Foraging Behavior

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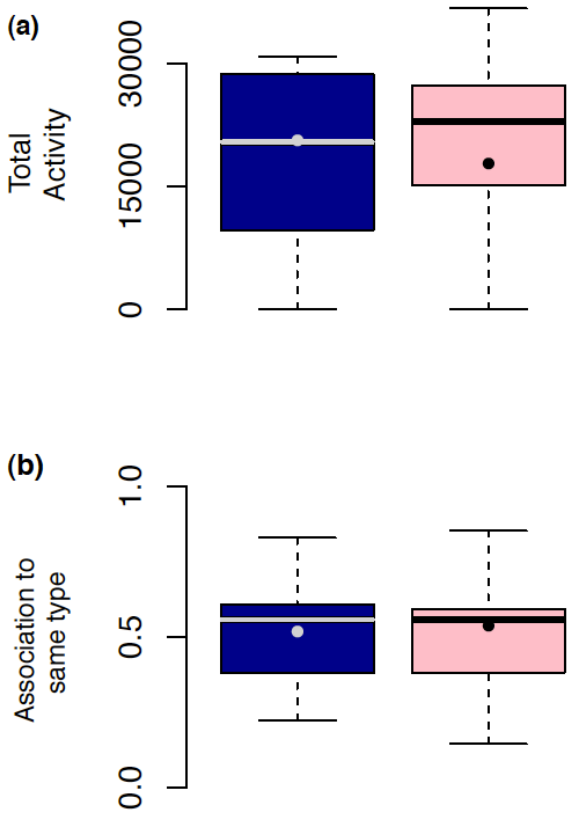


Figure S1. Relationship between pair-type and (a) foraging activity and (b) pre-manipulation social assortment. Birds from conflicted pairs (left, blue boxes, n=14) and compatible pairs (right, pink boxes, n=20) did not differ in their (a) total activity at feeders and (b) association with others of the same tag type (excluding associations between pair members) before the experiment began. Dots show mean, mid-lines show median, box shows interquartile range (IQR), whiskers shows range (with values outside 1.5 times IQR excluded) (See Fig. 2).

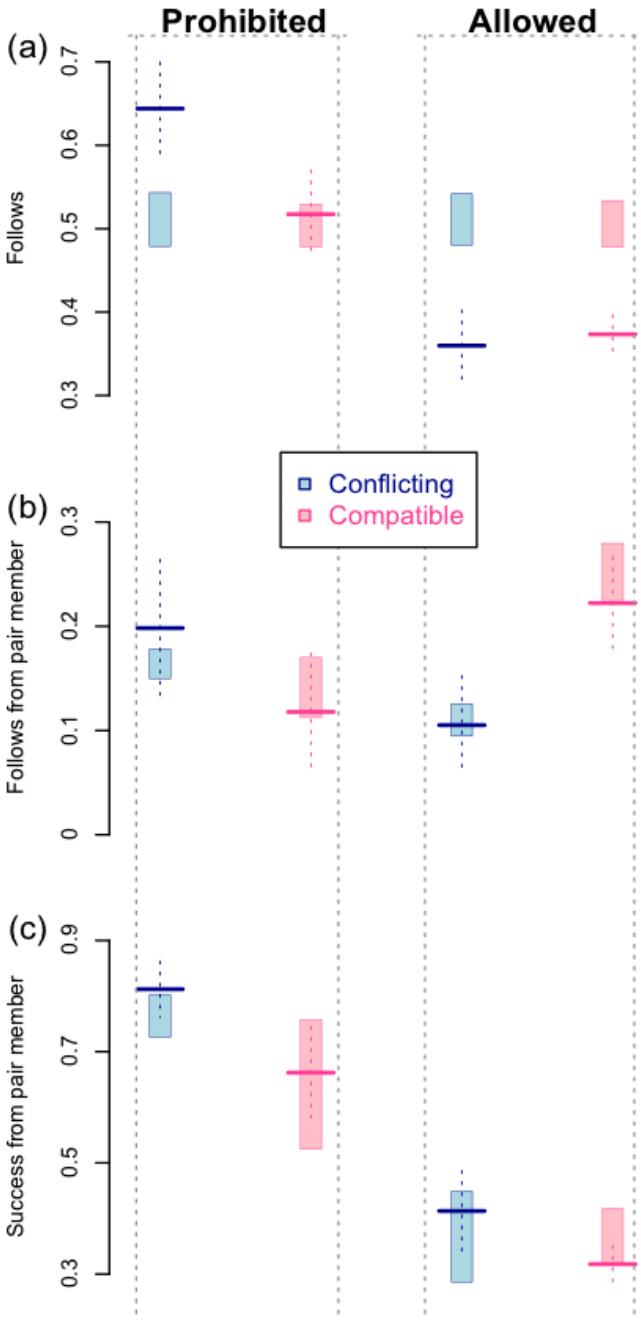


Figure S2. The observed metrics of following behaviour compared to the range expected from null models for focal individuals from conflicted pairs (blue) and compatible pairs (pink) in relation to whether the focal individual was prohibited or permitted access (left and right columns respectively, see header). Horizontal lines plot the observed mean of any given measure over the considered individuals with dotted lines showing the standard error around this mean. Boxes show the 95% range of the means generated from the specific null models (see Supplemental Experimental Procedures); the observed value is judged to be significantly different from the null model if the horizontal line falls outside of the box. The panels (and associated y axes) show three different metrics of following behaviour: (a) the proportion of visits that are 'follows' i.e. within 2 seconds of any other individual leaving, (b) the proportion of 'follows' which come in sequence within a flocking event after their mate, and (c) the proportion of visits following their mate that come within 2 seconds (i.e. the proportion of scrounging attempts that are successful upon following their pair member) (See Results & Discussion - Social relationships influence social foraging strategies – Fig. 3).

Additional explanatory text for Figure S2

The results for the behaviour of birds from conflicting pairs at feeders prohibited to them (i.e. first column of Supplemental Fig. 2a, b & c) are discussed in depth in the main text (see Results & Discussion). Using the same null models (see Supplemental Experimental Procedures), the same analysis was also carried out for the behaviour of birds from conflicting pairs at feeders where they were allowed access, as well as the behaviour of individuals from compatible pairs at feeders they were allowed access to and those they were not (i.e. second, third and forth column, respectively, of Supplemental Fig. 2a, b & c). The following text explains the results of this in more detail.

Birds from compatible pairs at prohibited feeders did not adopt a following strategy more than expected under the null model (Supplemental Fig. 2A), as they could open the feeders themselves. Further, when at sites they were allowed to feed, both conflicted and compatible pair members followed their flock members less than expected under the null model (Supplemental Fig. 2A) as other birds followed them instead.

Assessing the extent to which birds followed their own pair member over other flock members of the same tag type as their pair member showed that birds from compatible pairs at prohibited feeders did not differ from the null model in the extent to which they followed their partners (Supplemental Fig. 2B). The same result was found for birds from compatible pairs at allowed feeders. This is likely due to the fact that, in both of these cases, their pair member could not open the feeder. Birds from compatible pairs at feeders they were allowed access to followed their pair members slightly less than expected (Supplemental Fig. 2B). This may occur as these individuals can both access the feeder so do not need to follow one another, and other flock members (who cannot access the feeder) may follow these individuals instead.

Similarly, upon visiting a feeder directly after their pair member, the proportion of such visits that came within two seconds (i.e. 'following') was not significantly different from expected under the null model when considering birds from conflicted pairs at allowed feeders, and birds from compatible pairs at both feeder types (Supplemental Fig. 2C). This is because birds at feeders they are allowed access to can open the feeder themselves, and thus have no reason to rapidly follow others within two seconds more than expected, whilst compatible pair members at prohibited feeders also do not benefit by following their pair member within two seconds as their pair member cannot open the feeder either.

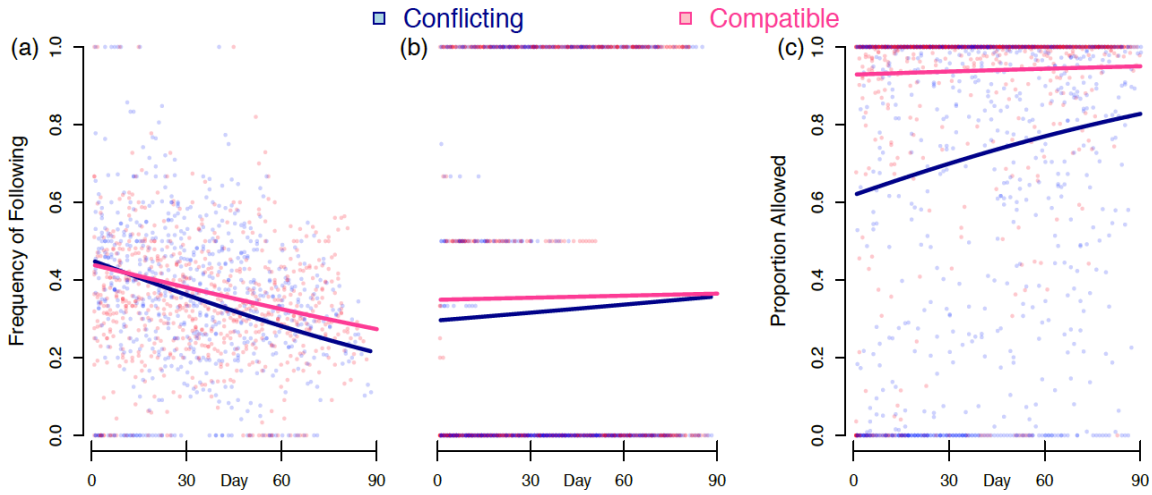


Figure S3. The change in foraging behaviour over time by individuals from conflicting pairs (blue) and compatible pairs (pink). (a) The change in the propensity for individuals to follow others (i.e. the frequency of following defined as the proportion of visits that come within two seconds of another individual) at feeders they are allowed access to over the number of days that individual has been observed at that feeder (x axis). Each point indicates the mean proportion of follows for an individual at a feeder site, and lines show the fit of GLMMs (See Supplemental Table 2 for full model & details). (b) The change in the propensity for individuals to follow others on their first visit of each day to a feeder, over the number of days that individual has been observed at that feeder (x axis), points and lines are analogous to (a). c) The proportion of individual's foraging activity that was at feeding sites they are allowed access to over the number of days that individual has been observed during the experimental period (x axis). Points indicate the mean proportion of correct activity for an individual that day, and lines show the fit of GLMMs (See Supplemental Table 2 for full model & details) (See Fig. 3).

Table S1. Results of binomial General Linear Mixed Models (GLMM), all including individual identity and unique pair number as random effects and assessing the effect on the binary response variable of whether the visit to prohibited feeder site was a 'follow' (i.e. within two seconds of a previous individual) by the fixed effects of (i) 'Day' i.e. the number of days the individual has previously visited the feeder and (ii) 'Pair type' i.e. whether the individual belonged to a conflicting or compatible pair and (iii) the interaction between these two factors. 'Model A' includes all visits to prohibited feeders whilst 'Model B' only includes the first visit to each prohibited feeder by each individual on each day.

Model	Term	Estimate	SE	z	p
A	Day	0.016	0.001	16.515	>0.001
	Pair Type	-0.286	0.338	-0.845	0.398
	Interaction	-0.005	0.002	-3.422	0.001
B	Day	0.031	0.005	6.288	>0.001
	Pair Type	-0.334	0.226	-1.477	0.140
	Interaction	-0.009	0.007	-1.386	0.166

Table S2. Results of binomial General Linear Mixed Models (GLMM), all including individual identity and unique pair number as random effects. Models A and B assess the effect on the binary response variable of whether the visit to the feeder site they were allowed access to was a 'follow' (i.e. within two seconds of a previous individual) by the fixed effects of (i) 'Day' i.e. the number of days the individual has previously visited the feeder and (ii) 'Pair type' i.e. whether the individual belonged to a conflicted or compatible pair and (iii) the interaction between these two factors. 'Model A' includes all visits to allowed feeders whilst 'Model B' only includes the first visit to each allowed feeder by each individual on each day. 'Model C' assesses the effect on the binary response variable of whether the detection was at a feeder site they were allowed access to. It uses the same fixed effect variables of 'Models A and B', but where 'Day' is measured as the number of days the individual has previously visited any feeder during the experimental period.

Model	Term	Estimate	SE	z	p
A	Day	-0.012	0.001	-20.422	0.001
	Pair Type	-0.043	0.203	-0.213	0.832
	Interaction	0.004	0.001	5.702	0.001
B	Day	0.003	0.004	0.864	0.387
	Pair Type	0.244	0.285	0.855	0.393
	Interaction	-0.002	0.004	-0.541	0.588
C	Day	0.012	0.001	52.118	0.001
	Pair Type	2.084	0.176	11.861	0.001
	Interaction	-0.008	0.001	-25.227	0.001

Supplemental Experimental Procedures

Identifying social associations

To identify which great tit pairs were non-randomly associated with one other, given their spatiotemporal occurrence, we used a restricted permutation method [S1] that swaps the observations of two individuals observed in different groups (flocking events), but with swaps restricted to only occur between groups at the same location (feeder) in the same time period (day) [S2]. We carried out 1000 swaps before re-calculating the association network, and this was run until 10,000 'null model' association networks had been calculated. Therefore, for each dyad there existed a distribution of 10000 association rates that could be expected given their individual gregariousness and spatiotemporal occurrence, and the overall structure of the network and group-size distribution. We then calculated a 'p-value' for each dyadic association rate, simply by determining the proportion of times the observed association rate (or higher) was achieved within the null model. The distribution of these p values was bimodal, with one mode centred around $p<0.01$, suggesting strong, non-random links existed within the system. Of these, 44 great tits were subsequently (i.e. in the following breeding season) found to belong to mated pairs of which both partners were RFID-tagged. 38 were associated with their partner during the experimental period, and 34 of them at $p<0.01$. These 34 individuals also held, in total, 41 'non-random' links (i.e. $p<0.01$) to birds who were not their mate (out of a total 1150 links from these 34 individuals to other birds). However, none of these other 'non-random' links were to one of the other 34 focal individuals, and in all cases the association to their pair member was the strongest out of all of their associations. Therefore, these 17 pairs of individuals were classified as breeding pairs that were non-randomly associated throughout the winter period, and were the focus of all further analysis

Measuring association based on tag type

We examined whether birds from conflicted pairs had different types of flock members (based on tag type) from those that might be expected, and whether they showed assortment to individuals who had access to the same resource locations as themselves. Excluding all associations between mated pairs within the network, we simply calculated the proportion of their weighed associations that were to other individuals of the same type as themselves. This is somewhat analogous to the EI (External/Internal) index of assortment [S3] used to compute the association that each individual has to other individuals of the same type (i.e. 'internal links') in comparison to those with the opposite tag type (i.e. 'external' links) by dividing ' the sum of associations to individuals of the opposite type minus the sum of associations to individuals of the same type' by 'the sum of all associations'. Whilst in the EI index +1 indicates a bird is only associated with others of the opposite type, +1 indicates it only co-occurs with others of the same type, and a score of 0 indicates that an individual is equally linked to those of the same and of the opposite type, our measure ranges from 0 to 1, where 1 indicates a bird only associated with individuals of the same type, 0

indicates co-occurrence only with those of the opposite type, and 0.5 indicates equal association to those of the same and opposite type. Indeed, repeating the analysis using the EI index gave the same results. Due to the non-independence of network data, we employed a node permutation test [S2], whereby the nodes (individuals) of the network were shuffled, individual assortment was recalculated, and the Mann Whitney U test was carried out. This process was repeated 10,000 times to determine whether the observed difference in assortment (Mann Whitney U test statistic) was higher than the 95% range of the values generated from 10,000 node permutations. . Further, using this permutation technique we found that birds from compatible pairs were significantly assorted by tag type (i.e. the mean individual assortment score, discussed above, was significantly higher than expected at random), whilst those from conflicted pairs did not show assortment.

Null models of following behaviour

The flap of the selective feeders re-locked only two seconds after no longer detecting an 'allowed' RFID tag number in order to avoid the flap inadvertently locking whilst the bird was still feeding. As a consequence, a bird arriving within this time period could gain access to the seed inside. This created potential for individuals to scrounge from feeders they were not prohibited from, by rapidly 'following' another individual within a flocking event. As the Gaussian mixture model assigned some flocking events to 'finish' within two seconds of another flocking event 'beginning', meaning the first individual could have scrounged following the final individual in the previous event (1.02% of all flocking events identified), we grouped flocking events occurring within 2 seconds of one another into a single event.

We then assessed how individuals from conflicted pairs performed this following behaviour to acquire seeds from feeders they were prohibited from, by comparing three metrics of interest (i, ii & iii – see below) from the observed data to those derived from null models that maintained which individuals occurred in which flocks, but permuted the temporal structure of the flocking event to assess the specific metric:

(i) Propensity to follow
For each individual belonging to a conflicted pair, we considered the proportion of visits that directly followed (i.e. came within two seconds) of another individual. The mean of this was compared to a null model aiming to determine the proportion of times these individuals would follow if they were random flock member occurring in the same time and place as they were recorded. Therefore, within each flocking event that these individuals where observed in, all flock members were assigned to the visitation pattern of another flock member, with no restrictions on which individual was assigned to which other individual (as swaps of visitations patterns were entirely random, and did not have to be reciprocal, they also allowed individuals to be assigned to their own visitation pattern). The proportion of times that each individual from a conflicted pair followed another individual was then recalculated, and a mean taken over

individuals. This was repeated 10,000 times to give the distribution of the proportion of visits that an individual from a conflicted pair would follow another individual if they had the same propensity to follow as other individuals within their flocking events. In sum, null model (i) randomly swaps which individuals adopted which activity patterns within the flock.

(ii) Propensity to follow their own pair member
For each individual from a conflicted pair, we calculated the proportion of each individual's 'follows' that came following their pair member. We compared the mean of this to null model again simulating individuals occurring in the same flocking events that they were observed, but randomly following other flock members based only on whether that flock member had opened the feeder or not (i.e. allowed or prohibited). Thus, we carried out the same permutation as described in (i), but with the additional restriction that individuals were only swapped to adopt the visitation pattern of another individual of the same tag type (odd or even) as themselves. We then recalculated the proportion of follows that each individual from a conflicted pair followed their partner, rather than another flock member. Again, this was repeated 10,000 times to determine the expected range of this metric if individuals with conflicted partners randomly followed any flock member who had opened the feeder. In sum, null model (ii) swaps individuals to adopt the activity pattern of another individual, but with the restriction that individuals with odd numbered tags can only be swapped with another individual with an odd numbered tag, whilst individuals with even numbered tags can only be swapped with another individual with an even numbered tag.

(iii) Success at following their pair member
Finally, we examined the proportion of times that these individuals arrived within two seconds after their conflicted pair member, upon arriving at the feeder after them (i.e. the proportion of times they were 'successful' at scrounging after their pair member had opened the feeder). A null model was therefore constructed to determine the distribution of the mean of this metric if each individual's success at following (i.e. arriving within two seconds) depended only on the tag type of the previous individual. Therefore, we maintained the order of the identities of the individuals within each flocking event, but randomly swapped the time gap that occurred between individuals arriving after one another. This also held the restriction that the time gap following a bird leaving the feeder could only be swapped with another instance of a bird of the same tag type (odd or even) leaving the feeder. Again, by recalculating the mean of the proportion of times that an individual arrived after its conflicted pair member within two seconds, we calculated the range expected if individuals were equally successful upon following their pair member or another bird who had opened the feeder. In sum, null model (iii) swaps the time gaps that occurred between each individual arriving after another individual with the restriction that the time gap which occurred following an even bird can only be swapped with other time gaps that occurred after an even bird left, and the time gap after an odd bird left can only be swapped with the time gap that occurred following another odd bird leaving.

All permutations were carried out 10,000 times independently on each flock. As well as carrying out these permutation tests considering individuals from conflicted pairs at feeders they were prohibited from (as described in 'i', 'ii', and 'iii' above), we also carried out the same tests for these individuals at feeders they were allowed access to, as well as for individuals from compatible pairs at both types of feeders (Supplemental Fig. 2 for results).

Supplemental References

S1. Bejder, L., Fletcher, D., and Brager, S. (1998). A method for testing association patterns of social animals. Anim. Behav. *56*, 719-725.

S2. Whitehead, H. (2008). Analyzing animal societies, (Chicago: University of Chicago Press).

S3. Krackhardt, D., and Stern, R.N. (1988). Informal Networks and Organizational Crises - an Experimental Simulation. Social Psychology Quarterly *51*, 123-140.

Chapter 8

General Discussion

General Discussion

Aims and Motivation

The social lives of wild animals are a central, and compelling, aspect of ecology and evolution (Alexander 1974; Wilson 1975). Due to modern technological and computational advances allowing the tracking and quantification of the social organisation of various animal taxa (Krause *et al.* 2007; Krause *et al.* 2013), numerous breakthroughs have recently been made in our understanding of these societies. In particular, this comes in terms of how individual properties and social relationships, along with ecological factors, structure social networks (Croft *et al.* 2008; Krause *et al.* 2015). Based on these insights, a framework has also emerged enabling the assessment of how the social organisation of wild animals relates to wider themes, such as the spread of information and disease (Godfrey *et al.* 2009; Aplin *et al.* 2012; Allen *et al.* 2013; VanderWaal *et al.* 2014; Aplin *et al.* 2015), fitness (McDonald 2007; Brent *et al.* 2013; Lehmann *et al.* 2016), and selection (Oh & Badyaev 2010; Farine & Sheldon 2015).

In this thesis, through the operation of a large-scale Radio Frequency Identification (RFID) system, I was able to collate high-resolution tracking information on wild songbirds, and quantify their social behaviour and the arising social networks. By constructing and employing empirically-parameterised null models to examine the contributions of various factors (i.e. social dynamics, individual characteristics, spatial factors), I aimed to assess the architecture of the social network, and how this carries over into shaping population structure. Motivated by concerns regarding confidence in understanding social networks and related processes due to a lack of experimental evaluation (James *et al.* 2009), I developed and implemented novel experiments to directly test the underpinning factors of social connections, as well as how these foraging associations can carry-over to influence sociality in other contexts, social information transmission, and individual behavioural and learning strategies.

The interplay between ecology and sociality

A classic model in ecology proposes that ecological selection pressures shape the spatial occurrence of individuals, and this in turn structures sociality (Crook 1970).

Fundamental research from as long as five decades ago has illustrated how differences in foraging resources broadly relate to interspecific variation in social systems, such as for weaver birds (Crook 1964), primates (Crook & Gartlan 1966; Eisenberg *et al.* 1972), and antelope (Jarman 1974). However, social interactions (e.g. competition, cooperation or mating) may also shape the distribution of individuals over space (Carpenter 1942; Sade 1972; Clutton-Brock 1974; Emlen & Oring 1977; Gehrt & Fritzell 1998). Therefore, social associations themselves may be a primary component in determining social structure.

Separating the influence of spatial patterns and social preferences remains a central challenge even in contemporary analyses of social structure (Pinter-Wollman *et al.* 2014; Shizuka *et al.* 2014). As the core data for this thesis were collected over a relatively large spatial scale, I was able to examine how spatial structure contributed to the group dynamics of foraging flocks (**Chapter 2**). Group composition is an important aspect of social life, and previous studies have, for example, demonstrated its role in movement synchrony (Aivaz & Ruckstuhl 2011), predator avoidance (Mathis & Chivers 2003) and foraging decisions (Aplin *et al.* 2014). Through generating null models of flock composition based on individuals' spatiotemporal occurrences, I illustrate how the observed assortment within immigrant and locally-born juvenile birds is largely determined by spatial structure. Further, the distribution of individuals also contributes towards the observed social assortment by age and segregation amongst the sexes (**Chapter 2**). In related work, I used a similar approach to illustrate the extent to which an individual's social behaviour (in terms of various social network metrics) is an outcome of its environment alone (**Appendix B**). Thus, in this way, environmental factors may determine the social experiences and pressures that individuals face (**Chapter 2**).

The influence of external factors on sociality is experimentally demonstrated in **Chapter 5**. By determining where separate individuals could access resources using novel automated RFID 'selective feeders', I show that the constraints placed on where individuals could feed, even over fine-spatial scales, influenced which birds they formed foraging flocks with. Therefore, whilst previous studies have demonstrated a relationship between environmental factors and social structure at the population (Davies & Hartley 1996; Sanchez-Prieto *et al.* 2004; Verdolin 2009) and individual

level (Chilvers & Corkeron 2001; Ansmann *et al.* 2012), this work confirms the causal relationship between the two. Whilst the work directly illustrates the impact of external perturbations on social networks, I show that the fission-fusion dynamics of the system allowed quick recovery of the network after the experimental treatment was ceased. Correspondingly, in another experimental study assessing the influence of ecological factors on this social system, we demonstrated how simulated predator attacks cause rapid group turnover within flocks, equivalent of up to 3hrs of standard foraging conditions (**Appendix C**).

Despite the strong influence of ecological factors on social structure, I also illustrate that fine-scale social dynamics influence wider social organisation. For instance, whilst spatiotemporal population structure may explain a significant proportion of non-random flock compositions, there is strong evidence that individuals choose to form flocks with those of the same age class and opposite sex (**Chapter 2**). Therefore, short-term decisions may also be based around social attraction and repulsion, and in this way regulate individuals' social experience. Individuals also were found to consistently occupy similar social network positions over time, and display repeatable social phenotypes over and above that which could be explained by their spatial locations alone (**Appendix B**).

Similar randomisation approaches into analysing observational data have also illustrated that song sparrow (*Zonotrichia atricapilla*) social communities are consistent over time, as flockmates in one year were also likely to be flockmates in following years (Shizuka *et al.* 2014). This appears to be due to both spatial range overlap and fine-scale social preferences (Shizuka *et al.* 2014). Yet, if individuals based their spatial choices around their social preferences, statistical approaches will struggle to separate the exact contribution of these interrelated processes. In **Chapter 3**, I use multiple lines of evidence to show that individuals breed nearer to those they were strongly associated with in the winter, even when correcting for spatial overlap. Also, breeding neighbours (i.e. those that share a territory boundary) were found to have higher prior social affiliation than non-neighbouring birds of the same breeding distance apart. Hence, I provide evidence that spatial structure and the fine-scale arrangement of individuals across the landscape are indeed based around social associations. Therefore, care is required when attempting to assess the independent contributions of individuals' social

preferences and their spatial distributions on the arising population structure, as spatial structure itself may be a product of social preferences. This finding also highlights how other analyses considering social preferences should carefully consider the rationale of accounting for spatial structure. For instance, if large females preferentially located themselves closer to large males due to favouring mating with these, controlling for space within the analysis may reduce, or even negate, any signal of active mating preferences, despite that these exist. Thus, spatial terms within a model could theoretically absorb patterns of interest. If this issue was not identified, this would result in a failure to properly detect behavioural processes governed by individuals' social preferences shaping their spatial occurrence.

Finally, strong social relationships are known to be a fundamental component of many complex animal societies, and therefore we may expect selection to act on individuals to maintain these. I show that when mated pairs of birds were experimentally separated so they could not access the same feeding stations as one another, individuals prioritised their relationship with their mate over maximising their own access to resources (**Chapter 7**). Therefore, whilst individual-based theories predict that animals should base their foraging around maximising energy intake (Charnov 1976; Pyke 1984; Stephens & Krebs 1986), I show how birds forgo optimizing consumption and instead base their spatial foraging decisions around sustaining their social relationships. Previous work has suggested wild primates may also prioritize group cohesion when making foraging decisions (King *et al.* 2008; Kazahari 2014). Yet, by experimentally imposing a clear conflict of preferences between two individuals, I demonstrate that individuals' will base their foraging decisions around preserving a single key relationship. Their decisions, in turn, influenced the structure of their social network in relation to the wider population, as their key social relationships also determined who else they would form flocks with. Therefore, these findings provide experimental evidence for feedback between social structure itself and the social associations which underpin it.

Carry-over of social structure

It has recently become widely acknowledged that a wide range of population-level processes may be interconnected with fine-scale social structure. Therefore, the social network approach may offer new insights into the influence of social interactions on

various aspects of ecology and evolution (Krause *et al.* 2015). For instance, within the studied great tit (*Parus major*) population, spatial structure during the breeding season is known to underpin numerous processes, such as mating opportunities, cooperation, responses to selection, timing of breeding and phenology (Garant et al. 2005; Grabowska-Zhang et al. 2012a; Patrick et al. 2012; Cole et al. 2015; Firth et al. 2015a; Hinks et al. 2015). As discussed, I show that social structure during the winter carries over to shape the breeding population structure upon which these processes are based (**Chapter 3**). Therefore, social structure, during a fission fusion period, may carry-over into spatial decisions at a crucial time (as individuals defend a territory and raise a brood). This may mean prior social networks have broad consequences in determining which environments individuals will be subjected to in the future. As individuals of all demographic classes and over all years appeared to shape their breeding positions around their previous social associations, this suggests that the future benefits of this may be broad, potentially including reduced aggression and increased cooperation between neighbours (Grabowska-Zhang *et al.* 2012a; Grabowska-Zhang *et al.* 2012b; Snijders *et al.* 2015), or increased mating opportunities if individuals are more likely to mate with familiar (Choudhury & Black 1994; Senar *et al.* 2013) and proximate (Patrick *et al.* 2012; Firth *et al.* 2015) conspecifics.

Experimentally imposing whom individuals formed foraging flocks with showed that foraging associations carried over into associations during breeding site prospecting (**Chapter 5**). This suggests a potential mechanism for the carry-over between winter social structure and the resultant breeding spatial structure. Further, how interaction patterns in one context may relate to another is currently of interest to furthering the understanding of sociality as well as general network theory (Lehmann & Ross 2011; Chan *et al.* 2013). Whilst drawing conclusions regarding the causal links between different social contexts using only observational data would be challenging, this experiment clearly demonstrates that social foraging directly influences other aspects of sociality (**Chapter 5**).

Indeed, while it has been widely recognised that experiments directly manipulating social networks are necessary in furthering the understanding of the fundamental properties of social structure, this remains largely unaddressed (James *et al.* 2009). Further, experiments also offer the ability to test the causality of patterns and determine

how interaction patterns and social behaviour of individuals respond to perturbations. Whilst other approaches, such as simulating perturbations and assessing potential outcomes for the social network (Lusseau 2003; Williams & Lusseau 2006; Manno 2008), are useful, they cannot incorporate the various potential behavioural responses of individuals (Flack *et al.* 2006). By removing individuals from the network while recording the social associations amongst individuals, I was able to assess how birds alter their social behaviour in response to the loss of their flock members (**Chapter 4**). Thus, whilst observational work within this system found that individuals exhibit a high degree of consistency in their social network positions over time (**Appendix B**), individuals can flexibly shift their social phenotypes upon removal of their associates. Further, the experimental approach used illustrated that the dynamic behavioural responses were driven by experiencing actual loss, rather than simply suffering disturbance. In this way, I provide evidence for compensatory social changes occurring upon the loss of an individual's social connections (**Chapter 4**). This indicates that the decrease in network connectivity predicted by the loss of individuals may be ameliorated by the remaining individuals' flexible responses and redundancy within the network (Naug 2009; Goldenberg *et al.* 2016).

Broadly, whilst the removal of individuals may be useful for assessing social structure (Flack *et al.* 2006; Thomas *et al.* 2008; Naug 2009), such experiments are often practically or ethically challenging (Lusseau *et al.* 2006). Further, removals also may have inadvertent effects independent of social structure through altering population size and composition (Flack *et al.* 2006; Naug 2009). Therefore, to exclusively determine the influence of social structure on wider processes, methods that enable associations to be broken, created, or maintained are needed, such as the direct manipulation of foraging associations (**Chapter 5**).

I was able to use this unique experimental system of manipulating foraging associations amongst wild birds to consider how the transmission of social information may depend upon the social network (**Chapter 6**). Social information use has been widely reported throughout the animal kingdom and is a key component in understanding animal behaviour (Dall *et al.* 2005; Rieucau & Giraldeau 2011; Gruter & Leadbeater 2014). Due to recent advances in examining information transmission, it is now possible to quantify how information flows through different components of the social networks of

wild animals (Hoppitt *et al.* 2010; Hoppitt & Laland 2011; Farine *et al.* 2015). However, examining the direct impact that changes to social structure may have for information flow has remained difficult (Webster *et al.* 2013). Further, as information use relates to various aspects of fitness, individuals may be expected to shape their social associations around gaining information (Laland 2004), yet disentangling this process from a simple correlation between social structure and information acquisition is challenging. I demonstrate how imposed changes to the social network can influence the pathways of information flow, as individuals were more likely to learn the location of new, unrestricted, ephemeral food patches (accessible to all birds) from those they were imposed to forage with (**Chapter 6**). Further, I demonstrate how individuals display a social learning strategy, whereby even when accounting for changes in social associations, they are most likely to acquire novel information from those who provide relevant information to them on a day-to-day basis. This preference was maintained even in contexts where information from all individuals was equally valid. Therefore, through combining the experimental manipulation of foraging associations with statistical techniques enabling the assessment of information flow through different social connections, I reveal how changes to social networks alter the pathways of information flow. Such findings expand the currently limited pool of knowledge regarding how social network structure and social learning strategies influence information flow in wild populations (Laland 2004; Hoppitt & Laland 2011; Aplin *et al.* 2015).

Similarly, through creating a mismatch between an individual's own preferences and the preferences of those they hold strong social relationships with, I showed that flexible behavioural strategies may develop to mitigate this trade off (**Chapter 7**). Within the selective feeder system deployed for the experiments in Chapters 5-7, birds could follow another individual (within 2 seconds) to scrounge from feeders even if they were not individually allowed access to them. I show that birds that were not allowed to feed at the same location as their mate increased both the flexibility and the learning rate of this scrounging strategy, as they attempted to maintain their pair-bond. Therefore, although an individual's own phenotype and the environment may influence the expression of social foraging strategies (Giraldeau & Beauchamp 1999; Bates & Chappell 2002; Rands *et al.* 2003), this experiment clearly demonstrates the consequences of social relationships for the flexibility and learning of these strategies.

The consequences of individuals shaping their own actions around their social relationships are conceivably broad, and could extend into various aspects of decision-making and behaviour, even if this is contrary to individuals' own preferences (**Chapter 7**). Interestingly, I also provide evidence that the scrounging behaviour was facilitated by their pair member, which may suggest that individuals can develop cooperative strategies to reduce the conflict of interests arising from differences in their preferred foraging locations. Further investigation of the occurrence and maintenance of cooperation within wild animal social networks would now be of much interest to advancing the understanding of the ecology of social systems, as well as the evolution of cooperation itself.

Further work

As discussed, there is considerable evidence that social connections amongst wild birds within this study system have various important implications. Nevertheless, the links between social networks and fitness remain uninvestigated. Previous studies within a variety of taxa have illustrated a link between wild animals' social network phenotypes and subsequent fitness (McDonald 2007; Formica *et al.* 2012; Brent *et al.* 2013; Wey *et al.* 2013; Nunez *et al.* 2015; Lehmann *et al.* 2016). However, our understanding of the causes of these relationships is not as developed as our documentation of their existence. Indeed, studies often struggle to account for sampling issues and externally driven causes of covariance between fitness and network position due to (i) being carried out within a relatively small number of individuals or focusing on a single, interdependent, social group (ii) a lack of information regarding within-individual changes in social network position resulting in relatively low confidence in estimates of social phenotypes, their plasticity and temporal variation in them, and (iii) assessing social networks at a spatiotemporal scale which does not allow environmental factors, and the spatial correlations within them, to be properly accounted for.

The study system on which the work in this thesis was based provides an exceptional opportunity to investigate how individual variation in social network positions relates to fitness. For instance, considering the current data set on great tits (*Parus major*), the success of 4497 breeding attempts by 2413 individuals present in the social network data have now been recorded. Further, 2614 of the individuals recorded within the social network data were ringed as chicks. Therefore, many individuals have been

tracked over their entire lifespan. This quantity of data would be sufficient to implement statistical techniques that measure the relationship between different aspects of individuals' sociality and various components of their fitness. Through employing null models similar to those used in **Chapter 2 and 3**, it would be possible to account for population spatial structure, both during the winter and the breeding season (as measures of reproductive success are also known to be spatially auto-correlated) within the framework of the social network. Furthermore, due to the detailed information available on individuals' traits, these data also provide the opportunity to examine the extent to which the relationship between sociality and fitness depends on an individual's characteristics (e.g. sex, age, immigrant status). Almost 1500 birds have been observed in more than one year's social network, and 817 observed in multiple years in both the social network data and the breeding data. Therefore, this would allow large scale and high resolution analysis of the fitness consequences of network positions *within* individuals.

Visualizing the raw data (Fig 1) illustrates consistent links between social network phenotypes and fitness components over all years. For instance, birds with more social connections (high centrality), but relatively weaker bonds (low average strength) are more likely to survive from one winter to the next, and are also more likely to breed (Fig 1a). Further, the broader position of an individual within the network beyond their dyadic associations may also be important. Among breeding birds, those occupying social network positions which bridge the shortest 'path' between others (high betweenness) and those whose flockmates are weakly associated with one another (low clustering coefficient) lay larger clutches and fledge more offspring (Fig 1b). As variation in individual seed consumption alone (i.e. usage of the RFID-feeders) has no carry over onto any measured fitness parameters (**Appendix A**), the relationship between social network position (recorded at the same feeders) with these fitness measures (Fig 1) is particularly intriguing.

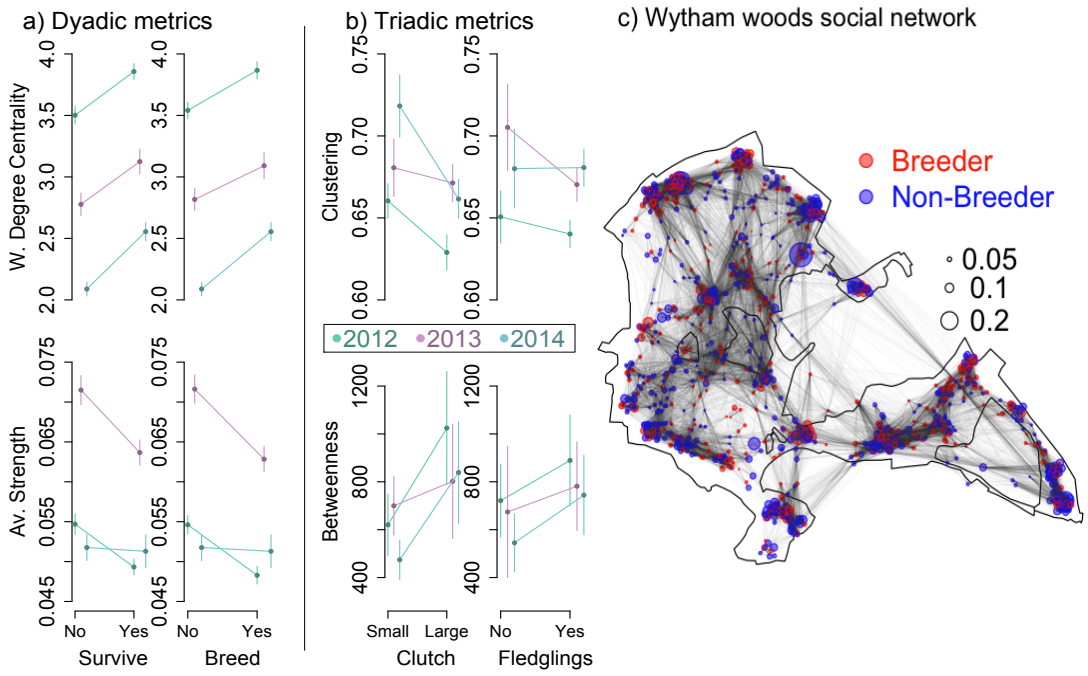


Figure 1: Preliminary analysis of the relationship between social network metrics and fitness components in great tits in Wytham Woods, 2012-2014. Left hand plot shows mean (±SE) for four node-level metrics in each of the three years, for four dichotomous characterisations of fitness components. The data are not adjusted for other effects. Right hand plot shows a map of Wytham Woods with the population-wide social network for one winter (2011-12) overlaid. Red = bred in 2012, Blue = non-breeder 2012; node size = average weighted strength, edge weight = strength of association, position = average winter position (jitter ~20m).

Whilst such patterns are highly suggestive, the apparent effects may differ if the influence of other factors was accounted for. For example, local population density varies significantly across space, and may simultaneously relate to the network centrality of individuals as well as determinates of fitness, such as the quality of the environment and the amount of competition experienced. Therefore, applying null model approaches similar to those described in this thesis (particularly **Chapters 2 & 3**) will enable separation of the effects of social network position and other environmental effects on subsequent individual fitness.

Nevertheless, even with extensive analysis, the direct causal effects of social phenotypes on individual fitness would remain uncertain. Within this study population, this could be addressed using the selective feeder system, which allows the fine-scale

experimental manipulation of social networks amongst spatially overlapping individuals (**Chapters 5-7**). By enforcing different social phenotypes on individuals (through controlling where/when individuals can access food) whilst allowing other environmental factors to remain constant across the different experimental treatment groups, it would be possible to establish the direct causal effects these social positions have for individual fitness within wild populations. Further, the mechanisms underpinning this relationship could also be elucidated during such experiments by simultaneously assessing processes related to social network position and potentially influential to fitness, such as access to information (Aplin *et al.* 2012; Aplin *et al.* 2015), pair bonding (Psorakis *et al.* 2012; Culina *et al.* 2015), neighbour familiarity and territory acquisition (Grabowska-Zhang *et al.* 2012a; Grabowska-Zhang *et al.* 2012b; Farine & Sheldon 2015). Finally, as social phenotypes are known to be heritable (Radersma *et al.* In prep) by assessing the fitness outcomes for individuals exposed to different social treatments, the response to selection on individual network position could be estimated. In this way, how variation in environmental factors may determine the mode and direction of these selective pressures, and hence maintain variance in individual behaviours, could also be examined.

Wider applications of understanding sociality

Whilst furthering the understanding of social networks and related processes may offer various new insights into ecology and evolution, it also presents some practical applications (Makagon *et al.* 2012). Indeed, whilst attention has been given to exploring how spatial structure can influence conservation efforts in terms of dispersal, gene flow, or extinction (Ferriere *et al.* 2004), the role of social structure remains less examined. Nevertheless, **Chapter 3** illustrates how prior social networks carry over into shaping spatial structure during the breeding season. Further, as individuals appear to shape their breeding positions around their close winter associates (**Chapter 3**), the current conservation practice of playing conspecific calls to attract birds to particular breeding locations (Ward & Schlossberg 2004; Scott & Lee 2013) could potentially be improved by playing calls of familiar individuals.

A particularly relevant concept is how perturbations to one social context within animals systems may carry over into another. Studies of mammals have demonstrated that networks considering the same individuals, but different kinds of interactions, show

correlations in overall structure and dyadic relationships (Chaverri *et al.* 2007; Drewe *et al.* 2009; Madden *et al.* 2009; Lehmann & Ross 2011; Silvis *et al.* 2014), as well as individual network positions (McCowan *et al.* 2008). Indeed, external factors or perturbations influencing specific interactions can have consequences for other dimensions of social structure (Madden & Clutton-Brock 2011). This social carry-over is demonstrated experimentally to occur within wild birds (**Chapter 5)**. Due to the correlations that exist between different social contexts, it has been suggested that using affiliative networks within captive primates to predict or mitigate aggressive interactions could improve their welfare (McCowan *et al.* 2008). Further, given the relationship between roosting association networks and foraging structure in wild bats (Chaverri *et al.* 2007; Chaverri *et al.* 2013; Silvis *et al.* 2014), it is also important to understand how habitat disturbance to one of these contexts could have negative implications for the other, for example the destruction of roosting sites disrupting social foraging (Silvis *et al.* 2014).

Human-induced loss of individuals is an issue that is likely to affect many wild animal populations. Therefore, it is valuable to attempt to understand the social consequences of this. In marine mammal populations, the social network approach has been used to illustrate how removal of the most socially central individuals, which may mimic hunting practices, may disrupt network connectivity (Lusseau 2003; Williams & Lusseau 2006). In wild elephant (Loxodonta africana) populations, loss of the matriarchs through poaching may potentially reduce the ecological information available to the groups (McComb *et al.* 2001). Interestingly however, recent work has illustrated that elephant social structure may be afforded some resilience against poaching as maternal social roles are actively replaced by those of their daughters (Goldenberg *et al.* 2016). Through taking an experimental approach, **Chapter 4** gives direct evidence for birds adjusting their social network position upon experiencing removal of their flock mates, and these behavioral changes may compensate for the social consequences of flockmate loss. How the selective removal of individuals influences the social network is also relevant to wildlife disease dynamics (Weber *et al.* 2013), as disease transmission may depend upon the associations amongst individuals (Godfrey *et al.* 2009; VanderWaal *et al.* 2014). Hence, knowledge of disease transmission network structure, and its response to perturbations, may improve the use of selective removals to reduce disease spread in wild populations. Indeed, previous

attempts to reduce disease spread have been hampered by insufficient understanding of disease transmission dynamics (Hamede *et al.* 2009; Lachish *et al.* 2010).

If the loss of individuals reduces the opportunity for social interactions, this may also reduce the opportunity for social information spread, e.g. regarding predator recognition (Griffin 2004) or breeding habitat selection (Doligez *et al.* 2002; Danchin *et al.* 2004), and potentially even increase extinction risk (Schmidt *et al.* 2015). Further, understanding how information flows in natural systems is of broad interest (Whiten & Mesoudi 2008). **In Chapter 6**, the experimental approach enables us to directly show that changes to social structure carry over to influence the pathways of information transmission. Further, I also demonstrate that individuals prioritize learning from individuals who provide relevant information on a regular basis, even in contexts where information from all individuals is equally valid. Indeed, social transmission may cause individuals to disregard their own information and simply copy one another (Dall *et al.* 2005). These 'information cascades' may even have negative consequences if the diffusing information is not beneficial (Giraldeau *et al.* 2002; Rieucau & Giraldeau 2011). Thus, understanding this component of social transmission also has various immediate practical applications, such as assessing how wildlife responds to human interference (Whitehead *et al.* 2004). For example, dolphins that socially learned to take food handouts from humans appeared to be potentially more likely to be involved in harmful boat strikes (Donaldson *et al.* 2012). There may also be implications for captive animal welfare (Makagon *et al.* 2012), such as in determining the social spread of stress-related behaviour (feather pecking) in poultry (Nicol 1995). Finally, just as it may aid animal welfare, understanding social networks also has implications for human systems, as social integration has been shown to strongly relate to biomarkers of physical health (Yang *et al.* 2016) as well as mortality risk (Holt-Lunstad *et al.* 2010) and well-being (Flori *et al.* 2006; Smith & Christakis 2008).

General Conclusion

In recent years, applying the social network approach to animal societies has revealed many new insights into their overall structure and the properties of the social relationships within them (Croft *et al.* 2008; Whitehead 2008; Krause *et al.* 2015). Together, various theoretical, technological and computational developments have enabled these advances by providing a clear framework to address, and suitably

analyze, the social network data generated from innovative tracking devices (Krause *et al.* 2007; Krause *et al.* 2013). Whilst the direct influence of social networks on wider processes has remained relatively less well explored, the continued discussion of this issue, and clear progression of relevant methods, appears indicative of imminent, considerable, progress.

In particular, automated experimental treatment of individuals (**Chapters 5-7; Appendix C**), will allow a wide variety of social manipulations to be applied and assessed. For instance, monitoring the spread of disease whilst experimentally imposing set rules on dyadic associations, or assigning selected individuals to particular network positions, would allow the sophisticated dissection of contagion dynamics. On a larger scale, different fine-scale social manipulations treatments could be applied over replicate networks. Such an approach, combined with examining processes of interest, would allow assessment of the social conditions that promote the adoption and spread of culture, or the maintenance of cooperation. In this thesis, I outline the appropriate analytical techniques, as well as introducing novel experimental approaches, for answering various outstanding questions surrounding animal social systems. I utilise this framework to disentangle, and emphasize, the important interplay between ecology and sociality. I demonstrate how social networks, and the individuals within them, respond to perturbations (such as the loss of individuals, or externally imposed segregation). Further, I was able to demonstrate that social structure is directly, and influentially, linked with the spatial distribution of individuals, transmission of social information, and the expression and learning of individual social and foraging strategies. Given the advances made, and the conclusions formed, these findings now create a platform for a broad range of future work intended to further our appreciation of the biological importance of social connections amongst wild animals.

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Appendix A

Individual variation in winter supplementary food consumption and its consequences for reproduction in wild birds

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Individual variation in winter supplementary food consumption and its consequences for reproduction in wild birds

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The provision of wild birds with supplementary food has increased substantially over recent decades. While it is assumed that provisioning birds is beneficial, supplementary feeding can have detrimental 'carry-over' effects on reproductive traits. Due to difficulties in monitoring individual feeding behaviour, assessing how individuals within a population vary in their exploitation of supplementary food resources has been limited. Quantifying individual consumption of supplementary food is necessary to understand the operation of carry-over effects at the individual level. We used Radio Frequency Identification (RFID) technology and automated feeders to estimate individual consumption of supplementary winter food in a large wild population of great tits *Parus major* and blue tits *Cyanistes caeruleus*. Using these data, we identified demographic factors that explained individual variation in levels of supplementary food consumption. We also tested for carry-over effects of supplementary food consumption on recruitment, reproductive success and a measure of survival. Individual variation in consumption of supplementary food was explained by differences between species, ages, sexes and years. Individuals were consistent across time in their usage of supplementary resources. We found no strong evidence that the extent of supplementary food consumption directly influenced subsequent fitness parameters. Such effects may instead result from supplementary food influencing population demographics by enhancing the survival and subsequent breeding of less competitive individuals, which reduce average breeding parameters and increase density-dependent competition. Carry-over effects of supplementary feeding are not universal and may depend upon the temporal availability of the food provided. Our study demonstrates how RFID systems can be used to examine individual-level behaviour with minimal effects on fitness.

Over recent decades, the feeding of wild birds has increased in popularity in many areas and is now a multi-million dollar global industry (Jones and Reynolds 2008). However, only recently has attention been paid to the potential consequences of substantial supplementary feeding of wild birds. Since winter food availability is a major determinant of mortality and population regulation in seasonal temperate environments (Lack 1954), the widespread and reliable availability of food for wild birds may have effects at the individual level, and subsequently influence population-level demographics (Robb et al. 2008a). The consumption of non-natural food resources may alter the body condition of individuals in ways that affect their performance in the subsequent breeding season (i.e. 'carry-over effects' – Harrison et al. 2011). For instance, supplementary feeding may cause earlier egg laying and increased fledging success (Svensson and Nilsson 1995, Robb et al. 2008b), improved egg quality (Blount et al. 2002, Reynolds et al. 2003), increased clutch size (Rooney et al. 2015), survival (Brittingham and Temple 1988, Norris 1993) and reduced dispersal (Orell and Ojanen 1979).

Supplementary feeding may also have negative effects on reproduction. During the breeding season, supplementary feeding can lead to a reduction in average clutch and brood size in great tits and blue tits, and reduced hatching success in the latter (Harrison et al. 2010). Further, supplementary feeding during the winter can have carry-over effect on subsequent life-history stages. Plummer et al. (2013a) reported a reduction in reproductive success in blue tits supplemented over winter with fat, documenting reduced mean offspring weight, size and survival in comparison to

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control populations. Thus, estimating the long-term effects of supplemental feeding of wild birds, and the mechanisms involved, is not straightforward.

Effects of food supplementation during the non-breeding season on reproductive traits could arise from either (or both) individual-level carry-over effects or effects on demography, e.g. by increasing overall survival rates. Whilst considerable variation may exist in the extent to which individuals within a population use supplementary resources (Robb et al. 2011, Bonter et al. 2013), most previous work has been limited to assuming individuals access supplementary food equally, due to difficulties in monitoring individual feeding behaviour (Harrison et al. 2010, Plummer et al. 2013a, b). Robb et al. (2011) found evidence of individual variation in supplementary food consumption using stable isotope analysis, but indirect techniques are limited in terms of the resolution that individual variation can be measured at. The classification of birds as supplemented versus non-supplemented in experimental and control treatments is likely to be a simplification, as many factors influence feeding patterns in wild birds. For example, dominance hierarchies during feeding affect the ability of willow tits *Poecile montanus* to gain mass during cold days (Koivula et al. 1995), while blue tits are subordinate to great tits in monopolising food resources and roosting sites (Dhont and Eyckerman 1980). Dominance hierarchies also exist with respect to age, sex and relative body size where older, male and larger-bodied individuals respectively, typically dominate each demographic class (Garnett 1981, Nilsson and Smith 1988, Sandell and Smith 1991). Dispersal status could also affect individual exploitation of supplementary food, due to dispersing (i.e. immigrant) birds being less competitive (Nilsson and Smith 1988) or having fewer social links to acquire information on food resource location in novel environments (Aplin et al. 2012).

In this study, we fitted Passive Integrated Transponder (hereafter 'PIT') tags to birds that could be detected by Radio Frequency Identification (hereafter 'RFID') antennae fitted to bird feeders. RFID technology enables standardised, contactless and non-invasive study of behaviour in wild animals. We used this approach to collect detailed, individual-level data on the feeding behaviour of a large population of blue and great tits supplemented through the winter with sunflower seeds. We estimated the individual consumption of seeds over the course of two years to address three aims. First, we quantified individual winter seed consumption levels, determined how consistent individuals were in their use of supplementary resources, and examined the relative importance of demographic factors in explaining the observed variation. Second, we tested for individual-level carry-over effects of winter supplementary feeding on subsequent life-history parameters, some of which have been assessed at the population level (Harrison et al. 2010, Plummer et al. 2013a, b). We examined whether winter seed consumption affected probability of recruitment, as well as of being observed in future – our best estimate of survival. For females that did breed, we assessed whether seed consumption had an effect on lay date, clutch size and egg mass. Finally, we looked for evidence of carry-over effects of seed consumption on later reproductive stages to consider potential carry-over effects in males as well as females via provisioning effort.

Material and methods

Seed consumption data

Data were gathered from a long-term study population of blue and great tits in Wytham Woods, Oxford, UK (51.7°N, 1.3°W), a 385 ha mixed deciduous woodland. Each individual was ringed with a standard BTO metal ring and fitted with a PIT tag (IB technology, Aylesbury, UK). It is estimated that 85–90% of great tits present in the woods were tagged during the study period (Aplin et al. 2014), although the proportion of blue tits tagged may be smaller. Tags were moulded into a split plastic colour ring with an internal diameter of 2.3 mm for blue tits and 2.6 mm for great tits. Sixty-five seed feeders were distributed in a grid throughout the site, at intervals of 250 m. Each feeder had 2 seed dispensing openings fitted with RFID antennae perches. Antennae remotely detected the RFID code of PIT tags fitted to individual birds that visited the feeder, recording these to a data logger. The detection range of each antenna was approximately 5 cm, meaning individuals were highly likely to only be recorded if they perched on the antennae to take a seed from the feeder.

During two consecutive winters (3 December 2011 to 27 February 2012 and 1 December 2012 to 3 March 2013), birds were provided with husked black sunflower seeds each Saturday and Sunday (Jacobi Jayne, Kent, UK). Mean monthly temperatures within the wood were similar across both winters and broadly in line with the long term average. December to February values were 4.8, 5.1 and 3.5°C in 2011/2012 and 4.6, 3.2 and 2.4°C in 2012/2013 (Environmental Change Network 2015). Feeders were programmed to automatically open pre-dawn and close post-dusk over the weekend, and were closed during weekdays. No birds could access supplementary food during this time and were therefore dependent upon foraging for natural foods within the wood, such as beech mast and invertebrates. While it is possible that some individuals may feed in adjacent gardens during the week, very few feeders are located within 1 km of the woodland edge. Since the birds in our study area are relatively sedentary during winter (Matechou et al. 2015), we are confident that the vast majority of birds were not exploiting alternative supplementary food resources during the week. The design of this study was part of a larger project investigating the winter behaviour of the wild tit community. Although providing intermittent access to supplementary food in this way should still allow assessment of the factors governing individual variation in supplementary food exploitation, it may reduce the extent to which the consequences of food exploitation (e.g. fitness) can be generalised to constant-provisioning scenarios. However, whilst some research has investigated the influence of constant provisioning (at least at the population level), the consequences of a less stringent feeding regime, which may be reasonably common under less standardized situations such as garden bird feeding, has not been investigated. Similarly, whilst some previous studies of supplementary feeding may have provided food every day, most have not quantified individual-level access to feeders, making it difficult to determine the consistency that birds actually accessed the supplementary food. Our study design also enabled us to assess whether

employing an RFID tracking system, which has many uses for studying avian ecology (reviewed by Bonter and Bridge 2011), based on supplying food to attract tagged individuals to RFID loggers over intermittent periods, can indirectly influence life-history variables.

Feeders logged each record of a bird at a frequency of 1/3 s, resulting in multiple records per bird per visit. We developed an algorithm that assessed the distribution of inter-visit intervals (the gap between two consecutive records) to infer the number of seeds taken. For each bird, the inter-visit intervals has a bimodal distribution, with a very large peak at ≤ 1 s, and a second peak at around 60 s. These peaks relate to within-visit intervals and between-visit detections respectively. This distribution occurs because birds typically visit a feeder to obtain a single seed, which they consume after flying into nearby vegetation (resulting in a temporal gap between each seed collected), but the RFID loggers record the presence of birds up to 3 times per second. To remove multiple records in the data that constitute a single visit, we identified the inter-visit interval corresponding to the lowest value between the two peaks in the distribution (i.e. the least common interval). We repeated this for each individual and calculated the 95% range of this value across all individuals combined (Fig. 1a). These values enabled us to assign visits to one of three categories (Fig. 1b): A) intervals that are part of the within-visit distribution of intervals, B) intervals that are uncertain (those that fell within the 95% range of minimum values), C) intervals that are part of the between-visit distribution of intervals. Interval 'B' ranged from 5 to 23 s in 2011/2012 and 5 to 24 s in 2012/2013, and accounted for 2.3% of the data in both years. Interval 'C' accounted for 29.1% of the data in 2012 (1 594 924 unique visits) and 27.9% of the data in 2013 (1 118 004 unique visits). We used the number of records for each bird with an inter-visit interval greater than 23 s in 2012 (which included 2567 individuals) and 24 s in 2013 (1964 individuals) as an estimate of the number of seeds consumed. We used R, ver. 3.1.2 (R Development Core Team) for all analyses. Thresholds used to calculate inter-visit intervals were almost identical for both species. The energetic content of the seeds we provisioned was estimated to be 1.05 kJ seeds^{-1} (average husked, dry weight energetic content = 19.9 kJ g^{-1}, average seed mass = 0.0528 g, J. Jayne pers. comm). Sunflower seeds are also high in protein (0.2 g g^{-1}) and vitamin E (0.35 mg g^{-1}, USDA 2007).

Reproductive data

Birds breeding in nest boxes throughout the woods were monitored from April to July, where 1 April was considered as day 1 for data analysis. Nests were monitored on a weekly basis until eggs were discovered within each active box. Where more than one egg was present in a nest, lay date was estimated by back-calculating from the day of observation, based on the assumption that blue and great tits lay one egg per day (Perrins 1996). Mean egg mass was calculated to the nearest 0.1 g by weighing a minimum of 3 eggs per clutch prior to incubation (Rahn and Ar 1974). Clutch size was recorded as the maximum number of eggs counted within the nest after commencement of incubation, unless a larger number of eggs or chicks were recorded during hatch checks. We recorded hatch date by visiting each nest every other day from the expected hatch date until hatching occurred.

Parents were identified in one of two ways. When chicks were aged between 7 and 11 d, the detachable front of each box was replaced with an identical front, to which an RFID antenna was attached around the entrance hole, powered by a concealed 9 V battery. If the parents were PIT tagged

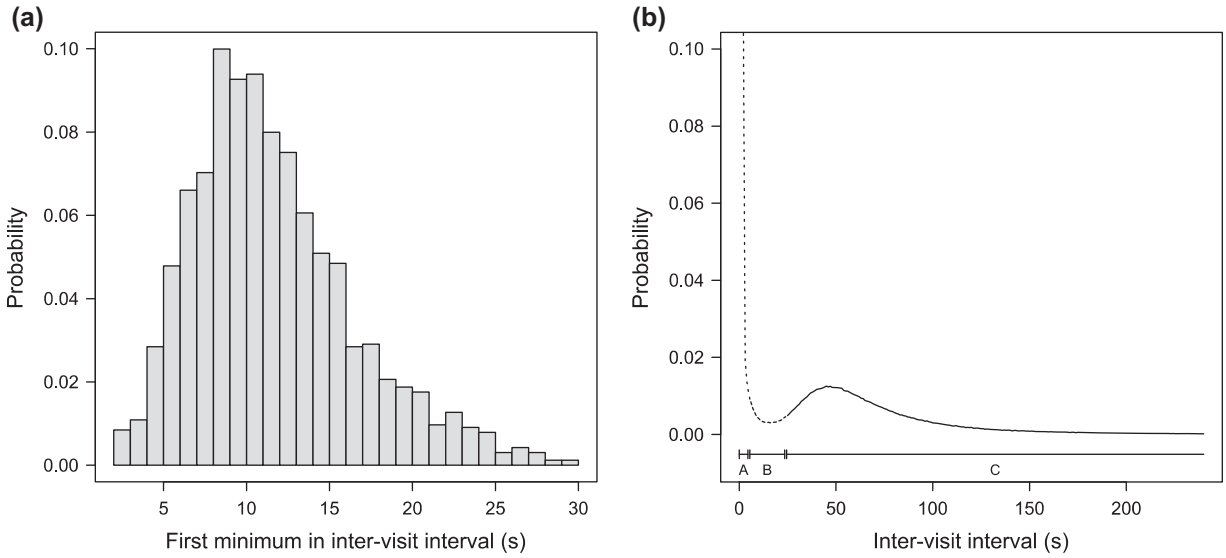


Figure 1. (a) Frequency distribution of the inter-visit interval corresponding to the minima between the two peaks in the distribution across all individuals and (b) probability distribution of inter-visit intervals for remotely-detected feeding data from a population of great tits (n = 1240) and blue tits (n = 1672) combined. The regions A to C in this graph identify intervals that correspond to the within-visit recording interval, intervals that cannot be allocated to within or between visit, and intervals correspond to between-visit intervals. Thus, only the occurrence of a gap between records that falls within the region of area C is used when estimating the number of seeds taken by each individual.

prior to breeding, their identities were remotely recorded as they entered the nest box to provision the chicks. The RFID fronting was left on each nest for a maximum of 1.5 h. If the fronting method failed to identify both parents, they were caught at the nest box using a spring-loaded trap when chicks were aged 11–15 d. Adults were ringed and tagged if unringed upon capture, and sexed by plumage traits and the presence of an incubation patch or a cloacal protuberance in females and males respectively (Svensson 1992). For breeding birds detected remotely, we inferred age and sex from previous breeding attempts or from the previous capture data of the partner. We also inferred the sex of great tits previously only captured outside of a breeding season based on plumage traits (Svensson 1992). Because blue tits cannot be sexed with certainty outside of the breeding season, remotely-detected blue tits that were not previously captured, or whose partner was not previously captured during a breeding season were left unsexed. All breeding birds were aged as adults (age $>$ 1 yr) or first years, based on plumage traits (Svensson 1992).

We classified the dispersal status of each individual as local if they were originally ringed as a chick within the study site, or an immigrant if not (Table 1). While a small number of birds breed in natural cavities, estimates of recapture rates of tits in Wytham Woods suggest that the great majority of birds breed in boxes (Lachish et al. 2011, Kidd et al. 2015). In addition, we defined birds as 'winter residents' if they were observed on at least 10 out of 12 weekends each winter, representing all birds recorded on greater than the population median number of weekends (i.e. the right hand of the bimodal distribution – Supplementary material Appendix 1, Fig. A1). We classified birds as breeding recruits if they were detected at a nest box during the spring following the winter in focus.

All chicks were ringed and fitted with a PIT tag age 15 d (hatch = day 1), and weighed to an accuracy of 0.1 g. Fledge checks were conducted one week after the expected fledge date. We calculated fledging success as the number of young fledged divided by the clutch size of each box. Because oak tree *Quercus* sp. density within the territory of each nest box is known to be a predictor of reproductive success (Wilkin et al. 2009), we controlled for this in our analysis by counting the number of oak trees greater than 50 cm diameter at breast height within 75 m of each nest box.

Data analysis

Individual variation in supplementary food consumption

Considering each species separately, we examined how demographic characteristics; namely sex, age, and dispersal status affected individual seed consumption levels. Annual seed consumption was strongly related to the number of weekends that a bird was observed at the feeders. Therefore, using the demographic characteristics as explanatory variables, we fitted linear mixed models (LMMs) using the lme4 package (Bates et al. 2014), setting the estimated number of seeds each bird consumed each weekend as the response variable (which was normally distributed – Fig. 2) and including individual identity as a random term. This also enabled us to determine individual consistency in exploitation of supplementary food resources by calculating the total variation that was accounted for within repeated measures of the same individual (Nakagawa and Schielzeth 2013). To account for differences between the two years, year was included as a categorical fixed effect. Similarly, as reliance on supplementary foods is likely to increase through the winter as weather conditions harshen, and individuals may differ in their temporal occurrence through the winter, we also included weekend number/ID as a numerical fixed effect to control for this. Initially, we conducted this analysis on winter residents only (see above; great tit n = 788, blue tit n = 814). Restricting the analysis to winter residents ensured that birds had access to the supplementary food resources throughout the majority of the winter and reduced the likelihood that these birds were exploiting supplementary food resources outside of the study area. However, as this may exclude some birds that occurred in the woodland but did not utilize the feeders regularly, we also ran the same models for two other sets of individuals. Firstly we considered only birds that were subsequently recorded breeding (great tit n = 568, blue tit n = 549). By considering breeding birds we were able to include 'distance from nest box to most frequently-visited feeder' as an explanatory variable to assess the influence of spatial location. Secondly, we also ran the analysis for all birds (including breeding and winter residency status as explanatory variables; great tit n = 1240, blue tit n = 1672), to broadly assess if using subsets of particular interest or considering certain types of individuals had any effect. For all LMMs, we assessed support for variables based on breadth and position of confidence intervals and effect sizes, as per Nakagawa and Cuthill (2007).

Carry-over effects on recruitment to the breeding population

We also examined how individual recruitment to the breeding population that year was influenced by supplementary food consumption. Using 'recruitment' as the binary response variable, we used generalized linear mixed models (GLMMs) with a binomial error structure to estimate the effect of estimated yearly seed consumption (square root transformed to aid model convergence), whilst accounting for sex, age, dispersal status and year. We also added individual identity as a random effect to account for repeated individuals between years. Initially, we restricted this analysis to winter residents (defined above) because transient birds may consume less seeds and to control for known effects of winter residency on recruitment (Farine and Sheldon 2015, Matechou et al. 2015). We repeated the analysis in two ways. Firstly we included the number of weekends each bird was recorded as a fixed effect, permitting an assessment of the effect of increased presence even within winter residents. Secondly, we included all individuals in the population, but instead of using total seeds consumed, we used the rate of estimated seed consumption as the predictor variable. Consumption rate was estimated by dividing individual total winter seed consumption by the number of weekends they were detected at a feeder. This allowed us to gain an understanding of the influence of considering a subset of particular interest in comparison to the whole population. As a supplementary analysis, we also ran the same models but setting the binary response variable as whether a bird was observed following the winter. This provides a best estimate of survival, but is

Table 1. Variables contained within models to explain variation in individual seed consumption levels in a population of great tits and blue tits, and to test for carry-over effects of seed consumption on survival and breeding parameters.

			Models included as a variable							
Fixed predictors	Description/levels	Justification	SC	R	S	LD	CS	EM	NM	FS
Annual seed consumption	Continuous factor, great tit range 1–2201, mean 815 ± 468; blue tit range 1–1859, mean 527 ± 425.	Test for potential negative effects of seed consumption on survival and recruitment.		✓	✓	✓	✓	✓	✓	✓
Weekly seed consumption	Continuous factor, great tit range 1–240, mean 85 ± 37; blue tit range 1–213, mean 64 ± 37.	Test for potential negative effects of seed consumption on survival and recruitment.	✓							
Age	2-level factor, adult or first-year.	Age differences in seed consumption and age affects breeding parameters (Bouwhuis et al. 2009).	✓	✓	✓	✓	✓	✓	✓	✓
Sex	2-level factor, male or female.	Potential sex differences in seed consumption, and also in effects on breeding success.	✓	✓	✓					
Feeder distance	Linear distance from main feeder to breeding box. Continuous (to nearest 10 m), range 10–3350, mean 200.	Potential negative correlation between distance to main feeder and seed consumption.	✓			✓				
Weekends	Weekends an individual was detected (for yearly consumption) or the specific weekend detected (for weekly). Continuous, range 1–14.	Positive correlation between seed consumption and number of weekends observed at the feeder.	✓	✓	✓	✓	✓	✓	✓	✓
Box altitude	Continuous, range 60–166 m, mean 103 m.	Negative correlation between altitude and lay date, due to temperature decrease with altitude (Perrins 1970).				✓				
Dispersal status	2-Level factor, immigrant or resident.	Potential differential use of supplementary feeders between immigrants and residents, also differences in RS between the two groups (Nilsson and Smith 1988).	✓	✓	✓	✓				
Oak density	Number of mature oaks within 75 m of breeding box. Continuous, range 0–87.	Breeding success strongly linked to oak density in tits (Wilkin et al. 2009).					✓	✓	✓	✓
Lay date	Date of first egg, where 1 April = 1. Continuous, range 1–80 mean 17 (2012), 35 (2013).	Lay date affects clutch size, brood mass and fledging success (Norris 1993).					✓		✓	✓
Clutch size	Discrete count, great tit range 2–13, median 7; blue tit range 2–15, median 9.	Clutch size affects egg mass and brood mass (Perrins 1996).						✓	✓	
Year	2-level factor, 2012–2013.	Account for annual variation in seed consumption due to e.g. availability of natural food (Perrins 1966).	✓	✓	✓	✓	✓	✓	✓	✓
Random effects										
Individual	Multi-level factor. See results and SI for specifics of each model.	Test for individual consistencies in seed consumption across years and control for multiple observations of individuals across weekends and years.	✓	✓	✓	✓	✓	✓		
Box	Multi-level factor. See results and SI for specifics of each model.	Control for territory effects and use of boxes across both years.				✓	✓	✓	✓	✓

Model abbreviations: SC, seed consumption; R, recruitment; S, survival; LD, lay date; CS, clutch size; EM, mean egg mass, NM, mean nestling mass; FS, fledging success. See Supplementary material Appendix 1, Table A1.1–A2.4 for further details of model construction.

difficult to disentangle from dispersal (see Supplementary material Appendix 1, Table A4.1–A4.2 for details).

Carry-over effects on reproductive success

For breeding birds of each species, we considered how yearly supplementary food consumption influenced various measures of reproductive success. We fitted LMMs separately for the response variables lay date, clutch size, mean egg mass, mean nestling mass and overall fledging success, including individual identity and nest box as random terms. For lay date, clutch size and mean egg mass, only maternal seed consumption was considered. For mean nestling mass and fledging success, paternal seed consumption was also included (which showed a 0.38 and 0.50 correlation with maternal seed consumption for blue tits and great tits respectively). Further details of fixed effects are outlined in Table 1. We repeated each model with a) number of weekends each bird was detected included as a fixed effect and b) considering

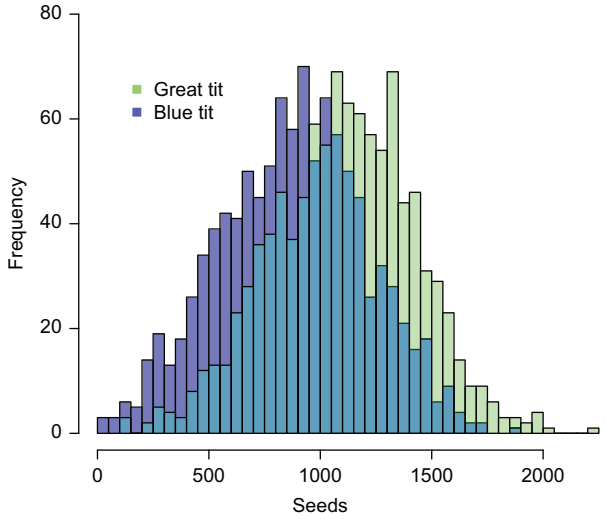


Figure 2. Frequency distribution of total estimated winter consumption of supplementary sunflower seeds in a winter resident population of great tits (green bars) and blue tits (blue bars). Turquoise (blend of blue and green) shows the smallest frequency of the two species when they overlap. Values are per bird per year, and only includes birds classed as winter residents of the study area (see Material and methods).

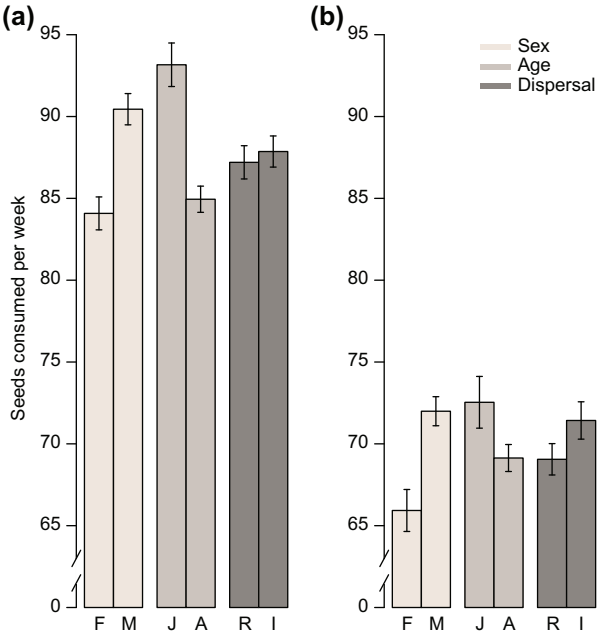


Figure 3. Variation in mean (± SE) estimated weekly consumption of supplementary seeds (averaged for each individual) by sex, age and residency status in a wintering population of (a) great tits and (b) blue tits. X axis abbreviations for sex: female (F) and male (M); age: juvenile (J) and adult (A); and dispersal status: resident – i.e. locally-born (R) and immigrant (I). Values are calculated using only birds classed as winter residents of the study area (see Material and methods).

rate of seed consumption instead of total seed consumption. Known re-nesting attempts, which were rare (< 2%), were excluded from all analyses.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4ch2c> (Crates et al. 2016).

Results

Individual variation in supplementary seed consumption

There was substantial variation in the extent to which birds within the population consumed seed from the supplementary feeders. In general, great tits consumed significantly more seeds (ca 35%) than blue tits (Fig. 3, Table 1). Considering the winter residents, the mean estimated annual seed consumption (± SD) in great tits was 1102 ± 323 (range 115 to 2201) and in blue tits was 876 ± 328 (range 15 to 1859, Fig. 2). Estimated seed consumption per weekend across all birds averaged 91 ± 37 in great tits and 64 ± 37 in blue tits.

Our model of variation in seed consumption identified several demographic factors that each explained a significant proportion of the variation (Table 2). In the resident population, first year birds tended to consume more seeds than adults, though this difference was only significant in great tits (Table 2, Fig. 3). In both species, the greatest difference in levels of seed consumption was found between the sexes, with males consuming significantly more than females. Dispersal status had no effect on seed consumption (Table 2, Fig. 3). We also found that increasingly more seeds were taken over weekends later in the season (Table 2), in line with predictions that usage of supplementary food may increase over the winter. Additional models that: a) restricted the analysis to breeding birds only and b) included the whole population, yielded very similar patterns (Supplementary material Appendix 1, Table A1.1 and A1.2). Individual consistency in the number of seeds consumed across observations (i.e. weekends) was reasonably high in both great tits (residents: $r = 0.33$, $n = 788$; breeders: $r = 0.38$, $n = 568$; overall: $r = 0.41$, $n = 1240$) and blue tits (residents: $r = 0.39$, $n = 814$; breeders: $r = 0.47$, $n = 549$; overall: $r = 0.46$, $n = 1672$). Individuals also showed similar levels of repeatability across weekends when each year was considered separately and also across years (Supplementary material Appendix 1, Table A2).

Carry-over effects on recruitment to the breeding population

For great tits, there was no evidence that seed consumption influenced recruitment to the breeding population of the winter residents (Table 3). This was also the case when including the number of weekends each bird was detected as a fixed effect in a model, or considering seed consumption rate of all individuals (not just winter residents) (Supplementary material Appendix 1, Table A3.––A3.2). The same result of no carry-over effects of seed consumption was found when an estimate of survival was considered instead of recruitment to the breeding population (Supplementary material Appendix 1, Table A4.––A4.3). Similarly, whilst a marginally significant (although

Table 2. Linear mixed model of factors affecting variation in estimated weekly winter supplementary seed consumption in a resident population of great tits and blue tits. Bold indicates the effects that are more than twice the standard error around the estimate.

	Great tit, n = 788			Blue tit, n = 814		
	Est.	SE	t	Est.	SE	t
Intercept	**78.608**	**1.558**	**50.454**	**56.471**	**1.699**	**33.241**
Age Relative to juveniles	**–8.795**	**1.135**	**–7.751**	–2.001	1.159	–1.726
Dispersal status Relative to immigrants	0.301	1.534	0.196	1.871	1.659	1.128
Sex Relative to females	**6.244**	**1.533**	**4.073**	**6.797**	**1.651**	**4.117**
Weekend Numerical from start of winter	**1.240**	**0.067**	**18.383**	**1.275**	**0.063**	**20.201**
Year Relative to 2013	**4.494**	**0.797**	**5.640**	0.043	0.755	0.057

not accounting for multiple testing) positive relationship was found between seed consumption and recruitment in winter resident blue tits, no evidence for carry-over effects was found when weekend occurrence was accounted for (Supplementary material Appendix 1, Table A3.1), or when considering seed consumption rate of all blue tits (Supplementary material Appendix 1, Table A3.2), as well as when considering survival (Supplementary material Appendix 1, Table A4.1–A4.3). When accounting for multiple tests on the data, no convincing evidence of carry-over effects of seed consumption onto recruitment (or estimated survival) was found within the population.

Carry-over effects on reproductive success

Estimated annual seed consumption in both sexes had no effect on any of the breeding parameters we tested in either species. Lay date increased with box altitude for both species. In great tits, adult and locally-born females started their clutches earlier than first-year and immigrant birds. In both species, there was a negative relationship between lay date and clutch size and in great tits there was a negative relationship between egg mass and clutch size. Clutch size was the key predictor of brood mass in both species and in great tits, there was a tendency for earlier hatched broods to be heavier. Mean nestling mass was the key predictor of fledging success for both species (Table 4). The same patterns were found when considering seed consumption rate, and when controlling for winter residency (Supplementary material Appendix 1, Table A5.1 and A5.2).

Discussion

Through the automated monitoring of individuals within a large community of wild birds, we identified factors that explained individual variation in the consumption of supplementary food resources. We then tested for individual-level carry-over effects of supplementary food consumption on a number of subsequent fitness parameters. There was substantial variation in the extent to which individuals exploited supplementary food resources and individuals were consistent in the degree to which they fed on supplementary food over both short (weekends) and long (years) time periods. Variation in supplementary food consumption was linked to a number of demographic traits at the individual level, but at this level, we found no evidence of carry-over effects of winter seed consumption on reproductive success. Our results suggest that negative effects of supplementary feeding demonstrated previously (Harrison et al. 2010, Plummer et al. 2013a, b) may have arisen through increased food availability influencing population demography, for example increasing the survival of low-quality individuals and potentially increasing resource competition during the breeding season. Additionally, temporally limiting the availability of supplementary food, as we did here, and which might occur in garden environments, may also prevent the development of carry-over effects.

Several factors predicted individual differences in supplementary food consumption. First-year birds consumed more seed than adults. Although adults may be expected to dominate younger birds for access to food resources, dominance

Table 3. Generalised linear mixed model of the effect of estimated total winter supplementary seed consumption on recruitment in a winter resident population of great tits and blue tits. p values reported are calculated under the default lme4 method (Bates et al. 2014).

	Great tit n = 788				Blue tit n = 814			
	Est.	SE	z	p	Est.	SE	z	p
Intercept	0.373	0.468	0.796	0.426	–1.698	0.423	–4.013	<0.001**
Age Relative to juveniles	0.046	0.153	0.297	0.766	–0.211	0.172	–1.228	0.219
Dispersal status Relative to immigrants	–0.217	0.138	–1.565	0.118	0.025	0.157	0.156	0.876
Sex Relative to females	–0.379	0.141	–2.684	0.007*	0.204	0.165	1.233	0.218
Seeds consumed	–0.002	0.014	–0.124	0.901	0.026	0.013	2.049	0.04*
Year Relative to 2013	–0.079	0.147	–0.535	0.593	0.022	0.147	0.148	0.883

Table 4. Summary of linear mixed models examining the effect of total estimated winter supplementary seed consumption on subsequent breeding success in a population of great tits and blue tits. Bold indicates the effects that are more than twice the standard error around the estimate.

Fixed effect	Lay date			Clutch size			Mean egg mass			Mean nestling mass			Fledging success		
	Est.	SE	t	Est.	SE	t	Est.	SE	t	Est.	SE	t	Est.	SE	t
Blue tit		**n = 284**			**n = 284**			**n = 265**			**n = 167**			**n = 167**	
Box altitude	**0.035**	**0.018**	**2.007**												
Mean brood mass													**6.814**	**2.106**	**3.236**
Clutch size							–0.003	0.003	–1.212	**–0.080**	**0.040**	**–1.986**			
Female age	–1.509	1.005	–1.501	0.144	0.229	0.630	0.010	0.012	0.854	–0.208	0.148	–1.406	–4.006	4.001	–1.001
Female dispersal status	1.394	0.929	1.501												
Distance from nest box to feeder	0.002	0.001	1.292												
Female annual seed consumption	0.000	0.001	–0.072	0.000	0.000	–0.583	0.000	0.000	0.802	0.000	0.000	–0.055	–0.001	0.005	–0.133
Lay date				**–0.104**	**0.014**	**–7.392**				0.009	0.010	0.843	–0.493	0.261	–1.889
Male age										–0.019	0.146	–0.128	1.341	3.915	0.343
Male annual seed consumption										0.000	0.000	–2.182	–0.004	0.005	–0.875
Oak density				0.008	0.007	1.050	0.000	0.000	–0.552	–0.002	0.004	–0.360	–0.068	0.118	–0.579
Year	**17.833**	**0.866**	**20.600**	**0.791**	**0.322**	**2.459**	**0.026**	**0.010**	**2.627**	0.355	0.224	1.587	**15.049**	**6.012**	**2.503**
Great tit		**n = 358**			**n = 358**			**n = 327**			**n = 208**			**n = 208**	
Box altitude	**0.043**	**0.016**	**2.791**												
Mean brood mass													**3.404**	**0.857**	**3.970**
Clutch size							**–0.011**	**0.004**	**–2.563**	**–0.221**	**0.083**	**–2.672**			
Female age	**–2.805**	**0.859**	**–3.267**	0.071	0.184	0.384	–0.016	0.015	–1.081	–0.406	0.300	–1.353	5.057	3.698	1.367
Female dispersal status	**1.907**	**0.828**	**2.302**												
Distance from nest box to feeder	0.001	0.001	1.014												
Female annual seed consumption	0.001	0.001	0.764	0.000	0.000	0.915	0.000	0.000	0.454	0.000	0.000	–0.216	0.003	0.004	0.736
Lay date				**–0.037**	**0.011**	**–3.291**				**0.101**	**0.019**	**5.196**	**1.036**	**0.253**	**4.090**
Male age										0.466	0.297	1.570	–1.501	3.547	–0.423
Male annual seed consumption										0.001	0.000	1.834	–0.001	0.005	–0.153
Oak density				**0.016**	**0.006**	**2.532**	0.000	0.001	0.719	0.014	0.009	1.507	0.050	0.112	0.450
Year	**19.492**	**0.736**	**26.480**	–0.117	0.274	–0.425	0.013	0.013	0.988	**–1.948**	**0.447**	**–4.360**	**–14.052**	**5.693**	**–2.468**

effects could still explain increased use of feeders by first-year birds. For instance, adult birds may be more efficient at locating natural food sources through experience, or more likely to monopolise natural food resources by excluding or usurping younger subordinates from rich patches (Krebs et al. 1972, Hegner 1985). Alternatively, basal metabolic rate (BMR) decreases with age across taxa due to physiological changes with age or through selection for low BMRs in food-limited environments (Hulbert and Else 2000, Broggi et al. 2007). Bouwhuis et al. (2011) showed that BMR declines with age in this population of great tits, although the effect (ca 4% decline comparing first year and older birds) is smaller than the difference in estimated seed consumption reported here. A reduction in BMR with age may partially explain why adult birds consumed less supplementary seed than first year birds.

Body size could in part explain the difference between species, as blue tits are around 45% smaller by mass than great tits. Similarly, sex differences in levels of seed consumption are consistent with body size-energetic demand theory, as males are on average 7% greater in mass (Bouwhuis et al. 2014) and 5% longer in wing length in both species. Also, female bills are on average shorter and shallower than males (Gosler 1987). This could make it more difficult for females to de-husk each seed to access the kernel, which may reduce average female seed consumption rate. Sex differences could also be explained by dominance, since in both species, males were found to exploit seed to a greater extent than females.

Individuals were markedly consistent in their exploitation of supplementary food across both weekends and years. Between 33–47% of the overall variation could be explained by individual identity, suggesting intrinsic differences between individuals, perhaps through behavioural tendencies such as personality (Aplin et al. 2013, 2014, 2015), could drive a large part of the observed variation in consumption patterns. Individual consistency in supplementary food consumption may also be explained by location within the wood. The distribution of beech mast (and other natural winter food resources), is non-random and likely to be consistent across time. Therefore, if individuals reside in the same areas of the wood across weekends and years, their dependency upon non-natural food resources is, similarly, likely to remain consistent across time.

Many factors may have prevented the development of carry-over effects in the population. Birds were only provisioned with supplementary food for two days per week. Even with limited weekly availability, individuals could still consume a substantial quantity of supplementary food, with mean values of 815 ± 468 and 527 ± 425 seeds per individual per winter in great tits and blue tits respectively. When accessible, great tits and blue tits consumed on average 40 ± 15 and 23 ± 15 seeds d^{-1} respectively, leading to an estimated gross energetic intake from supplementary food of 31.5 kJ d^{-1} (given a mean estimated energy content of 1.05 kJ $seed^{-1}$). In great tits, estimates of daily energetic expenditure (DEE) range from 88.7 to 105.5 kJ $(24\ h)^{-1}$ while provisioning young (Tinbergen and Dietz 1994, Tinbergen and Verhulst 2000) and from 50 to 150 kJ $(24\ h)^{-1}$ during egg laying (Stevenson and Bryant 2000, te Marvelde et al. 2012). DEE increases linearly with decreasing temperature, approaching 130 kJ $(24\ h)^{-1}$ at ambient temperatures close to 0°C (Sanz et al. 2000). Given this range of DEE estimates, the average energetic intake from sunflower seeds could provide up to 60% of an individual's daily energy requirements. We stress these are rough estimates, as DEE is influenced substantially by a wide range of environmental and intrinsic factors (Tinbergen and Verhulst 2000, te Marvelde et al. 2012).

How the estimated levels of seed consumption we calculate compare to environments where supplementary food is available continuously remains to be determined. A study of feeding in two Nearctic congeners; the black-capped chickadee *Poecile atricapillus* and tufted titmouse *Baelophus bicolor*, found that daily visitation rates at bird feeders ranged from 20–50 visits (Bonter et al. 2013). Assuming that each bird consumed one seed per visit, our daily estimates of seed consumption for blue tits and great tits are similar to those of chickadees and titmice. Therefore, our study population may have consumed around 70% less supplementary food than birds provisioned continuously throughout the winter. Further, birds require daily food to supplement their fat reserves as they can drop by as much as 10% each night (Macleod et al. 2005). By only supplying food for two days per week, natural population regulation processes are likely to have been in operation when food was not available (Lack 1954). Blue and great tits do not store food, so the benefits of supplementary food are likely only to be felt during, and shortly after the periods when it is available. In contrast, caching species such as marsh tits *Poecile palustris* and nuthatches *Sitta europea* could benefit substantially from supplementary food even when it is not available continuously. However, these species respond to the same foraging pressures as non-caching species (Farine and Lang 2013). Whilst previous studies have focussed on continuous provisioning, temporally limiting the supply of food could reduce carry-over effects (both positive and negative). Therefore, further research in now needed to investigate both the influence of different feeding regimes, as well as the relative frequency of typical feeding regimes practiced by the general public.

The seasonal availability of supplementary food may also be important in determining its potential to affect breeding. Here, we withdrew the supplementary food at the end of February so that, in line with Robb et al. (2008b), there was a period of at least 5 weeks between the cessation of supplementary feeding and the commencement of breeding. This gap between feeding and breeding enabled us to distinguish true carry-over effects from directly contemporaneous effects of the supplementary food on body condition and reproduction.

Supplementary food provisioning did not act as an ecological trap; birds were unlikely to use these food resources as a cue for breeding as, in contrast to Robb et al. (2008b), we found no evidence that the degree of individual-level exploitation of supplementary food led to earlier egg laying or increased fledging success. Another potential explanation as to why our findings contrast to those of previous studies is that birds in our study were provisioned with sunflower seeds as opposed to peanuts (Robb et al. 2008b) or fats (Plummer et al. 2013a, b). The nutritional profiles of supplementary foods vary substantially, not only in their energetic content, but also in the levels of vitamins, minerals and antioxidants. Sunflower seeds are particularly high in vitamin E, a key

antioxidant that Plummer et al. (2013b) found could prevent the negative carry-over effects caused by provisioning wild birds with a high-fat supplementary diet. The availability of sunflower seeds as a supplementary food in many ways mimics a large beech mast crop (seeds of beech tree *Fagus sylvatica*); a natural winter food source with substantial annual variation in availability, which both blue and great tits exploit to a large extent when available (Perrins 1966, Savill et al. 2010). The energetic content of beech mast and sunflower seeds are broadly similar, at 24.1 and 24.5 kJ g^{-1} in beech and sunflowers respectively (USDA 2007, Lebl et al. 2010). The abundance of natural winter food resources is widely understood to affect large scale population dynamics in tits (Perrins 1966, Kallander 1981). As such, providing sunflower seeds as supplementary food effectively results in an artificial increase in the frequency of years with high natural food abundance. Therefore, the type of food provisioned could also determine the potential to cause carry-over effects on individuals.

Conclusion

Using RFID technology, we were able to estimate individual consumption of supplementary food in a large wintering population of wild birds. Individuals were consistent in their use of supplementary food resources and variation was explained by species, age, sex, and individual identity. Our results suggest that the quantity of supplementary food consumed by individuals did not impact upon their subsequent reproductive behaviour. Therefore, we demonstrate that with a carefully-designed feeding regime it is possible to monitor the behaviour of birds at a fine scale without affecting their subsequent life histories.

Any negative effects of supplementary feeding are more likely to result from impacts on population-level demographic processes. We found no evidence for a relationship between seed consumption on recruitment or estimated survival with our study design. This suggests that an alternative mechanism could be causing negative effects from constant supplementary feeding, or feeding at more critical time periods (i.e. during breeding). Reduced breeding quality is likely to arise by increasing over-winter survival, which results in greater density-dependent competition, increased use of marginal territories or acquisition of territories by poor-quality individuals (Both 1998, Farine and Sheldon 2015). This mechanism is supported by the fact that first year birds, which are widely thought to be subordinate to older conspecifics, exploited the supplementary food to a greater extent than adults. In common buzzards *Buteo buteo*, supplementary feeding improved breeding success in suboptimal habitat (Rooney et al. 2015), which is likely to increase breeding density. Such density-dependent competition is known to have effects on breeding traits such as recruitment, clutch size and brood mass (Krebs 1970, 1971, Minot 1981, Both et al. 1999). When measured at the population level, these individuals negatively influence mean trait values, such as nestling mass, which can be interpreted as a negative outcome of supplementary feeding. However, this does not necessarily result in a decrease in the population in subsequent years, but rather is the result of natural population regulation processes.

Future experimental studies could attempt to manipulate both the availability and quality of supplementary food to a range of species. These should strive to measure not just the outcome of breeding attempts, but also demographic parameters of the population. The development of new technologies, such as RFID, offer exciting opportunities for experimental tests to explore the potential for supplementary feeding to cause carry-over effects. Feeders can be designed to selectively provision some birds, while excluding others from accessing the feeder (Firth and Sheldon 2015, Firth et al. 2015). This experimental design would limit potentially confounding effects such as year, time and space. Such studies will be valuable from both an ecological as well as an applied conservation perspective.

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Supplementary material (Appendix JAV-00936 at <www.avianbiology.org/appendix/jav-00936>). Appendix 1.

Appendix B

Consistent individual differences in the social phenotypes of wild great tits (*Parus major*)

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Consistent individual differences in the social phenotypes of wild great tits, *Parus major*

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Despite growing interest in animal social networks, surprisingly little is known about whether individuals are consistent in their social network characteristics. Networks are rarely repeatedly sampled; yet an assumption of individual consistency in social behaviour is often made when drawing conclusions about the consequences of social processes and structure. A characterization of such social phenotypes is therefore vital to understanding the significance of social network structure for individual fitness outcomes, and for understanding the evolution and ecology of individual variation in social behaviour more broadly. Here, we measured foraging associations over three winters in a large PIT-tagged population of great tits, and used a range of social network metrics to quantify individual variation in social behaviour. We then examined repeatability in social behaviour over both short (week to week) and long (year to year) timescales, and investigated variation in repeatability across age and sex classes. Social behaviours were significantly repeatable across all timescales, with the highest repeatability observed in group size choice and unweighted degree, a measure of gregariousness. By conducting randomizations to control for the spatial and temporal distribution of individuals, we further show that differences in social phenotypes were not solely explained by within-population variation in local densities, but also reflected fine-scale variation in social decision making. Our results provide rare evidence of stable social phenotypes in a wild population of animals. Such stable social phenotypes can be targets of selection and may have important fitness consequences, both for individuals and for their social-foraging associates.
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The application of social network analysis to animal populations has become an important component of the behavioural ecologist's toolbox, leading to novel insights into the potential costs and benefits of sociality. In particular, different social positions within animal groups can have associated advantages and disadvantages, including for social information use (Aplin, Farine, Morand-Ferron, & Sheldon, 2012), disease transmission (Godfrey, Bull, James, & Murray, 2009; Hamede, Bashford, McCallum, & Jones, 2009), mate choice (Oh & Badyaev, 2010), competition (D. Farine & Sheldon, 2015) and long-term reproductive success (Mcdonald, 2007). It therefore seems likely that social network position may be under selection; further, that there may be trade-offs associated with differing social behaviours (e.g. central individuals receive better social information, but are also more susceptible to diseases). However, while some studies have found some aspects of network position to be heritable (Fowler, Dawes, & Christakis, 2009; Lea, Blumstein, Wey, & Martin, 2010), surprisingly little is known about whether individuals are repeatable

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and consistent in their social network characteristics. Establishing whether individuals have consistent social phenotypes is important for understanding the degree of plasticity in social behaviour, can set an upper limit to heritability, and is an important first step in understanding the significance of social network structure for individual fitness outcomes.

Individual level variation in behaviour can be understood within the context of the animal personality literature, which focuses on broad trait categories including boldness, exploration behaviour, risk taking, aggression and sociability (Bell, Hankison, & Laskowski, 2009; Reale, Reader, Sol, McDougall, & Dingemanse, 2007). Consistent within- and between-individual differences have been extensively documented for exploration behaviour and boldness by assaying individuals in isolation (Bell et al., 2009; Dingemanse et al., 2012) and by using dyadic interactions for traits such as aggression (Blumstein, Petelle, & Wey, 2013). In contrast, individual variation in sociality has been quantified in a more limited range of studies and usually investigated with assays of shoaling tendency, separation tests or group size choice (Cote & Clobert, 2007; Cote, Fogarty, & Sih, 2012; Harcourt, Sweetman, Johnstone, & Manica, 2009; Mills & Faure, 2000; Reale et al., 2007). Social networks provide a new opportunity by which to study sociability in a complex social context, with a set of standardized, well-understood metrics (Sih, Bell, & Johnson, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

Individual variability in social behaviour may also have implications for the evolution and maintenance of other personality traits, for example if individuals adopt stable social roles that are fine-tuned through positive feedback loops or frequency dependence (Bergmuller & Taborsky, 2010; Wolf, van Doorn, Leimar, & Weissing, 2007). A relationship between social behaviour, social structure and other individual level behavioural traits has been found in fish (Croft et al., 2009; Pike, Samanta, Lindstrom, & Royle, 2008; Schurch, Rothenberger, & Heg, 2010), sleepy lizards, *Tiliqua rugosa* (Godfrey, Bradley, Sih, & Bull, 2012) and great tits (Aplin et al., 2013; Snijders et al., 2014). In great tits, birds with higher scores for the personality trait 'exploration behaviour' are more central in winter and spring social networks (Aplin et al., 2013; Snijders et al., 2014). Aplin, Farine, Mann, and Sheldon (2014) tested how these individuals made social decisions when flocking, and found that fast explorers used less social information and showed less social cohesion, suggesting a mechanism by which broad-scale differences in social structure may emerge (also see Boogert, Farine, and Spencer (2014)).

An assumption of individual consistency in social behaviour is therefore important for a range of questions in studies of social networks and animal personality. Yet networks are rarely repeatedly sampled, with studies often drawing inferences about social structure and dynamics despite little or no replication. Two exceptions include recent studies in wild yellow-bellied marmots, *Marmota flaviventris* (Blumstein et al., 2013) and captive spotted catsharks, *Scyliorhinus canicula* (Jacoby, Fear, Sims, & Croft, 2014). In Blumstein et al. (2013) a moderate repeatability was found for a measure of aggressive interactions, with social networks measured over several years ($R = 0.22$), but there was no relationship between social aggression and the individual level personality trait of defensive aggression. Jacoby et al. (2014) measured social associations in replicated groups of captive juvenile sharks, quantifying repeatability across different habitat treatments. Network strength was repeatable ($R = 0.46$), with little plasticity across treatments, and largely driven by stable individual level preferences for aggregating in specific group sizes. The authors suggested that this consistent behaviour provided evidence for social personality types in sharks; however, the relatively short-term nature of the measurements (14 days) limited broader conclusions.

Here we investigated social behaviour in a PIT-tagged population of great tits over three winters. This large-scale study provided a unique opportunity to assess individual consistency in social network position over both short-term (week to week) and longer-term (between years) timescales, by using a grid of feeding stations fitted with RFID antennae to capture 'snapshots' of the spatiotemporal flocking patterns of a population of 729–1053 individuals. We first collected 13–14 replicated foraging social networks for each year, and measured individual repeatability in network attributes within each winter season. Second, we combined within-year sampling periods to construct a foraging social network for each winter, and measured between-year individual repeatability in the same network attributes. Repeatabilities were compared across age and sex classes. Finally, we compared our repeatability estimates to those calculated from permutations that controlled for the spatial location of individuals in each sampling period. This approach corrected for any potentially confounding interaction between social networks and spatiotemporal differences in local population density (Farine et al., 2015). This allowed us to identify the relative contributions to social network position of spatial influences (including dispersal, settlement and movement decisions (Cote & Clobert, 2007; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010), and more fine-scale variation in social decision making.

METHODS

Study Site and Species

The study was conducted over 3 years (December 2011–March 2014) in a population of great tits in Wytham Woods, Oxfordshire, U.K. (51°46′N, 01°20′W). This population has been the subject of a long-term breeding survey since its establishment in 1947, with 1018 great tit nestboxes installed throughout the core area. The provision of artificial nestboxes allows birds to be trapped as nestlings and breeding adults, with trapped birds fitted with both a metal leg ring from the British Trust for Ornithology and a plastic leg ring containing a uniquely identifiable passive integrated (PIT) tag from IB Technology, Aylesbury, U.K. Birds were aged and sexed upon capture using either previous breeding records or plumage coloration. Over winter, great tits form loose fission–fusion flocks of unrelated individuals, with groups moving between patchy and ephemeral food sources, including bird feeders. In this period, mist netting at regular intervals targeted birds immigrating into the population, such that the large majority of wintering individuals were ringed and PIT-tagged. See Aplin et al. (2013) and Matechou, Cheng, Kidd, and Garroway (2015) for a formal analysis of what percentage of the population was tagged in winter, estimated at over 90% in 2011–2012.

Field Observations

Data were collected in three winter seasons: from 3 December 2011 to 27 February 2012 (Year 1), 1 December 2012 to 3 March 2013 (Year 2) and 30 November 2013 to 2 March 2014 (Year 3). Bird feeders were filled with unhusked sunflower seed and deployed at 65 locations, each approximately 250 m apart throughout the study site (Fig. 1a). These feeding stations opened from before dawn to after dusk for 2 consecutive days in every 7, resulting in 26 days of data collection over 13 sampling periods in

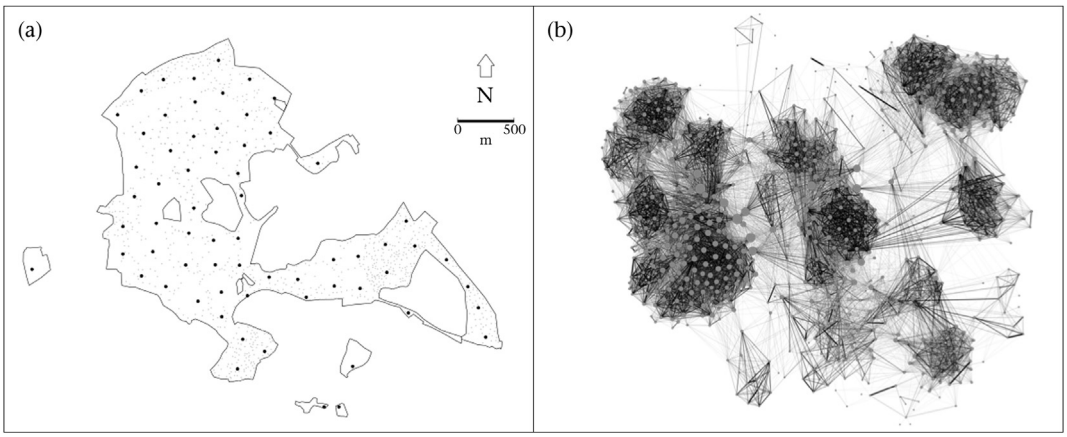


Figure 1. (a) Map of the study site showing the location of 65 feeding stations, each approximately 250 m apart and opening to scan for PIT-tagged great tits for 26–28 days of data collection over each of three winters. Smaller points on the map show the 1018 artificial nestboxes installed in the woodland. (b) An example of a social network constructed using this information on spatiotemporal foraging behaviour; the network is shown for the entire 2013–2014 winter period. Each node is one of 816 individuals and links between nodes are scaled between 0 (never observed in the same foraging flock) to 1 (always observed in the same foraging flock). Node size is scaled by unweighted degree (1–226).

the first winter (2011–2012) and 28 days of data collection over 14 sampling periods for the second and third winters (2012–2013, 2013–2014). Each feeding station had two access points fitted with a radio frequency identification (RFID) antenna and a data-logging device that scanned for PIT tags every 16th of a second. When great tits landed on the feeding station, their unique 10-digit hexadecimal PIT-tag code was registered and recorded on the data-logging hardware with an associated time and location, providing detailed spatiotemporal snapshots of individual foraging behaviour.

Social Networks

In each season, simultaneous sampling thus captured the weekly flocking choices of foraging individuals. We used a Gaussian mixture model to detect clusters of visits in these spatiotemporal data streams (Psorakis, Roberts, Rezek, & Sheldon, 2012). This method detects high-density periods of feeding activity (gathering events) without imposing subjective and artificial assumptions about the temporal boundaries of groups. This provided data on the identity of birds in each group, and was used to calculate an average group size for each individual in each sampling period and over the winter season. Social associations were assigned based on their presence in the same gathering event, similar to a gambit of the group approach (Franks, Ruxton, & James, 2010; Whitehead & Dufault, 1999). Association strengths for each dyad were calculated using the simple ratio index, where associations are scaled between 0 (never observed in the same foraging group) to 1 (always occurred in the same foraging group) (Cairns & Schwager, 1987). This approach is consistent with previous work on this population (see Aplin et al., 2015; Aplin et al., 2013; Farine, Garroway, & Sheldon, 2012). Social networks were then created for each sampling period, resulting in a total of 41 networks, containing an average of 561 (409–851) individuals. Social networks were also created for each winter season, summing data from all within-season sampling periods to create three networks containing 1053 (Year 1), 729 (Year 2) and 816 (Year 3) individuals (e.g. see Fig. 1b). Network construction and analysis were performed in R v.3.1.1 (R Core Team, 2012) using the asnipe package (Farine, 2013).

In addition to average group size, three social network metrics were calculated for each individual in each sampling period and season: unweighted degree, overall association strength (weighted degree) and betweenness. These metrics respectively measure: (1) the number of conspecifics with which the focal individual was observed foraging, giving an idea of overall gregariousness (see Fig. 1b, in which nodes are scaled by unweighted degree); (2) the total interaction rate for the focal individual with all other individuals, representing a focal measure of individual sociability; and (3) the number of shortest paths from all individuals to all other individuals that pass through the focal individual, important for the spread of information and disease (Croft, James, & Krause, 2008). Clustering coefficient was also calculated for individuals for each winter; this metric requires extensive observations of group membership to show interindividual variation and could not be reliably calculated for within-season sampling periods. It is representative of the extent to which nodes tend to cluster together to form distinct cliques, indicating how 'tight-knit' individuals are in their groups. All social network analyses were done in R packages sna (Butts, 2008).

Statistical Analysis

We assessed both within-year and between-year variation in social phenotypes by calculating individual level repeatability in social network metrics and group size. Repeatability is a measure of the total variation that is reproducible among repeated measures of the same individual (Nakagawa & Schielzeth, 2010), giving an indication of the consistency of individual phenotypes. Yet network metrics are not independent of other individuals in the social network, and will vary with sampling effort, population size and density. We first dealt with these possible sources of error by collecting the data for each repeated network in the exact same way, with the same sampling intensity and effort. Second, we calculated repeatability in two ways. A linear mixed-effects model (LMM) was used to calculate the intraclass correlation coefficient (ICC), with repeatability adjusted to account for population size, network density and date of each repeated measure (Nakagawa & Schielzeth, 2010). The square root of each measure was taken, except for betweenness, which was modelled as an exponential

function. This normalized the distributions, and repeatability was estimated from the variance of the individual random effect divided by the sum of the individual-level variance and the variance of the random error. Repeatability significance was estimated with Markov chain Monte Carlo sampling using restricted maximum likelihoods and default priors in the R package MCMCglmm (Hadfield, 2010). This method has the advantage of being easily comparable with most previous studies (e.g. see Bell et al., 2009), but should be interpreted with caution for network measures with a more global scope, such as betweenness. Using this method, repeatability estimates were further compared across age and sex classes. Individuals were aged (adult/first year) and sexed (male/female) using either previous breeding records or plumage coloration. Differences between classes were determined by calculating pairwise differences in *Z*-transformed repeatability estimates and assessing whether confidence intervals, CI, overlapped with zero (Nakagawa & Schielzeth, 2010).

We also calculated repeatability using methods described in Wilson, Krause, Dingemanse, and Krause (2013), with a null model based on repeated node-based randomizations of the networks. This test explicitly controls for the nonindependence of data within networks, and compares the sum of the variances for individuals' network positions across observed networks (SV_O) to the sum of individual level variances in position from randomized networks SV_R (Wilson et al., 2013). Individuals were ranked within each network and scaled between 0 and 1. Individual network positions were thus relative to all others in that network, with small values of SV_O indicating a similar relative ranking across all repeated samples. Significance was determined by comparing the SV_O for each network measure to a frequency distribution of SV_R values generated from 10 000 node randomizations of observed data.

A component of an individual's social phenotype might simply result from choices about where and when to forage. For example, if individuals differ in their propensity to settle in areas of different density, then, given that population density is expected to influence many aspects of social networks, a component of the interindividual variation will result from such individual settling decisions. To identify the influence of such spatial effects, we designed a spatiotemporal null model that aimed to estimate the expected individual repeatability if individuals simply differed consistently in their occurrence at different feeding locations, but were not repeatable in their behaviour within these locations. To create this null model we carried out 1000 permutations of each network that maintained which locations (feeders) and time periods (weekends) each individual was recorded, but randomized their social phenotype within these spatiotemporal choices. In each permutation, each individual was assigned to one of the locations where it was observed, where the probability of being assigned to each location was generated by their activity at each one (number of flocks they were observed in). On the majority of occasions (65%), individuals were only present at one location on a given weekend.

Following this assignment, the identity of individuals within the same locations during the sampling period was randomly swapped, so that each individual adopted the phenotype of another individual occurring at that feeder that weekend, Thus, in each permutation, individuals were assigned a new social phenotype (network metric). This permutation procedure maintained the structure of the data and the same variation in network metrics, but removed the link between observations of the same individual across multiple replicates. This represents a null model in which the effects of individual locations in space and time (at the scale of weekend samples) are retained, but no other individual differences. Estimation of repeatability (using the LMM approach) was then drawn from each permuted data set, and the 95% range of these estimations illustrated the expected range of repeatability if individuals just differed in their spatiotemporal occurrence, but not in their social choices.

Ethical Note

All work was subject to review by the local ethical review committee at the Department of Zoology (University of Oxford) and also adhered to U.K. standard requirements. The work was conducted as part of a larger ongoing research project at Wytham woods, and all birds were caught, tagged and ringed by appropriate BTO licence holders.

RESULTS

Within each winter season, individuals were observed in a median of 11 (Year 1), 10 (Year 2) and 12 (Year 3) sampling periods, with 9835 (Year 1), 6853 (Year 2) and 7940 (Year 3) measures derived from 1053 (Year 1), 729 (Year 2) and 816 (Year 3) individuals. Over each full winter, the median range encompassed three feeding stations with eight moves between feeders (also see Aplin et al., 2013; Fig. 1a); there was no difference in the distance or type of spatial movements undertaken by males and females, but first-years moved more than adults (see Appendix Fig. A1).

Birds were significantly consistent in all measured social behaviours. In all years, group size (Year 1: $R = 0.43$; Year 2: $R = 0.64$; Year 3: $R = 0.60$), degree (Year 1: $R = 0.46$; Year 2: $R = 0.61$; Year 3: $R = 0.58$) and association strength (Year 1: $R = 0.41$; Year 2: $R = 0.64$; Year 3: $R = 0.63$) were moderately to highly repeatable. Betweenness (Year 1: $R = 0.19$; Year 2: $R = 0.18$; Year 3: $R = 0.38$) was less consistent, with a higher variability (Fig. 2). Males and adults were significantly more repeatable than females and birds in their first year in all measures except betweenness, for which the results were less consistent (Tables 1 and 2). However, the differences in absolute repeatabilities were small, ranging between 0.01 and 0.14 for age differences and between 0.01 and 0.06 for sex. Furthermore, the 95% CIs overlapped for all but one metric (see Appendix Fig. A2), suggesting that the biological importance of these differences may be relatively minor compared to the overall effect of individual differences in social phenotype. Population size, network density and date were included as fixed effects in all models. Population size and network density both had a significant effect in all but two models, but date was less consistent (see Appendix Tables A1 and A2). Finally, when the repeated within-year networks were analysed using a network randomization method (Wilson et al., 2013), the results for network metrics were similar, with significant repeatability in all metrics, but with highest repeatability in degree centrality and association strength (see Table 3).

It was also possible to calculate individual consistency in social behaviour between years, with 565 great tits observed in at least two winters, and 210 individuals observed in all 3 years. Similarly high repeatabilities were observed for degree ($R = 0.55$, 95% CI 0.54–0.56), group size ($R = 0.51$, 95% CI 0.50–0.52), association strength ($R = 0.57$, 95% CI 0.567–0.574) and clustering coefficient ($R = 0.43$, 95% CI 0.41–0.44; Fig. 3). Estimated repeatability for betweenness was slightly lower, with a higher variance ($R = 0.33$, 95% CI 0.28–0.36; Fig. 3, also see Appendix Fig. A3 for an alternative visualization). Again, results were similar for the network metrics when using the test statistic SV_O, with significant repeatability for all measures, but with the highest repeatability in degree and strength (see Table 3).

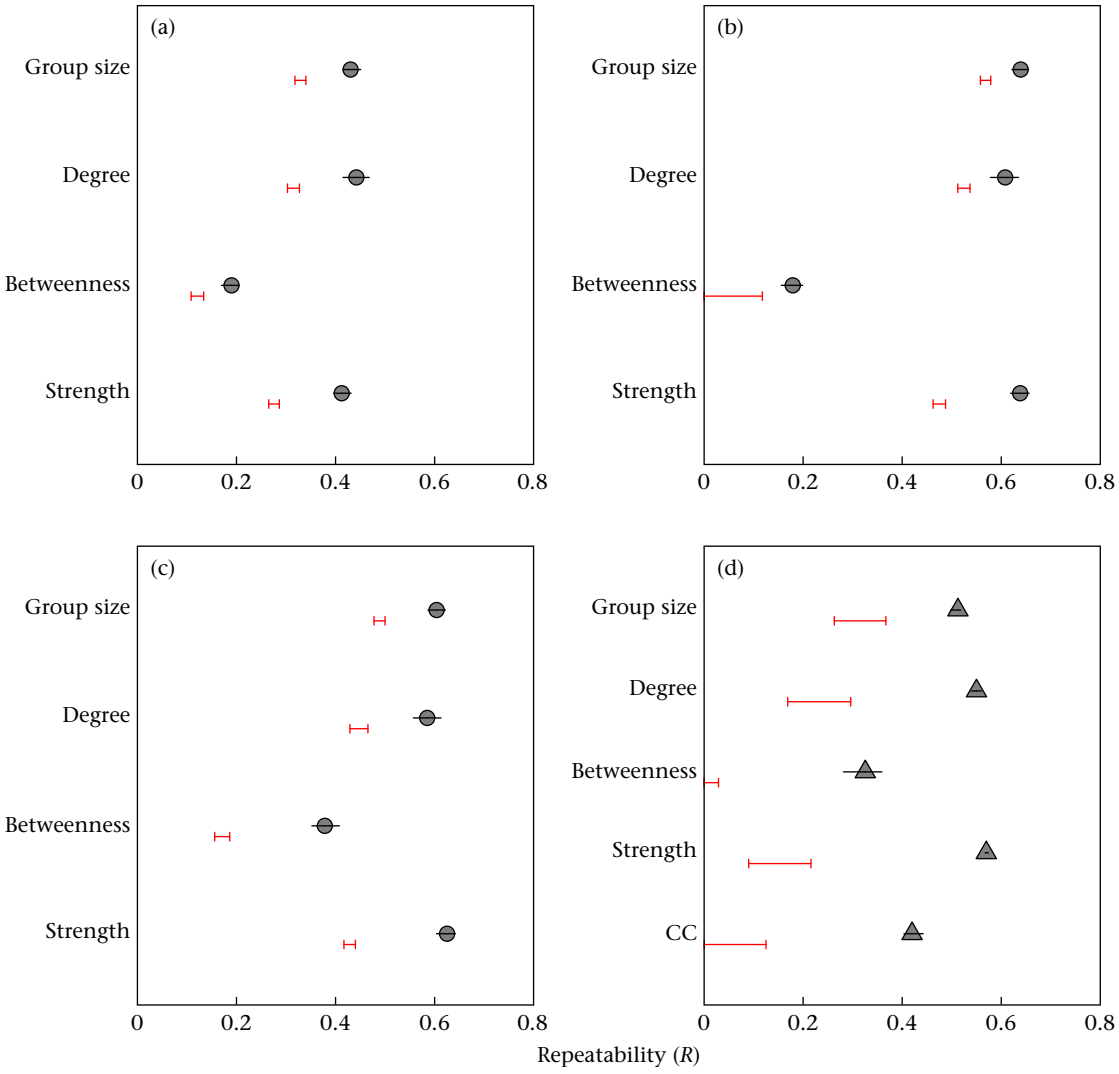


Figure 2. Repeatabilities and 95% confidence intervals for average group size and four social network metrics: degree, betweenness, association strength and clustering coefficient (CC; between years only for the latter). Results are shown for three winter data collection periods (within-season repeatability): (a) 2011–2012 winter; (b) 2012–2013 winter; (c) 2013–2014 winter. (d) Results compared across 3 years (between-year repeatability). Estimates whose confidence intervals do not cross 0 (*y*-axis) are significantly repeatable at the $\alpha = 0.05$ level. Horizontal red lines show 95% range of the repeatability estimates calculated from 1000 data randomizations controlling for spatial location.

For both within- and between-year estimates of repeatability, the four measures of social behaviour were compared to repeatability estimates calculated after the data were randomized within sampling period and within location. This spatially constrained null model explained variable amounts of the individual repeatability for different phenotypes. For example, within years, it accounted for only 1–19% of the within-individual consistency in betweenness centrality, but 35–55% of the consistency in an individual's average group size. This pattern was reflected in the between-year individual consistency, with very little of the repeatability in betweenness centrality due to spatial location, but with 32% of repeatability in average group size due to location. Yet in all cases, the repeatability estimate calculated from the observed data was higher than the 95% range of those generated from the spatially constrained permuted data sets, suggesting that local variation in social phenotypes

Table 1
Differences in the repeatability of social behaviour by sex

Metric	$N(N_o, N_i)$ male	$N(N_o, N_i)$ female	R_{male}	R_{female}	Effect size	Trend
Group size	10906 (706)	10186 (735)	0.48	0.45	0.83 (0.77,0.89)	M>F
Degree	10906 (706)	10186 (735)	0.49	0.45	0.95 (0.89,1.02)	M>F
Strength	10906 (706)	10186 (735)	0.49	0.44	1.58 (1.48,1.68)	M>F
Betweenness	10906 (706)	10186 (735)	0.08	0.09	0.60 (0.55,0.66)	F>M

M: male; F: female. All 41 repeated social networks across 3 years were used to calculate repeatability estimates for sex, additionally controlling for year (1–3). Differences are considered significant when 95% CIs for effect sizes do not overlap with zero. Sample size (*N*) shows both total number of observations (N_o) and number of individuals (N_i), and effect size shows 95% CIs.

Table 2
Differences in the repeatability of social behaviour by age class

Metric	$N(N_o, N_i)$ Fy	$N(N_o, N_i)$ Ad	R_{Fy}	R_{Ad}	Effect size	Trend
Group size						
Year 1	4441 (503)	5318 (514)	0.40	0.45	1.11 (1.02, 1.19)	Ad>Fy
Year 2	1237 (152)	5579 (573)	0.63	0.64	0.19 (0.13, 0.25)	Ad>Fy
Year 3	4016 (405)	3924 (411)	0.59	0.61	0.44 (0.37, 0.52)	Ad>Fy
Degree						
Year 1	4441 (503)	5318 (514)	0.42	0.47	1.11 (1.03, 1.19)	Ad>Fy
Year 2	1237 (152)	5579 (573)	0.60	0.63	0.51 (0.44, 0.57)	Ad>Fy
Year 3	4016 (405)	3924 (411)	0.54	0.64	1.60 (1.47 1 .73)	Ad>Fy
Strength						
Year 1	4441 (503)	5318 (514)	0.38	0.43	1.69 (1.56, 1.81)	Ad>Fy
Year 2	1237 (152)	5579 (573)	0.61	0.65	1.74 (1.61, 1.86)	Ad>Fy
Year 3	4016 (405)	3924 (411)	0.60	0.65	1.78 (1.62, 1.93)	Ad>Fy
Betweenness						
Year 1	4441 (503)	5318 (514)	0.54	0.46	−1.0 (−1.08, −0.92)	Fy>Ad
Year 2	1237 (152)	5579 (573)	0.17	0.18	0.14 (0.06, 0.21)	Ad>Fy
Year 3	4016 (405)	3924 (411)	0.37	0.45	1.99 (1.80, 2.18)	Ad>Fy

Age categories can change from first year (Fy) to adult (Ad) for individuals between years, so each year is presented separately (13–14 sampling periods). Differences are considered significant when 95% CIs for effect sizes do not overlap with zero. Sample size (*N*) shows both total number of observations (N_o) and number of individuals (N_i), and effect size shows 95% CIs.

contributed significantly to within-individual repeatability in social network position (Fig. 2).

DISCUSSION

When sampled throughout three winter seasons, individual great tits were repeatable in their social behaviour and social network phenotype. In two recent studies, the mean repeatability of the network metric 'strength' was 0.22 in yellow-bellied marmots (Blumstein et al., 2013) and 0.46 in captive spotted catsharks (Jacoby et al., 2014). This measure had a repeatability in our system of $R = 0.41–0.62$ depending on the year analysed, suggesting that great tits have a comparatively high consistency in social behaviour. A recent meta-analysis of behavioural consistency across various taxa also placed the average repeatability of all behaviour at 0.37 (Bell et al., 2009), indicating that individual great tits were relatively highly consistent in their group size choice ($R = 0.45–0.65$) and gregariousness (degree: $R = 0.46–0.63$). Repeatability was more moderate for the social network measures of betweenness ($R = 0.18–0.38$). Overall, when taken in combination with previous studies, these results suggest that network metrics tend to be consistent at the individual level. This is of fundamental importance for our understanding of the interaction between individual behaviour and social structure in animal social networks.

When within-individual consistency was measured across 3 years using winter-long social networks, similarly high repeatability measures were observed for group size ($R = 0.51$), degree ($R = 0.55$) and association strength ($R = 0.57$). Significant repeatability was further observed in clustering coefficient ($R = 0.43$) and betweenness ($R = 0.33$). That repeatability estimates tended to be higher when measured across years, as opposed to when measured within years, may indicate that winter-long social networks may provide the most accurate estimate of individual social phenotypes in this system, or alternatively that the most consistent individuals are more likely to survive from year to year; these hypotheses need further investigation to disentangle. Overall, however, our results demonstrate that social behaviour is stable over both short and long timescales.

Such within- and between-individual variation in social phenotypes may have important implications for the evolution and ecology of sociality. More central network positions have been shown to be associated with various benefits, including social information transfer (Aplin et al., 2012) and reproductive success (Mcdonald, 2007; Oh & Badyaev, 2010), but may also expose social individuals to higher rates of competition (Oh &

Table 3
The observed (O) and randomized (R) sum of the variances (SV) of individual social position in the repeatedly sampled networks

Group	Metric	No. of samples	SV_O	S_R	*P*
2011–2012	Degree	13	50.24	83.86 (80.75, 87.77)	<0.001
	Strength	13	51.43	83.94 (82.18, 85.73)	<0.001
	Betweenness	13	69.02	83.85 (80.19, 87.31)	<0.001
2012–2013	Degree	14	22.29	55.65 (53.62, 57.96)	<0.001
	Strength	14	21.61	55.73 (54.42, 57.13)	<0.001
	Betweenness	14	46.54	55.09 (52.93, 57.85)	<0.001
2013–2014	Degree	14	28.80	61.81 (58.8, 65.13)	<0.001
	As. Strength	14	25.84	61.83 (60.21, 63.52)	<0.001
	Betweenness	14	48.82	61.74 (58.88, 65.34)	<0.001
Between-year	Degree	3	22.93	46.98 (40.57, 54.2)	<0.001
	Strength	3	21.06	47.05 (43.30, 50.94)	<0.001
	Betweenness	3	30.30	46.96 (40.61, 46.97)	<0.001
	Clustering C.	3	28.19	49.52 (41.99, 56.33)	<0.001

Smaller values of SV indicate a higher individual repeatability in network metrics, and mean and 95% range are shown from 10 000 node randomizations of each observed network.

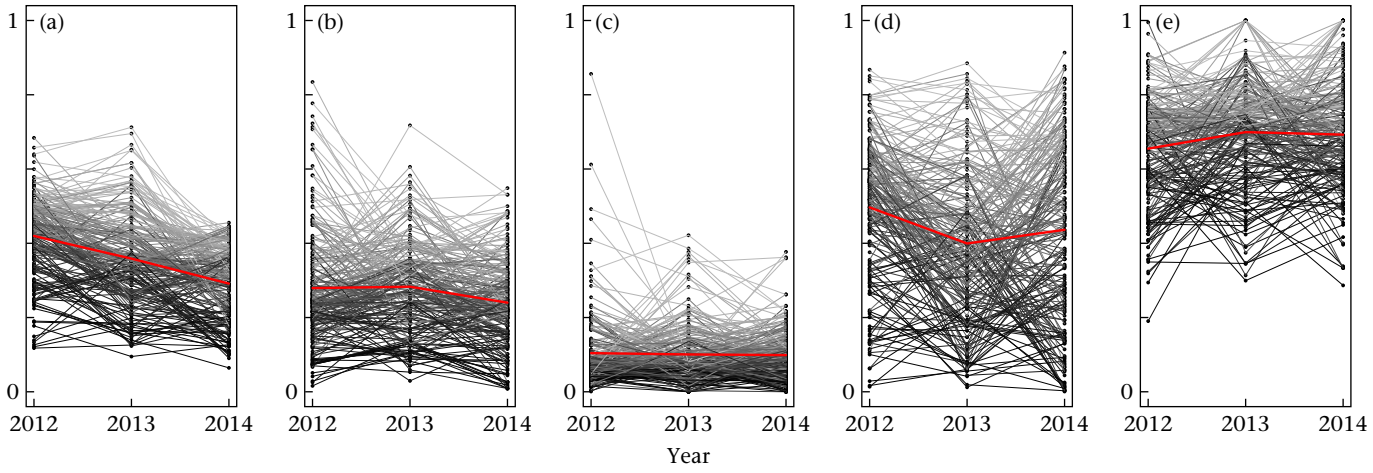


Figure 3. Repeatabilities for 210 individuals observed over three winter seasons of social network data collection. Scores are scaled between 0 and 1 for all individuals within each season. Points are individuals and grey lines connect their scores in each year. Red lines show the average score for all individuals in each year. Five winter-long measures of social behaviour are shown: (a) average group size ($R = 0.51$), (b) degree ($R = 0.55$), (c) betweenness centrality ($R = 0.33$), (d) strength ($R = 0.57$) and (e) clustering coefficient ($R = 0.43$).

Badyaev, 2010) and disease (Christley et al., 2005). It thus seems likely that there is functional significance to variation in social network position, with life history trade-offs leading to the evolution of consistent individual differences in social behaviour (Dall, Houston, & McNamara, 2004; Krause, James, & Croft, 2010). Given that repeatability can indicate the upper limits to heritability, our results further suggest that individual great tits could show heritable differences in sociality, an avenue that merits further study.

While territoriality is low over the winter period, our woodland study site varies in microhabitat quality and in local population density. It is thus likely that some of the consistency in social behaviour is related to individual differences in space use (Shizuka et al., 2014). Such differences may also explain the slightly higher repeatability of males and adults, which tend to make fewer spatial movements than females and first-years, although this is also consistent with across-species patterns of behavioural repeatability (Bell et al., 2009). We applied spatially constrained randomizations to disentangle these effects and showed that while some individual differences could be explained by spatial location, an additional component of social behaviour was driven by within-location flock membership choices. However, habitat choices might also be a reflection of social phenotypes. Tits use social information from conspecifics when making dispersal and settlement decisions (Nocera & Forbes, 2010; Nocera, Forbes, & Giraldeau, 2006; Pajero, White, & Danchin, 2007; Parejo et al., 2008). Individuals could potentially differ in this decision making based on individual differences in sociability (Blumstein, Wey, & Tang, 2009; Cote, Clobert, Brodin, Fogarty, & Sih, 2010), as observed in common lizards, *Lacerta vivipara* (Cote & Clobert, 2007) and mosquito-fish, *Gambusia affinis* (Cote, Fogarty, et al., 2010), in which more asocial individuals tend to stay in low-density patches and disperse when local population sizes become high. Future work could potentially explore these interactions with a combination of captive and wild translocation experiments, measuring individual variation in social behaviour across different contexts.

In summary, our study provides one of the few demonstrated examples of consistency in social network position, with birds maintaining relatively stable group sizes and network metrics over multiple timescales. This variation in social behaviour was partly attributable to individual differences in spatial location and space use, but a significant amount of between- and within-individual variation remained even when controlling for these factors. We can therefore identify individual social phenotypes, a vital first step in showing the adaptive significance of social network structure in wild animals. Future work should aim to quantify the potentially diverse fitness consequences associated with different social phenotypes, and further investigate how such selection can shape the evolution and ecology of animal social networks.

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Appendix

Table A1
Outputs of linear-mixed models showing fixed effects for four network measures in each of three winter seasons

Year	Metric	Term	Estimate	Lower 95% CI	Upper 95% CI	*P*
2011–2012	Group size	PS	0.0005600	0.0003021	0.0008281	<0.001
		ND	4.5827078	0.8800015	9.1275491	0.04
		Date	−0.0179925	−0.0242837	−0.0106679	<0.001
	Degree	PS	0.004594	0.003924	0.005316	<0.001
		ND	58.828297	47.716612	68.944029	<0.001
		Date	−0.013392	−0.031308	0.003472	0.150
	Betweenness	PS	−0.4221	−0.5185	−0.3003	<0.001
		ND	−1438.6215	−3161.8210	227.9183	0.098
		Date	1.5072	−1.2775	4.3902	0.282
	Strength	PS	0.0005202	0.0002851	0.0008156	<0.001
		ND	0.6342989	−3.4182792	4.3784652	0.744
		Date	−0.0141429	−0.0206190	−0.0076515	<0.001
2012–2013	Group size	PS	−0.0001.661	−0.0003.982	0.0007.208	0.166
		ND	12.65	10.52	14.76	<0.001
		Date	0.0000330	−0.003750	0.003693	0.984
	Degree	PS	0.004958	0.004346	0.005538	<0.001
		ND	38.830534	33.520697	43.934455	<0.001
		Date	0.004751	−0.004275	0.014303	0.330
	Betweenness	PS	−1.416	−1.600	−1.237	<0.001
		ND	−6398	−8086	−4641	<0.001
		Date	−0.0003055	−2.729	3.064	0.988
	Strength	PS	0.0000085	−0.0002321	0.0002308	0.916
		ND	10.33	8.006	12.29	<0.001
		Date	0.002167	−0.001562	0.005576	0.238
2013–2014	Group size	PS	0.0005122	0.00000268	0.000933	0.026
		ND	14.8	11.79	17.78	<0.001
		Date	0.008140	0.005077	0.01103	<0.001
	Degree	PS	0.004869	0.003660	0.006124	<0.001
		ND	58.437816	50.106302	67.543610	<0.001
		Date	0.000447	−0.007223	0.008739	0.892
	Betweenness	PS	−0.2347	−0.4745	0.01216	0.060
		ND	−2178	−3952	−425.4	0.012
		Date	0.8131	−0.8573	2.431	0.338
	Strength	PS	0.0007248	0.0003058	0.001189	<0.001
		ND	12.12	9.476	15.29	<0.001
		Date	0.00991	0.007116	0.0129	<0.001

Three fixed effects are included in each model: total population size (PS) for each sample, total network density (ND) for each sample and the date of each sample. Individual identity was included as a random effect in all models.

Table A2
A comparison of repeatability scores in three seasons of data collection

Model variation	Network metric	Year 1: 2011–2012	Year 2: 2012–2013	Year 3: 2013–2014
As reported in paper	Average group size	0.430	0.639	0.605
	Degree	0.456	0.625	0.585
	Betweenness	0.189	0.179	0.376
	Strength	0.413	0.639	0.624
Including sample size for each individual	Average group size	0.428	0.631	0.601
	Degree	0.440	0.592	0.579
	Betweenness	0.481	0.138	0.327
	Strength	0.409	0.606	0.590
Removing individual with <50 observations	Average group size	0.455	0.644	0.597
	Degree	0.450	0.618	0.558
	Betweenness	0.520	0.173	0.487
	Strength	0.409	0.614	0.574

The results from three model variations are presented: (1) repeatability estimates as reported in the paper, with a linear mixed model including individual identity as a random effect and population size, network density and date as fixed effects; (2) the linear mixed model additionally including the number of observations for each individual on each weekend sampling period as a fixed effect; (3) the linear mixed model as above, but removing all individuals with fewer than 50 observations.

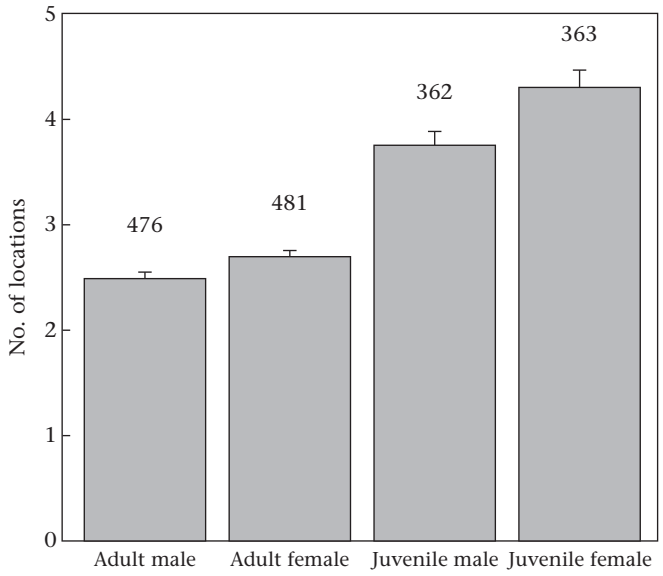


Figure A1. The average number of locations per year where individuals of the different age and sex classes were observed foraging. Lines show SEs and data are used from three winter seasons. Numbers show the number of unique individuals recorded in each class.

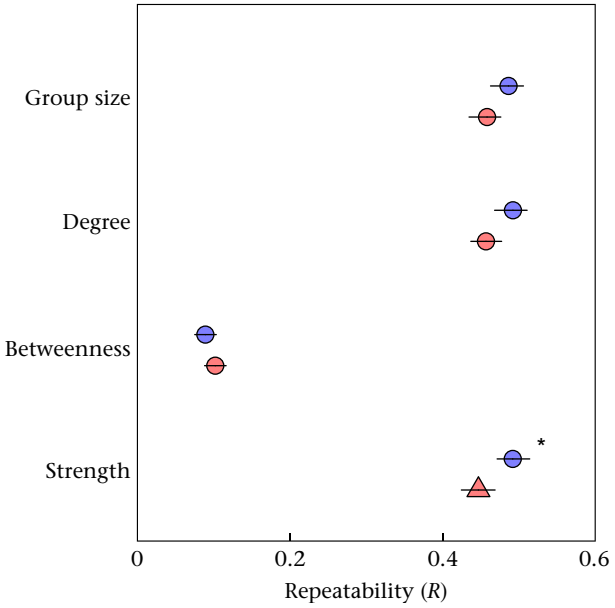


Figure A2. The repeatability measures for the different sex classes, showing the 95% confidence interval for each measure. Nonoverlapping confidence intervals at the 95% level are marked with an asterisk. Group size and degree measures do not overlap at the 84% confidence interval (nonoverlapping 84% confidence intervals are equivalent to a *z*-test at the 0.05 level). All 41 repeated social networks across 3 years were used to calculate repeatability estimates, additionally controlling for year (1–3). Blue nodes are males; red nodes are females.

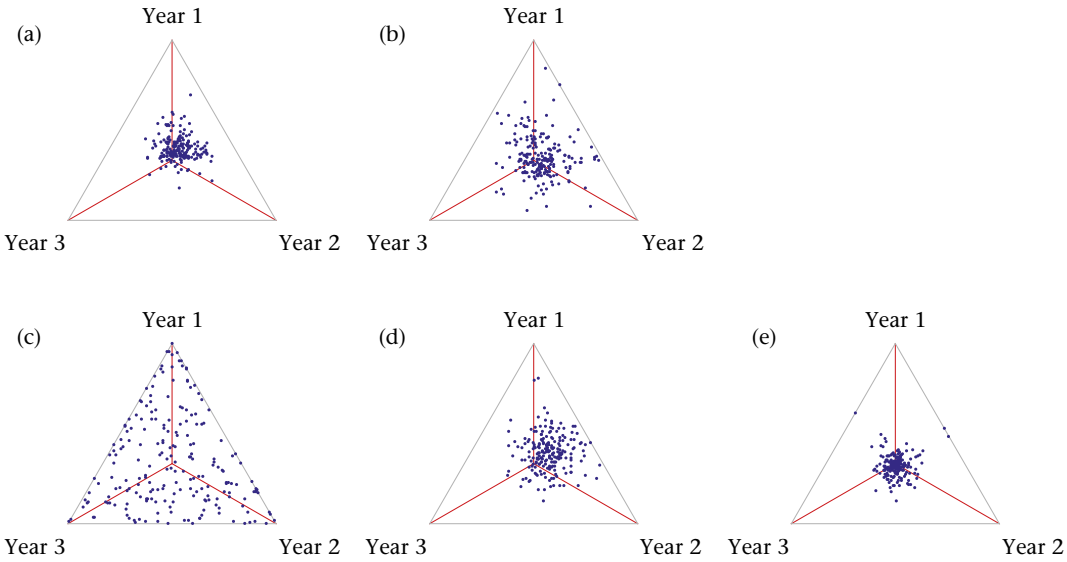


Figure A3. Simplex plots of repeatabilities for 210 individuals observed over three winter seasons of social network data collection. Each point represents one individual, and a perfect correlation between all three seasons is the central intercept of axes. Data are scaled between 0 and 1 within each season. Five winter-long measures of social behaviour are shown: (a) average group size, (b) unweighted degree, (c) betweenness centrality, (d) association strength and (e) clustering coefficient.

Appendix C

Nonlethal predator effects on the turn-over of wild bird flocks

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Nonlethal predator effects on the turn-over of wild bird flocks

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Nonlethal predator effects arise when individuals of a prey species adjust their behaviour due to the presence of predators. Non-lethal predator effects have been shown to affect social group structure and social behaviour as well as individual fitness of the prey. In this experimental study, we used model sparrowhawks to launch attacks on flocks of wild great tits and blue tits whilst monitoring their social dynamics. We show that nonlethal attacks caused instantaneous turn-over and mixing of group composition within foraging flocks. A single experimental 'attack' lasting on average less than three seconds, caused the amount of turn-over expected over three hours (2.0–3.8 hours) of undisturbed foraging. This suggests that nonlethal predator effects can greatly alter group composition within populations, with potential implications for social behaviour by increasing the number of potential interaction partners, as well as longer-term consequences for pair formation and emergent effects determined by social structure such as information and disease transmission. We provide the first evidence, to our knowledge, based on in depth monitoring of a social network to comprehensively support the hypothesis that predators influence the social structure of groups, which offers new perspectives on the key drivers of social behaviour in wild populations.

Predation has long been argued to be a major selective force in evolution, affecting numerous biological properties, including mating systems, socio-spatial structure, group organization and social behaviour[1–4]. However, most attention in the study of predation effects has been given to lethal effects of predation, while nonlethal effects through the mere presence of predators have received much less attention[5–7]. Nonlethal effects, also sometimes referred to as 'risk effects'[8], arise when prey alter their behaviour in response to the presence of predators[5,9]. Such effects have been most clearly demonstrated through substantial changes in prey density and population demography caused by predators that were experimentally rendered nonlethal. For example, Peckarsky and collaborators[8] 'disarmed' predatory stone flies (*Megarcys* sp. and *Kogotus* sp.) by gluing together their mouthparts. They then compared the demography of predator free populations of mayflies (*Baetis bicaudatus*) with those of mayfly populations with either nonlethal predators or un-treated, and hence lethal, predators being present. Nonlethal predator effects have been reported for a variety of species and meta-analyses of the existing literature suggest that the impact of 'intimidation' by predators on prey demographics can be even considerably stronger than direct consumption[7,9,10].

The most common behavioural responses to predation risk include changes in habitat use[11,12], movement patterns[13–15], vigilance[16,17], escape distance[18], and foraging behaviour[19,20], which can lead to reduced energy income, lower mating success and increased vulnerability to other predators[10]. The formation of groups can be an effective anti-predator response[1,21,22] and the effects of predator presence on group formation and group size have been demonstrated empirically in many studies[23–25]. The resulting group size of prey species has direct consequences for the behavioural activity of the group members. For example, in mixed-species flocks, the amount of scanning undertaken by individual birds –a measure of vigilance behaviour- decreases with increasing flock size[17,23], allowing individuals to dedicate more time to active foraging[26,27].

If individuals of a species differ in their vulnerability to predation or their foraging demands, starvation-predation risk trade-offs can result in differential foraging decisions in response to the presence of predators. For example, Cresswell[28] observed than juvenile redshank (*Tringa totanus*) preferentially fed in more profitable but also more risky areas while adults avoided those risky areas. Similarly juvenile male dolphins (*Tursiops aduncus*) are more likely to accept high predation risk to achieve higher energy intake[29]. When disturbed by predators young red knots (*Calidris canutus*) were also more likely to resume foraging at the same place, while adults left the areas[30]. Sex is another source of inter-individual variation in foraging decisions under

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vaying predation risk which might even lead to sex-selective predation[31]. When resource availability is high, female skylarks (*Alauda arvensis*) are more likely to stay in a risky area while males will leave sooner[32]. In cercopithecoid primates the number of males in multi-male groups increases with increasing predation pressure, suggesting a trade-off between male reproductive success—which is higher for males that can monopolize females in single-male groups—and optimal group sizes to minimize the effects of predation[33].

However, while predator presence has been shown to differentially affect foraging decisions and grouping behaviour of different phenotypes, the consequences of predation risk on the social relationships in foraging groups is still unknown. For example, social interactions in tit flocks are non-random and social relationships formed in these flocks are indicative for pair formation during the breeding season[34–37]. Changes in the social composition of these foraging flocks could, therefore, have consequences on the pair formation and, hence, mating success. Furthermore, individuals in foraging flocks might provide valuable information about population density and structure, habitat quality, or foraging opportunities, and this, too, will be affected by group composition.

In this study, we investigated how nonlethal predator effects influence the composition of winter flocks of foraging great tits (*Parus major*) and blue tits (*Cyanistes caerulaeus*). We determined whether simulated attacks of predators have a direct effect on flock stability and turn-over rates. We achieved this through exposing individually tagged tits at automated feeding stations to attacks by models of sparrowhawks—their natural predators—and comparing (a) individual responses and (b) changes in flock membership with control situations in the absence of predator threats. Specifically, we examined whether individuals were more likely to leave a feeding area after a simulated sparrowhawk attack, whether they took longer to return to the feeding area, and whether attacks increased the turn-over rates of birds present in the feeding area.

Methods

Study site and subjects. This field experiment was carried out in Wytham Woods (51°46′ N, 1°20′ W), a mixed deciduous woodland area of ca 385 ha, near Oxford, UK. Birds have been monitored in this area since the early 1960 s as part of a long-term population study[38]. The study species, great tits and blue tits, are small passerine birds which are territorial during the breeding season but form multi-species flocks – together with other (numerically much less abundant) tit species during the winter months[38]. Routine data collection during the breeding season (April–June) consists of nestbox checks to record breeding activity. Breeding adults and nestlings are ringed with uniquely numbered metal rings from the British Trust for Ornithology and standard morphometric information is recorded. In addition to the ringing effort during the breeding season, mist nets are used for catching and ringing non-breeding adults and immigrant birds throughout the winter. Since 2011 all breeding blue and great tits, and any birds caught in the non-breeding season were additionally fitted with plastic split rings containing passive integrated transponder tags (henceforth PIT-tags; from IB Technology, Aylesbury UK). It was estimated that over 90% of great tits in the area carry PIT tags[39]. For blue tits this proportion is probably slightly lower (see Supplementary Information). Each PIT tag contains a unique ten-character hexadecimal code that can be read by a radio frequency identification (RFID) antenna. A grid of 65 sunflower seed feeders that opened every weekend from September to February has been installed in the study area. Each seed feeder was fitted with an RFID antenna that recorded the time, place, and the identity of all visiting PIT-tagged individuals. Out of these 65 feeders, eight were selected for experimental treatment (experimental feeder, Fig. 1).

Design of the model predator. The model predator consisted of a plastic bird model (length 350 mm, wingspan 560 mm) representing a flying male sparrowhawk; previous research has demonstrated that passerines perceive such models as potential predators, and respond with anti-predatory behaviour and increased vigilance that is not shown towards non-threatening objects of the same size[40,41]. Eurasian sparrowhawks, *Accipiter nisus*, are forest living raptors that hunt primarily on small passerine birds[42]. They are the principal predators of tits in the study area[43]. All models were hand coloured in order to closely match the natural colour patterns of sparrowhawks. Two rollers were fitted to the back of the sparrowhawk model, allowing it to run along a coated 2 mm steel cable. At each of eight selected experimental feeder sites we installed four predator units by fixing a plastic box (600 mm × 400 mm × 420 mm) to a tree at a height of 3.5 to 7 m and running a steel cable from the box over the seed feeder to a second box fixed to another tree at the other side of the feeder at a height of 1 to 2 m (Fig. 1). The boxes and cables were attached to the trees two weeks before the start of the experiment and left there until the end of the study. The distance between the upper box and the lower box varied between 8 m and 17 m, with an inclination between 8° and 26°. The open side of each box was concealed by a set of dark green curtains. During the experiment, the hawk model was placed in the upper box, hidden behind the curtain, where it was held in place by a small hook. A solenoid fitted within the box was positioned to lift the hook upon activation. Triggering the solenoid therefore allowed the hawk model to run down the steel cable (driven by gravity), making an 'attack' by swooping over the feeder and landing in the lower box, where it remained concealed behind a curtain for the rest of the day. Releases were triggered automatically via an electronic circuit board (Stickman Technology Inc., Southampton) that was connected to the RFID antenna at the feeder, thus allowing the sparrowhawk to be released upon the RFID antenna detecting a given PIT tag. The speed of the model hawks over the feeders varied between approximately 4 and 11 ms^{-1}, which is slower than real sparrowhawks during attacks (up to 16 ms^{-1})[42], though the strong response of the tits, along with previous research demonstrating the effectiveness of these models[40], make us confident that the sparrowhawk models were perceived as a threat. Models were only maintained and set by the experimenters between 19:00 and 21:00 h (outside of bird feeding times) to avoid experimenters causing disturbance. Thus, on each feeder site, the maximum number of attacks per day was limited to four: one on each line.

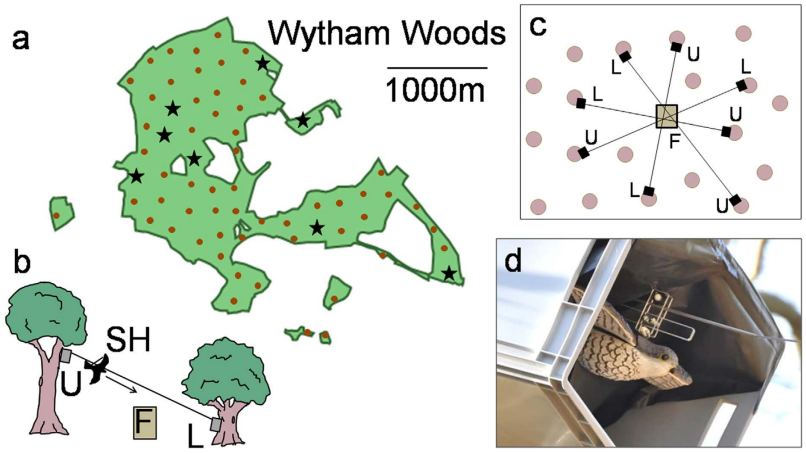


Figure 1. (**a**) Map of the study area Wytham woods, Oxfordshire (created in *Mathematica* 10.2 from Wolfram Research Inc., http://www.wolfram.com/). A grid of 65 seed feeders (brown dots) was deployed every weekend from September to February. Eight feeders (stars) were selected for simulated sparrowhawk attacks. (**b**) Sketch of a sparrowhawk unit, consisting of a sparrowhawk model (SH) and a steel cable running from an upper box (U) over the feeder (F) to a lower box (L). Sparrowhawks were released automatically upon detection of predefined PIT tagged individuals by the RFID antenna attached to the feeder. (**c**) At each experimental site we installed four sparrowhawk units next to a seed feeder, by fixing four upper boxes and four lower boxes to surrounding trees (grey disks), enabling up to four predator attacks per day. (**d**) Photo of a sparrowhawk model in an upper box. During the experiment the hawk model was hidden behind a curtain.

Experimental procedure. Experiments were conducted on consecutive weekends from 09/02/2013 to 04/03/2013 (season 1) and 15/11/2013 to 23/02/2014 (season 2) with the exception of 27–29/12/2013. The experimental protocol differed slightly between seasons. During season one, six experimental feeders were opened on Friday and all visits of PIT tagged birds were logged. Out of all birds visiting the feeder on that day we randomly selected five potential 'target birds' for the next day. Saturday was an experimental treatment day, whereby the feeder's circuit board was programmed to release a model sparrowhawk (with a probability of 0.05) upon the RFID antenna detecting a target bird. Once the first hawk was released, further hawks were only released by visits of the same focal individual (i.e. it became the sole target bird) for that weekend. Once birds were chosen as target birds they were excluded from the list of potential target birds for all following weekends. The motivation for this selection procedure was to distribute releases of hawks more evenly over the day and to ensure that all birds had a similar chance of experiencing an attack. By conditioning the release on the presence of a bird at a feeder, we avoided 'null releases' at times when no birds were near the feeder as well as ultimately simulating more realistic attacks, as hawks whooshed over the feeders only when a bird was perched upon it. On Sunday the birds were subjected to the same experimental treatment with the same target bird as on Saturday. On Saturday and Sunday all 65 seed feeders in the study area were open and logged bird visits. On Monday, experimental feeders were opened again for logging of post-experimental activity but no sparrowhawks were released on that day. During the second season of the study, the procedure differed in that there was only one day of predator attacks per weekend, with pre-experimental logging at five experimental feeders on Friday, predator treatment on Saturday and post-experimental control logging on Sunday. To allow combined analysis of season 1 and 2, we excluded the second day of experimental treatment from season 1 (thus excluding 19 model hawk releases) from further analysis, therefore analysing one day of predator treatment over all weekends. Overall, sparrowhawk models were released at 8 different feeder sites on 22 different weekends, resulting in a total of 112 sparrowhawk attacks.

Identifying Flocks. Feeding activity at feeders is highly variable over time and clearly deviates from expectations for random activity[35]. During winter months, tits form mixed species foraging flocks[44,45] and burst of activity at a feeder signify the arrival of such a flock. We used a machine learning algorithm based on a Gaussian mixture model[35,46] for identifying instances of flocking. This algorithm searches for temporal regions of increased activity at the feeder and divides the continuous time stream of recorded visits into discrete gathering events, reflecting those 'bursts' of activity. Gathering events lasted between 1 and 2373 s (median = 208 s, IQR: 109–295 s) and comprised between 1 and 28 birds (median = 4, IQR: 2–7). For each gathering event we assumed a 'gambit of the group' approach[47] by considering that every bird that visited the feeder during this gathering event at least once was associated with every other bird detected during the same gathering event at the same feeder.

Demography and sample. Blue tits and great tits that were fitted with PIT tags and were recorded by the antenna at the feeder during a gathering event were considered as being present during this gathering event. Further, birds might have been present without showing up in the data set if they (i) were members of non-focus species, (ii) did not carry PIT-tags, or (iii) were present in the area of the feeder but did not land on the antenna. Thus, we acknowledge that the detected birds represent only a sample of the total number of present birds, and the actual number of birds might have been higher than the reported numbers in all conditions. We assume that all birds present during a gathering event with a model sparrowhawk release are likely to notice this event. The

112 attacks were, thus, experienced by 281 different birds. Out of these birds 129 (46%) experienced only a single attack while the remaining birds were present repeatedly (median 2 times, IQR: 1–3), totalling up to 705 observed responses of birds to model predator attacks. In those cases where birds experienced more than one attack, the median time gap between attacks was 7 days. Great tits made up 60% of the birds at the feeders during attacks and blue tits 40% (only these two species were considered). As those tits forage and roam in mixed-species flocks[44,45], where individuals of both species freely mix and interact with each other, we performed all tests on the combined data set of both species. Sexes were almost equally represented with 38% males, 34% females and 28% birds of undetermined sex (yearlings that were not subsequently seen breeding). Most of the birds (68%) were yearlings –i.e. birds that hatched in the previous breeding season, while the remaining 32% were adults.

Measures of turn-over. In order to quantify the change in group composition between successive gathering events we calculated three measures. The index *change* (I_c) relates the number of individuals that were present in both gathering events to the number of individuals that were present in either event as

$$I_c = \frac{|(B \cup A) \setminus (B \cap A)|}{|B \cup A|}, \tag{1}$$

where B (as in "Before") is the set of individuals present in the first gathering event and A (as in "After") is the set of individuals present in the second gathering event. The term $X \cup Y$ denotes the union of the two sets X and Y, the term $X \cap Y$ denotes the intersection of the sets X and Y, the term $X \setminus Y$ denotes the complement or difference set of all those elements in X that are not elements of Y and $|X|$ is the cardinality of the set X, i.e. the number of elements in X. That is, the index *change* gives the proportion of individuals that were not present in both events. The index *blending* (I_b) relates the relative number of individuals which were present in both events to the number of individuals present in either event and is given by

$$I_b = \frac{|B \cap A| \times |B \cup A \setminus B \cap A|}{dm}, \tag{2}$$

where $dm = (|B \cup A|/2)^2$ if $|B \cup A|$ is even and $\frac{|B \cup A - 1|}{2} \times \frac{|B \cup A| + 1}{2}$, otherwise. In other words, blending gives a value of zero if there is either no or complete overlap in the animals present before and after an attack and a value of one if those animals present both before and after the attack comprise 50% of all birds present. Finally, we calculate a *mixing* index (I_m) as $I_m = 1 - P_m$ where P_m gives the probability of getting such an overlap, or one smaller than the observed one, if all individuals that were recorded during either of the gathering events were in the surrounding of the feeder for the whole period in question and visiting the feeder at random. P_m is calculated as the tail probability of getting the observed or a smaller intersection of two sets A and B of size a and b, respectively, by independently sampling first a and then b elements from a pool of u elements, which is given by

$$P_m = \sum_{i=1}^{a} \frac{b!(u - b)!(u - a)!}{(b - i)!(u - a - b + i)u!} \binom{a}{i}, \tag{3}$$

with $a = |A|$, $b = |B|$, and $u = |B \cup A|$. For all three indices, a value of zero indicates perfect overlap, which is achieved when exactly the same set of individuals was observed in both gathering events. For the *change* indices a value of one indicates complete turnover with none of the individuals present in the first event being also present in the second event. The mixing index takes into account that an overlap of zero could also be due to chance if birds visit the feeder at random, though as the probability of a null overlap might be relatively small (depending on the total number of birds present), the *mixing* index will be close to one in such a case. For the blending index a value of one indicates maximal blending while zero indicates either perfect overlap or no overlap of individuals between the before and after events. Graphical explanations of the turn-over indices are given in Supplementary Figs S5 and S6 and a graphical illustration of how the three turnover indices compare to each other is provided in Supplementary Fig. S7.

Statistical analysis. We used a matched control design, where each experimental treatment was matched with two control treatments at the same location and at a comparable time of the day (time-matched control): a pre-experimental control on the day before the attack and a post-experimental control on the day after the attack. If it was not possible to take the control from days directly before or after the attack (in a few cases there were no recordings on those days), we made controls at appropriate dates as close in time to the attack date as possible (see Supplementary Table 4a–c for details). With this matching procedure we control for seasonal differences (as every attack event is matched with a gathering event close in time), local differences in feeder popularity (as we match each attack with a gathering event at the same feeder) and differences in foraging activity along the course of the day (as we matched events at comparable daytimes).

For Individual-level analyses of the birds' responses we employed general linear mixed model (GLMM) comparisons. For the latency to return after an attack (or matched control) we used a linear model with identity link, Gaussian error term, condition (attack or control), season, age class (yearling or adult), species (great tit or blue tit), time of the day, the number of previously experienced attacks and numbers of birds present during the attack as fixed factors and feeder location, weekend and bird identity as random factors. The full model was compared with a restricted model without the factor condition with a likelihood ratio test on the model deviances. For the binary outcome variables, i.e. whether a bird returned after an attack to the same feeder at that day ("return") and whether a bird returned after an attack during the first post-attack gathering event ("immediate return"), we used

generalized linear mixed models with logit link functions and binomial error terms and the same predictor variables as before. This analysis was carried out with the statistical software R[48], using the functions lmer and glmer of the package lme4[49]. Parameters were estimated using the Maximum Likelihood method.

In addition to an analysis of individual responses we performed a group-level analysis where the main response variables of interest were measures of group turn-over before and after the simulated predator attack. We employed the same time-matched control design as for the individual-level analysis, yet as group composition in mixed species tit flocks changes quickly[50,51], differences in the composition of groups between subsequent gathering events after hawk attacks and after the matched control events could be due to the longer temporal delay of the former. We therefore introduced a second set of matched controls. In this, we matched each attack event with another gathering event on a previous or successive day at the same feeder, where the time gap between the matched control event and its follow-up event was as close as possible to the time gap between the attack event and its follow-up event (gap-matched control). With this gap-matched control we created a set of control samples where the median gap times to the successive gathering events were 440 s (IQR: 257–771 s) for the pre-attack control and 437 s (IQR: 270–787 s) for the post-attack control, which was very close to the median gap-time between the attack and follow-up events of 451 s. Having controlled for temporal and local variation in bird activity by design, we used Wilcoxon tests for paired samples to compare responses in experimental and control treatments.

As this study was a field experiment with unrestricted access to the feeder, individual identity of the birds present was beyond our control. Overall, 46% of the birds recorded during the experiment experienced only a single attack event and the median number of times birds were present during attacks was two. For a field study with unrestricted access this is, in our opinion, a low level of repeated measures on the individual level and we can say that differences in experience with the model hawks were modest. More importantly, for the measures of group turn-over the level of analysis is in our case the foraging flock, as we measure the time gap between flocking events and the proportional change in flock composition. In total we had only a single instance (out of 112 attacks), where the same combination of individuals was present twice. We argue that this is a level of repeated measures that can safely be ignored for the kind of group-level analysis provided below. Throughout the text we give median values together with the 50% inter-quartile range (IQR). We performed multiple significance tests (Wilcoxon tests for paired samples), as we compared the response to an attack both with a pre- and a post-treatment control. As diverging results for pre- and post-treatment comparisons would have led to different conclusions, we recommend interpreting the reported p-values of those tests against a Bonferroni corrected significance level $\alpha' = 0.016$.

Ethical statement. All work was subject to review and approved by the local ethical review committee at the Department of Zoology (University of Oxford) and also in accordance with the UK standard requirements and the ASAB guidelines for the use of animals in research. The work was conducted as part of a larger ongoing research project at Wytham woods, and all birds were caught, tagged and ringed by appropriate BTO licence holders.

Results

Behavioural responses. Birds reacted strongly to the attacks of the model sparrowhawks and usually left the feeder within seconds after the release of the sparrowhawk model (median = 3 s, inter-quartile range, IQR: 2–3.5 s). In order to classify the birds' responses to attacks by a model predator, we defined three response types: a bird was said to 'return' within the given day if the first observation of this bird after an attack was made at the same feeder where it witnessed the attack; a bird was said to 'move' within the given day if the first observation of this bird after an attack was made at a different feeder; and a bird was said to 'disappear' if the bird was not observed after the attack at any feeder for the rest of the day. In 522 cases (74%) a bird returned after an attack, while in 77 cases (11%) a bird moved to another feeder and in 106 cases (15%) the bird disappeared for the rest of the day (Supplementary Table S1). All our observations are restricted to those birds which were fitted with pit tags (estimated as roughly 90% of the population based on capture-recapture data[39]) and which visit the feeders. The time gap between the end of the attack event and the subsequent gathering event was more than twice as long (median = 451 s, IQR: 257–877 s) than the time gap between time-matched control events and their successive gathering event (pre-attack: median = 131 s, IQR: 26–325 s, post-attack: median = 164 s, IQR: 54–356 s). These differences are both significant (Wilcoxon tests for paired samples, pre-attack: $N = 112$, $T_s = 744$, $p < 0.001$, post-attack: $N = 112$, $T_s = 1267$, $p < 0.001$).

Individual-level effects. In order to investigate whether an 'attack' by a model sparrowhawk had an effect on the likelihood of a bird returning to the same feeder after the attack, we used a likelihood ratio test for comparing the deviances of a full GLMM and a restricted model not containing the experimental condition (attack versus control). Birds were less likely to return on the same day to the feeder where they witnessed an attack than were birds in both pre- or post-attack control trials ($\Delta_{Dev} = 84.0$, $df = 1$, $p < 0.001$, and $\Delta_{Dev} = 75.6$, $df = 1$, $p < 0.001$, Supplementary Table S3). Birds were also less likely to be detected in the first gathering event after an attack at the same feeder than were birds in both pre- or post-attack control trials ($\Delta_{Dev} = 93.6$, $df = 1$, $p < 0.001$, and $\Delta_{Dev} = 91.3$, $df = 1$, $p < 0.001$). Finally, those birds that did return to the feeder after an attack did so only after a longer time delay compared to the pre- and post- attack matched control conditions ($\Delta_{Dev} = 202.7$, $df = 1$, $p < 0.001$, and $\Delta_{Dev} = 132.9$, $df = 1$, $p < 0.001$, respectively).

Flock composition. Comparing the number of birds in the first post-attack gathering event we found fewer birds at feeders after model hawks attacked (median = 2, IQR: 1–4) than in both the time-matched control condition (pre-attack: median = 4, IQR: 2–7, Wilcoxon test for paired samples: $N = 112$, $T_s = 3695$, $p < 0.001$, post-attack: median = 5, IQR: 2–8, $N = 107$, $T_s = 3003$, $p < 0.001$), and the gap-matched control (pre-attack: median = 3, IQR:1–7, $N = 112$, $T_s = 2967$, $p = 0.003$, post-attack: median = 3, IQR:1–6, $N = 112$, $T_s = 2187$,

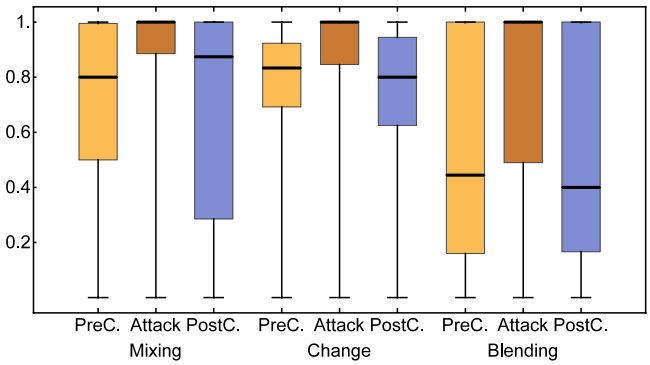


Figure 2. Time-matched comparisons for group turn-over. Three measures of turn-over in group composition in the experimental condition after a simulated attack (Attack), in a pre-treatment matched control condition (without a sparrowhawk model release) at the same feeder and time of day on a day before the attack (PreC), and in post-treatment control at the same feeder and time of day on a day after the attack (PostC). Indices of zero indicate no change in group composition and indices of one or close to one indicate complete turn-over with no overlap in group membership (see text for definitions for the measures). Bold bars give the median, boxes the inter-quartile range, and whiskers the range.

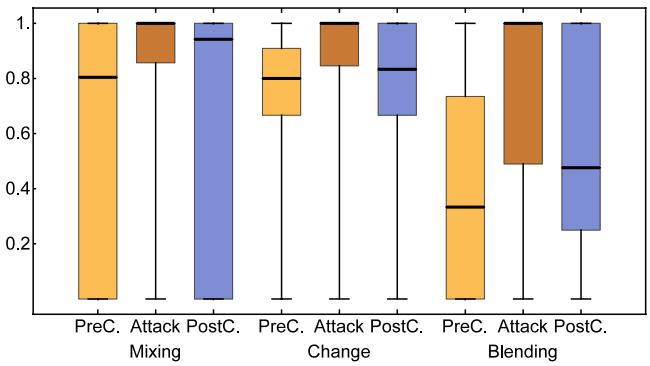


Figure 3. Gap-matched comparisons for group turn-over. Three measures for turn-over in group composition in the experimental condition after a simulated attack (Attack) and in two gap-matched control conditions without sparrowhawk release at the same feeder on a day before the attack treatment (PreC) and the day after the attack treatment (PostC) with a comparable time gap between control event and follow-up event to the time gap between attack event and the follow-up event in the *Attack* condition. Indices of zero indicate no change in group composition while indices of one or close to one indicate complete turn-over with no overlap in group membership, or maximal blending; bold bars give the median, boxes the inter-quartile range, and whiskers the range.

$p = 0.013$). Comparing birds present during the attack events and the post-attack gathering events, 26% of the birds present during the attack were not present afterwards. In order to investigate whether this corresponds with the expected value given continuous changes in group composition, we calculated three indices quantifying different aspects of turnover in flocks (See Methods and Supplementary Figs S5–S7). We found that turn-over after model hawk attacks was significantly higher than in the time-matched control condition, and this was true for both pre- and post-experimental controls and all measures for turn-over (Wilcoxon tests for paired samples, pre-attack: $N = 102$, change: $T_s = 895$, $p < 0.001$, blending: $T_s = 3089$, $p < 0.001$, mixing: $T_s = 902$, $p < 0.001$, post attack: $N = 98$, change: $T_s = 632$, $p < 0.001$, blending: $T_s = 2592$, $p < 0.001$, mixing: $T_s = 703$, $p < 0.001$, Fig. 2). Furthermore, rates of turn-over after attacks were also significantly higher than in the gap-matched control condition (pre-attack: $N = 103$, change:, $T_s = 674$, $p < 0.001$, blending: 103, $T_s = 2961$, $p < 0.001$, mixing: 103, $T_s = 479$, $p < 0.001$, post-attack: $N = 104$, change: $T_s = 882$, $p = 0.002$, blending: $Ts = 2139$, $p = 0.001$, mixing: 842, $p = 0.003$, Fig. 3), suggesting that the higher turn-over is not only due to the increased latency to return after a model hawk attack.

As flock composition changes continuously, with birds leaving and other birds joining[50], a gradual decrease in membership overlap with increasing time can be observed. Therefore, on finding that predator attacks induce instantaneous turn-over, we considered the amount of turnover, in terms of undisturbed foraging time, that a single predator attack generated. We calculated the three measures of turn-over (change, blending and mixing rates) for all subsequent flocking events at the respective feeder for the rest of the day. By fitting exponential functions to the observed indices, we were able to estimate the expected increase in the turn-over of group composition

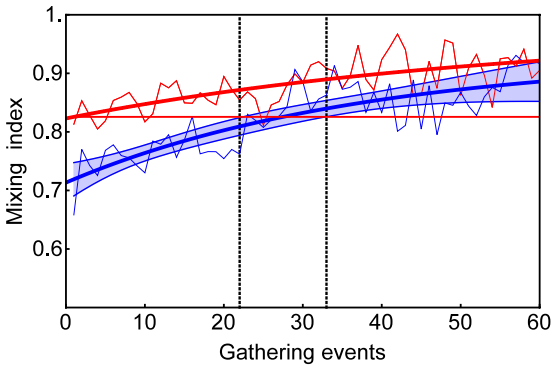


Figure 4. Mixing index for successive gathering events after an attack event in the experimental condition (red dot-dashed line) and after the matched control event in the post-experimental control condition (solid blue line). The bold line gives the fit of an exponential function to the mixing indices after all control events. The shaded area gives the 95% confidence interval for the estimated function for the control condition. Thin red and blue lines give the median values over all attack and control events. The horizontal line indicates the estimated mixing index for the first post-attack gathering event and the intersections between this line and the 95% CIs for the control condition were taken as the upper and lower estimates (dotted grey lines) for the time-effect that the attack had on the mixing index. On average, the distance between two consecutive gathering events equates to 6.5 minutes (392 s). Figures indicating the effect on the 'blending' and 'change' indices are provided in the online supplementary material.

(Fig. 4). Based on this, we estimate that each single model predator attack generates the same change as we would otherwise expect, under normal conditions, after between 18.5 and 25 gathering events; the same blending expected after between 22.3 and 34.6 gathering events, and the same mixing as expect after between 22 and 33 gathering events. Given the distribution of gathering events in time (linear model fit to the median latencies for the first 35 post-event gathering events: $R^2 = 0.998$, Supplementary Figure S9), this equates to the instantaneous change in group composition after a predator attack corresponding to the change expected after 2.0–2.6 hrs, the blending after 2.5–3.8 hrs and mixing index after 2.3–3.3 hrs, under standard, non-manipulated, conditions.

Discussion

Using a large-scale field experiment, we demonstrate the nonlethal effects of simulated predator attacks on the behaviour of wild birds. As an immediate response to the sudden appearance of a model predator, the birds left the site. Birds were less likely to return to the site after an attack than in matched control situations and if they returned, they did so only after a considerably longer delay. As not all birds returned and new birds joined the flock of birds remaining at the feeder, this lead to an increased turn-over in group composition at the feeder site. The effect of an unsuccessful predator attack on the turn-over in group composition was rapid and extensive, and—depending on the chosen measure—equated to the turnover expected for 2.0–3.8 hrs of undisturbed foraging. Given a day length of eight to nine hours during winter, this corresponds to 22–47% of the time potentially available for foraging.

These estimates are associated with some uncertainty but, regardless of the measure of turn-over considered, the appearance of the model predator had a considerable effect on the turn-over within these flocks. As a caveat we want to mention the possibility that some of the undetected birds might have stayed in the vicinity of a feeder after an attack. A discussion of this scenario is given in the online supplementary material. An increased turn-over in group composition can affect the effective size of the social interaction network[52] and, on the individual level, the number of potential interaction partners. It has been shown previously that changes in foraging associations in great tits carry over into other social contexts[53,54]. Increasing the number of interaction partners, and the rate at which these change, has the potential to influence many processes within populations with both negative and positive effects for individual fitness. For example, interacting with more conspecifics before the breeding season implies, on the one hand, meeting more potential mating partners and, on the other hand, meeting more competitors of the same sex. Both effects can have direct implications for an individual's social behaviour and its future mating success. Further, the distribution of social interactions is often implicated–at least in theory–in emergent processes such as information or disease transmission, and recent work on tits has demonstrated effective social learning predicted by social structure[55]. Clearly, predator-driven changes in the rate of social association and turnover could have implications for such processes, even if this remains to be demonstrated empirically.

Predation is a strong mortality factor in mixed species tit flocks[56] and sparrowhawks are amongst the main predators of tits in the study area[43]. Morse[57] estimated that each individual tit may witness one sparrowhawk attack per day, with an estimated success rate of 12%[42]. Birds can reduce the risk of falling prey to hawks by increasing vigilance, staying closer to cover, moving less or hiding, though all these measures for evading predation also reduce foraging efficiency. That is, the birds have to trade off safety against foraging, and the balance between risks of predation and starvation is under constant selection pressure[3,40,58–61]. Whether a trade-off in tit flocks exists between safety and a favourable flock composition with respect to specific individuals remains unknown. Although we could not address this question with our study, such trade-offs between safety and social

requirements could be elucidated by systematically altering the frequency of predator attacks, or by longitudinal studies if responses to predators change as the breeding season approaches. Finally, pair formation, which intensifies in spring, might require that pair members condition their decision (e.g. whether to stay or to go) on the response of their partner. As a recent study has shown that great tits opt to forage at sub-optimal patches in order to stay together with their preferred social partner[53], it seems plausible that decisions about leaving an area due to increased predator presence might be influenced by the partner's response as well. We observed some instances where mated pairs of birds were present during attacks (summarized in Supplementary Table 1), but the small number of these occasions prohibited any analysis in this direction.

In order to describe the predation risk effects on the behaviour and habitat use of prey species, Brown and colleagues[62] coined the term "ecology of fear". Here, we suggest extending this to a "socio-ecology of fear" when considering the effects of predation risk on social behaviour and group composition. Several empirical studies have shown that predation risk can influence individuals' decisions to join groups[24,25]. Recently, Croft and colleagues[63] found that under high predation pressure males guppies (*Poecilia reticulata*), which are more vulnerable to predation than females, form separate shoals in shallower and safer habitats, demonstrating that predation pressure can even lead to social segregation of the sexes. Predation risk effects on social behaviour are, however, not confined to foraging aggregations but have been debated for breeding colonies[64], and empirical studies delivered evidence for such effects[22,65,66].

Predators have direct impact on the population dynamics and individual behaviour of their prey species. The very evident and drastic impact of mortality caused by direct predation has led to most research primarily focusing on the consequences of elimination of individuals from the population. More subtle effects of predator presence have been studied predominantly in the context of foraging[61,67]. Here, we argue that nonlethal predator effects on social behaviour and social structure deserve more attention, as it is likely that they, in turn, have a strong influence on population level processes, as well as individual fitness by exerting sizeable influence on the social system and social interaction patterns of the prey species.

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Author Contributions

B.C.S. and B.V. planned and designed the study, B.V. and J.A.F. collected and analysed the data, all three authors wrote the paper. All authors gave final approval for publication.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

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Appendix D

The influence of nonrandom extra-pair paternity on heritability estimates derived from wild pedigrees

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The influence of nonrandom extra-pair paternity on heritability estimates derived from wild pedigrees

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Quantitative genetic analysis is often fundamental for understanding evolutionary processes in wild populations. Avian populations provide a model system due to the relative ease of inferring relatedness among individuals through observation. However, extra-pair paternity (EPP) creates erroneous links within the social pedigree. Previous work has suggested this causes minor underestimation of heritability if paternal misassignment is random and hence not influenced by the trait being studied. Nevertheless, much literature suggests numerous traits are associated with EPP and the accuracy of heritability estimates for such traits remains unexplored. We show analytically how nonrandom pedigree errors can influence heritability estimates. Then, combining empirical data from a large great tit (*Parus major*) pedigree with simulations, we assess how heritability estimates derived from social pedigrees change depending on the mode of the relationship between EPP and the focal trait. We show that the magnitude of the underestimation is typically small (<15%). Hence, our analyses suggest that quantitative genetic inference from pedigrees derived from observations of social relationships is relatively robust; our approach also provides a widely applicable method for assessing the consequences of nonrandom EPP.

KEY WORDS: **Extra-pair copulations, misassigned paternity, pedigree error, pedigree simulation, quantitative genetics, SNP.**

Estimating the heritability of traits in wild populations is fundamental in determining responses to selection, as well as understanding patterns of genetic variation (Lynch and Walsh 1998). Wild bird populations have been a popular subject for such work, as family structure and hence relatedness among individuals can often easily be inferred through observations during breeding attempts, and pedigrees built over multiple generations (Merilä and Sheldon 2001). However, molecular genetic techniques have often demonstrated the occurrence of extra-pair paternity (EPP) in socially monogamous species (Griffith et al. 2002). Consequently, paternal links within the social pedigree may differ from those in the actual genetic pedigree, and therefore using social pedigrees for quantitative genetic parameter estimation may be problematic (Merilä et al. 1998; Keller et al. 2001; Charmantier and Reale 2005).

Initial investigations of the effect of pedigree error used empirical avian pedigrees, and compared estimates of heritability derived from midparent–offspring regressions using genetically correct pedigrees with those calculated from uncorrected pedigrees (Merilä et al. 1998; Keller et al. 2001). Although no substantial differences between social and genetic pedigree heritabilities were found, a trend of reduced heritabilities from social versus genetic pedigrees suggested that the error induced by EPP had the potential to decrease heritability estimates. Charmantier and Reale (2005) advanced this work by employing simulation techniques that bypassed potential underlying confounding effects

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within field data, and enabled consideration of how a range of EPP rates influence estimates of various heritabilities, which were derived using "animal models" (Henderson 1975). They showed that social pedigrees underestimate heritability most when EPP rates and trait heritabilities are high, as this increases the number of incorrect pedigree links, and causes extra-pair young (EPY) to strongly resemble their genetic sire, therefore decreasing the average resemblance between putative paternal relatives (Charmantier and Reale 2005). Nevertheless, the extent of underestimation remained small and it was concluded that social pedigrees were generally reliable when EPP rates ($\leq$20%) and trait heritabilities (0.1–0.4) were typical of those found in most bird species (Charmantier and Reale 2005).

Importantly, however, past work has assumed no relationship between the investigated trait and the misassigned paternities, and the extent to which this could decrease the accuracy of heritability estimates remains unknown (Keller et al. 2001; Charmantier and Reale 2005; Berenos et al. 2014). Indeed, a large body of research suggests that numerous morphological, behavioral, immunological, life-history, and reproductive traits are associated with extra-pair activity across many species of birds (Birkhead and Moller 1992; Moller and Ninni 1998; but see Akcay and Roughgarden 2007; Hsu et al. 2015). In such cases, this may result in additional bias in estimates of quantitative genetic parameters, as a result of the relationship between EPP and the trait being considered (Reid et al. 2014).

The primary objective of this study was to assess the validity of using social pedigrees for estimating the heritability of traits associated with EPP. Such traits may influence the gain, or loss (i.e., cuckoldry), of paternity in multiple ways. Therefore, first, we analytically derive how the trait values of the social and genetic fathers may influence heritability estimates from father–offspring regression. Second, we explore how animal model estimates of heritability are influenced by the degree, and mode, of nonrandom EPP within authentic populations using a permutation approach. As wild populations may differ in pedigree structure from both animal breeding designs and simple simulated pedigrees, which may also influence heritability estimation (Charmantier and Reale 2005; Quinn et al. 2006; Berenos et al. 2014), we utilized an extensive pedigree from a wild great tit (*Parus major*) population for which both a detailed social pedigree (gained through observations) and genetic pedigree (derived from large-scale SNP genotyping) was available (and for which there has been extensive previous quantitative genetic work (McCleery et al. 2004; Garant et al. 2008; Liedvogel et al. 2012; Santure et al. 2013)). This population has a typical pedigree structure and rate of EPP (12.7–14%) similar to the average of most other socially monogamous bird species (~11%; Blakey 1994; Griffith et al. 2002; Patrick et al. 2012). We combined this with simulation techniques that imposed five different EPP scenarios:

i Males with larger trait values gain more EPP (Hasselquist et al. 1996; Yezerinac and Weatherhead 1997; Johnsen et al. 1998).
ii Males with larger trait values suffer less cuckoldry (Smith et al. 1991; Kempenaers et al. 1992, 1997; Sheldon et al. 1997; Sheldon and Ellegren 1999).
iii Males with larger trait values gain more EPP and suffer less cuckoldry (Burley et al. 1996; Saino et al. 1997).
iv Males cuckold other males that are most dissimilar from themselves (Yasui 1998).
v Males cuckold other males that are most similar to themselves (Patrick et al. 2012; Forstmeier et al. 2014).

Through this, we highlight the extent to which social pedigrees (for which large quantities of data are available, and for which pedigree information is much easier, and frequently cheaper, to obtain) can be used in assessing heritability of traits that may correlate with paternal misassignment in wild pedigrees.

Methods

THEORY

Obtaining analytical results for the expected bias of animal model estimates would be challenging. However, analytical results for the expected bias of father–offspring regression estimates are possible. The difference between actual and estimated coefficients of kinship is at their most extreme for this type of comparison, and so these results should be considered as upper bounds on the degree of bias. The expected estimate of heritability from father–offspring regression is

$$E[\widehat{h^2}] = 2\mathrm{cov}\,(z, o)\,/\mathrm{var}\,(z)\,, \tag{1}$$

where z is the trait value of the social father and o the trait value of the offspring. Under the assumptions that (1) the social father's trait does not have a paternal effect; (2) there is no genetic correlation between the trait and female preference; and (3) there is no inbreeding, then $\mathrm{cov}(z, o) = \mathrm{cov}(z, a)/2$, where a is the breeding value of the offspring's genetic father. If we assume that mating behavior is determined directly by the studied phenotype, then

$$\mathrm{cov}\,(z, a) = h^2\mathrm{cov}\left(z, z'\right), \tag{2}$$

where z' is the phenotype of the genetic father. Denoting EPP events as $\delta = 1$ ($\delta = 0$ otherwise), where δ is also a random variable:

$$\mathrm{cov}\,(z, a) = h^2\mathrm{cov}\,(z, z\,(1-\delta) + \delta e)\,, \tag{3}$$

where e is the phenotype of the extra-pair male (EPM), which is not defined when $\delta = 0$. It can be shown (see Supporting Information) that

$$E[\widehat{h^2}] = h^2[1 + \bar{\delta}\gamma\left(\beta_{e|z} - 1\right) + \beta_{\delta|z}\Delta], \quad (4)$$

where $\bar{\delta}$ is the mean EPP rate, γ is the ratio of the variance in phenotype of cuckolded males compared to all males, $\beta_{e|z}$ is the regression of EPM phenotype on social father phenotype, $\beta_{\delta|z}$ is the regression of being cuckolded on the social father phenotype, and Δ the average difference between the phenotypes of EPMs and the social fathers they cuckold. Perhaps surprisingly, equation (4) implies that heritability estimates under nonrandom EPP would not differ from those under random EPP if patterns and rates of EPP were only determined by the phenotypes of potential EPMs. Under these conditions, equation (4) simplifies to

$$E[\widehat{h^2}] = h^2 - \bar{\delta}h^2 \quad (5)$$

because there is no relationship between social father and EPM phenotypes ($\beta_{e|z} = 0$), nor a relationship between social father phenotype and the probability of being cuckolded ($\beta_{\delta|z} = 0$) and so necessarily $\gamma = 1$. This result has been used previously to estimate $\bar{\delta}$ before the advent of cheap molecular markers (Alatalo et al. 1984). Under this scenario, animal model estimates should be biased downwards by no more than the EPP rate, as has been shown by previous simulation work (Charmantier and Reale 2005).

However, the bias is not simply determined by the EPP rate ($\bar{\delta}$) when patterns and rates of EPP are associated with the cuckolded male's phenotype. This can happen through two broad, but interacting, mechanisms. First, the phenotypes of EPMs and those they cuckold could be correlated, with a positive correlation ($\beta_{e|z} > 0$) reducing bias and a negative correlation ($\beta_{e|z} < 0$) increasing bias. However, a lower bound on $\beta_{e|z}$ is -1 if the variances in trait value for all males, EPMs, and cuckolded males are approximately equal, and so heritability estimates from animal models are unlikely to be biased downwards by more than twice the EPP rate, and most likely substantially less.

A second mechanism is if the probability of being cuckolded depends on the social father's phenotype. Here, bias will increase when the probability of being cuckolded decreases with trait vale ($\beta_{\delta|z} < 0$) and the phenotype of EPM is larger than the average ($\Delta > 0$) or vice versa. It should be noted that even if EPP is independent of EPM phenotype these two quantities will have different signs: if social fathers with low trait values get cuckolded ($\beta_{\delta|z} < 0$) then by necessity EPMs (which are drawn randomly from the population) will have larger trait values ($\Delta > 0$). However, if EPP also depends on EPM phenotype then this is not necessarily the case: as an extreme example, imagine two types of male with phenotypes 0 and 1 and that males with phenotype 1 neither gain nor lose EPP, but males with phenotype 0 lose all their paternity (to each other). Under this example $\beta_{\delta|v} = -1$, yet $\Delta = 0$. Under these conditions $E[\widehat{h^2}] = h^2$ (because $\gamma = 0$) and there is no bias; this makes intuitive sense because the social father of every offspring has the same phenotype as the genetic father. In contrast, if males with phenotype 0 lost all their paternity to males with phenotype 1 then $\Delta = 1$ and $E[\widehat{h^2}] = 0$ generating large biases.

STUDY SYSTEM

The empirical part of this study was conducted using the long-term study population of resident great tits in Wytham Woods, Oxford, UK (51°46′N, 1°20′W; Perrins 1965). The area contains ∼1020 nestboxes in fixed positions which are visited regularly throughout the breeding season (April–May) to record breeding attempts and performance, and identify/capture adults (between days 6 and 14 of nestling phase) and nestlings (after day 15) to mark with a unique BTO (British Trust for Ornithology) metal leg ring. Blood has been collected for a limited subsample of adult birds between 1985 until 2004 and for a much larger proportion onwards. As the majority of studies attempting to estimate heritabilities usually focus on adult traits this pedigree, which consists only of adult birds (therefore giving the realized paternity for males), is appropriate for this work.

PATERNITY ANALYSIS

A total of 2644 of the blood-sampled individuals were chosen for genotyping on an Illumina iSelect BeadChip (SNP chip) of 9193 Single-nucleotide polymorphism (SNP) (see Van Bers et al. 2012 for details). Following quality control, a linkage map of the great tit genome was constructed, with 4701 SNPs mapped to autosomes (van Oers et al. 2014). For computational reasons, a set of 1700 of the mapped SNPs were chosen for parentage analysis by selecting a third of evenly spaced SNPs on each chromosome to reduce interdependence. CERVUS 3.0 (Kalinowski et al. 2007) was employed to confirm social paternal pedigree links and identify previously unknown genetic links. For each offspring, the pool of candidate fathers included all genotyped males at least one year older than itself. Using 10,000 simulated mating events, paternity was assigned to the male with the highest paternity likelihood if they were assigned with high confidence (>99%) in CERVUS.

As this study was aimed at examining the possible effects of misassigned paternities, rather than data completeness (but see Charmantier and Reale 2005; Quinn et al. 2006) only individuals born between 2004 and 2009 (the period for which the large majority of data were available) and had both genetic parents known were included as offspring in the following analyses. Although this subset may have a reduced rate of EPP if social fathers are more likely to be sampled than EPMs, 12.5% of offspring were EPY. This is very similar to previous estimates based on analysis

of paternity among nestlings within this population (Blakey 1994; Patrick et al. 2012). In total, the pedigree contained 1553 genotyped individuals, made up of 593 offspring and 960 founders (i.e., parents of these including genotyped males known to have sired young between 2004 and 2009).

SIMULATIONS

We used simulation techniques to assess how the estimates of traits with heritabilities of 10, 30, 50, and 70% (a range spanning estimates often made for traits in wild populations) were influenced when linked to EPP through the five different mating scenarios. All analyses were run in R (R Development Core Team 2010). We generated traits of given heritabilities by simulating the phenotype for each individual down the genetic pedigree using standard methods (Lynch and Walsh 1998; Hadfield 2010). Then, to establish a given scenario of how the trait is linked to EPP (i.e., "EPP scenarios"—see Introduction), we used a permutation technique that maintained the structure of the observed genetic pedigree. This is desirable as pedigree structure may influence how paternity misassignment affects heritability estimates (Charmantier and Reale 2005; Quinn et al. 2006; Berenos et al. 2014), and this could potentially be exaggerated under nonrandom EPP. Thus, we simulated paternities conditional on the observed social pedigree and summary statistics regarding observed patterns of EPP (see below). We modeled the probability that the potential EPM i gains EPP in the brood of social father j, E_{ij}, following the logit-linear model (Smouse et al. 1999; Hadfield et al. 2006):

$$E_{ij} = \frac{e^{\lambda d_{ij} + \beta(z_i,\ z_j)}}{\sum_m \sum_{n \neq m} e^{\lambda d_{mn} + \beta(z_m,\ z_n)}}, \qquad (6)$$

where the denominator is the sum over all pairs of males (m and n) observed that year. To incorporate the likelihood that there are spatial constraints on the occurrence of EPP, d_{ij} was defined as the distance between the potential EPM and the social father, and λ as the rate of decline of the probability of EPP with distance. We investigated five EPP scenarios with different functional forms for $f(z_i, z_j)$, where z is trait value:

i. The trait of male i, that is, EPM trait values increase the probability of gaining EPP: $f(z_i, z_j) = z_i$.
ii. The trait of male j, that is, social father trait values decrease the probability of being cuckolded: $f(z_i, z_j) = -z_j$.
iii. A combination of (i) and (ii): $f(z_i, z_j) = z_i - z_j$.
iv. The absolute difference in trait values between the EPM and social father increases the probability of EPY within this brood: $f(z_i, z_j) = |z_i - z_j|$.
v. The absolute difference in trait values between the EPM and social father decreases the probability of EPY within this brood: $f(z_i, z_j) = -|z_i - z_j|$.

Finally, β represents the strength of the effect. Smouse et al. (1999) state in passing that β is analogous to the selection gradients defined by Lande and Arnold (1983). We show that this can be justified under our scenarios [i]–[iii] when the number of candidate fathers is large (Supporting Information).

We simulated the trait to have a standard deviation (SD) of one so that β can be roughly interpreted as a standardized selection gradient (note that β must be multiplied by two in scenario [iii] to get the standardized selection gradient).

Under each scenario, β was set as either 0, 0.1, 0.2, 0.4, 0.8, or 1.6; these values range from no association between the trait and EPP (or "zero selection") to strengths of association (or "selection") well above the range typically encountered in wild populations.

A number of extra-pair (EP) events (equal to the number observed in the genetic pedigree) were then drawn from the distribution defined by equation (6). However, note that this distribution is not multinomial because a social father can only be subject to one EP event (i.e., social fathers are sampled without replacement). Whether offspring are sired by an EPM is nonindependent within broods (Brommer et al. 2007; Morrissey and Wilson 2010). Therefore, at each successful EP event, one offspring was randomly assigned to the EPM. Then, the remaining offspring were assigned to the EPM given the known probability of additional young within an EP event were also EPY. Upon assigning individuals as EPY, their trait value was again calculated using the standard methods (Lynch and Walsh 1998; Hadfield 2010). Each combination of heritability, EPP scenario, and strength of the scenario (i.e., strength of relationship between the trait and EPP) within this was simulated 100 times, generating new starting traits on each occasion. We also calculated the statistics γ, $\beta_{e|z}$, $\beta_{\delta|z}$, and Δ identified as important in the analytical model (eq. 4). Further, to allow comparison to previous studies of EPP, we also report the difference (in terms of the number of SDs) between the traits of all EPMs and those of cuckold males. As the differences between these groups of males may influence the total SD, we use the SD of the group with the largest sample size.

HERITABILITY ESTIMATES

For the social, observed genetic, and simulated genetic pedigrees, the additive genetic variance (V_A) and residual variance (V_R) (Falconer and Mackay 1996) were estimated using the animal model (Henderson 1975; Lynch and Walsh 1998; Kruuk 2004) following a Bayesian Markov chain Monte Carlo method (Hadfield 2010). To enable the large number of simulations to be carried out, chains were run for 23,000 iterations after a burn-in of 3000 with a thinning interval of 10. The prior distribution for V_A was as a scaled 1000 $F_{1,1}$-distribution, and a flat improper prior was placed on V_R. Following this, narrow sense heritability estimates were calculated using the standard formula (Falconer

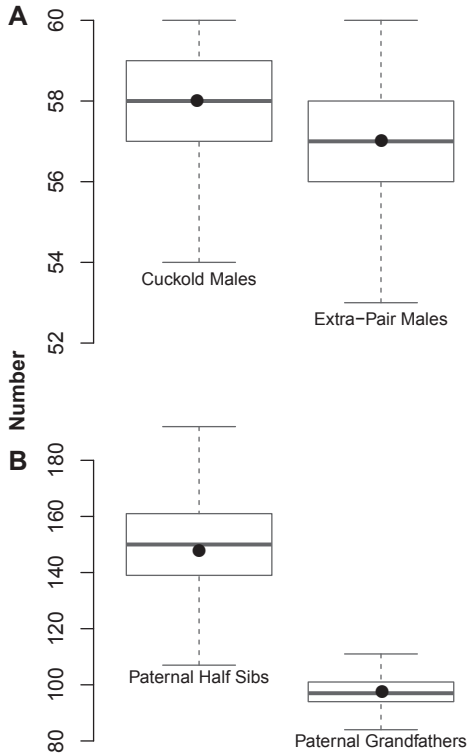


Figure 1. **Measures of pedigree structure related to paternity in (A) number of individuals and (B) number of links, from permuted pedigrees (box plots) and observed genetic pedigree (dots).**

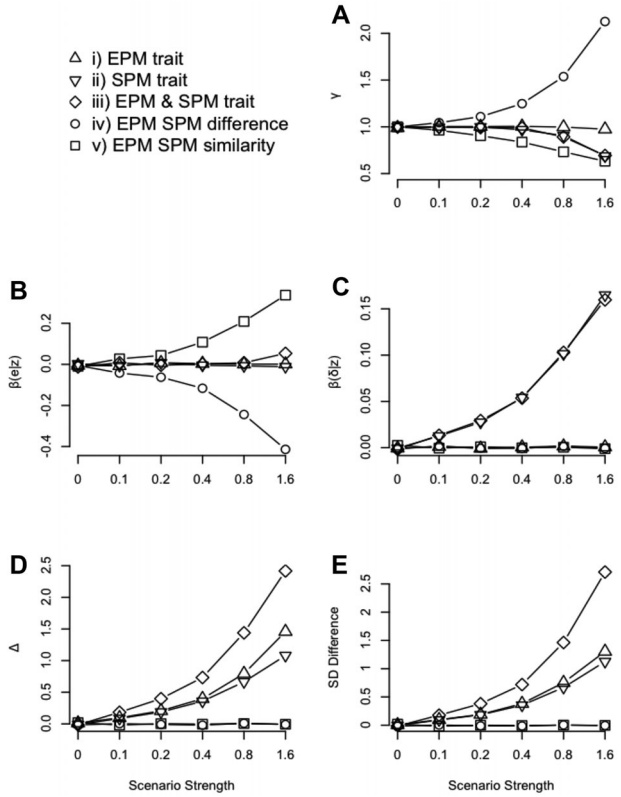


Figure 2. **The mean value of the pedigree statistics shown to be important to the analytical model (eq. 4). The *x*-axis shows the strength of the scenario (i.e., strength of relationship between the trait and EPP) which refers to β from equation (6). This is analogous to a linear standardized selection gradient for scenarios [i], [ii], and [iii] (Supporting Information). Trait heritability had no influence on these parameters so simulations of the same scenario and selection strength are pooled for clarity. (A) γ is the variance in phenotype of cuckolded males compared to all males, (B) $\beta_{(e|z)}$ is the regression of EP male phenotype on social male phenotype, (C) $\beta_{(\delta|z)}$ is the regression of being cuckolded on the social male phenotype, (D) Δ is the average difference between the phenotypes of EP males and the social males they cuckold. Finally, (E) shows the average difference between the phenotypes of all EP males and of all cuckold males (in terms of number of standard deviations - where standard deviation is calculated from the group with the largest sample size). However, the statistics in (E) are not directly included in the analytical model (eq. 4).**

and Mackay 1996). For each heritability ($n = 4$), EPP scenarios ($n = 5$), and different strength of these scenarios ($n = 6$), 100 simulated pedigrees were generated and analyzed.

Results

SIMULATED PEDIGREES

As we incorporated multiple parameters influencing the patterns of EPP observed in the genetic pedigree into our permutations of the social pedigree (see Methods), our genetic pedigrees simulated with no association between the male trait and EPP (i.e., zero selection) did not differ from the observed genetic pedigree in measurements of pedigree structure that could be influenced by such techniques (Fig. 1). This ensured that the simulation technique only applied differences through imposing a nonrandom relationship between the male trait and EPP. By not independently changing the underlying pedigree structure, we avoided the implications that this could have on heritability estimates.

The statistics identified as important in the analytical model (eq. 4) showed the expected trends given the different scenarios (Fig. 2). For example, when males lose paternity to others most dissimilar from themselves (scenario [iv]), the variation in cuckolded males phenotypes (γ) increases (as males with the most extreme traits are likely to lose paternity; Fig. 2A). Further, the relationship between the social fathers trait and the male that cuckolds him ($\beta_{e|z}$) becomes more negative in this scenario, yet, when males cuckold others most similar from themselves (scenario [v]), $\beta_{e|z}$ increases (Fig. 2B). Similarly, a relationship between the male's trait and suffering cuckoldry ($\beta_{\delta|z}$) is only generated when this was directly simulated (scenarios [ii] and [iii]; Fig. 2C). Finally, the mean difference between an EPM and the male he cuckolded (Δ) increased when the trait was either positively related to gaining EPP (scenario [i]) or negatively

related to suffering cuckoldry (scenario [ii]), but was largest when both of these processes were in play simultaneously (scenario [iii]) (Fig. 2D).

HERITABILITY ESTIMATES

Heritability estimates generated using social pedigrees were generally lower than those accurately derived from genetic pedigrees (Figs. 3, S1). This effect is most pronounced at high levels of heritability, although when expressed as a percentage difference, this pattern is not observed (as the analytical results suggest) (Fig. S2). Heritability underestimation does not increase with increasing selection for males with larger traits to gain EPP (scenario [i]; Fig. 3A). The slight increase observed for traits with high heritability is an artifact of simulating strong selection, as in these extreme circumstances, inhibiting a male from gaining EPP at his own brood causes males with low trait values to be more likely to be cuckolded (eq. 6). Indeed, heritability underestimation is increased when low trait values are related to cuckoldry but this effect is only observed at high strengths of selection and heritability $>10\%$ (Fig. 3B). When these two scenarios act in combination, heritability is underestimated even further (Fig. 3C) as the EPMs differ more from those they cuckold (Fig. 2D). This can result in $>10\%$ raw heritability drop (or 20% proportional decrease) at the most extreme points, which is similar to scenario [iv] (i.e., males cuckold others most dissimilar from themselves; Figs. 3D, S2). However, the increased underestimation in scenario [iv] is driven primarily by the negative relationship between the EPMs trait and the trait the male they cuckold (Fig. 2B). Notably, this relationship becomes positive if males cuckold others similar to themselves (scenario [v]), causing heritability underestimation to decrease beyond what is expected under random EPP (Fig. 3E).

Discussion

By combining an analytical approach with simulations using empirical data, we investigated how a nonrandom association between a trait and paternity misassignment may influence heritability estimates over a range of potential scenarios. We confirm that EPP generally causes social pedigrees to slightly underestimate heritability (Keller et al. 2001; Charmantier and Reale 2005). Crucially, however, we demonstrate that this can be influenced by the relationship between the focal trait and the occurrence of EPP (Fig. 3), and we highlight the mechanisms underlying this (eq. 4; Fig. 2).

Much literature links particular male characteristics to the gain of EPP (Griffith et al. 2002), but, interestingly this is not predicted to decrease heritability estimates (gained from parent–offspring regression) more than expected under random EPP (eq. 4). This is supported from simulations using animal models to estimate heritability (Figs. 2, 3). It is also commonly found that particular traits may relate to the likelihood of cuckoldry, for example, in our study species (great tit) for longevity, physical, and behavioral traits (Blakey 1994; Lubjuhn et al. 2007; Kawano et al. 2009; Patrick et al. 2012). Analytically, it is expected that this relationship may increase underestimation of heritability from social pedigrees (eq. 4; Fig. 2B), yet the empirically parameterized simulations illustrate that the effect is minor even when the selection acting through EPP is 0.8 or above. Although selection gradients are rarely calculated and reported in literature surrounding EPP, such high values are generally likely to be uncommon (Kingsolver et al. 2001). This selection was found to be equivalent to $\sim$0.6 SD difference between the trait values of cuckolded males and those gaining EPP (Fig. 2E), which is much higher than found for great tit breast stripe (0.16 SDs difference—Kawano et al. 2009), yet lower than some more extreme examples in related species, such as timing of blue tit (*Cyanistes caeruleus*) song (0.8 SDs difference—Poesel et al. 2006).

These first two EPP scenarios may act in combination, and this has been reported in multiple populations, although its prevalence is still debated (Akcay and Roughgarden 2007; Hsu et al. 2015). Under this scenario, heritability was underestimated by $\sim$10% (Fig. 3; proportional to a $\sim$13% total reduction—Fig. S2) when selection was 0.8 or above, therefore differing rather substantially from just a $\sim$5% (proportionately 7%) underestimate under random EPP (Figs. 3; S1). Similarly, this was also observed in a scenario where individuals cuckold others that are most different from themselves. This could, for instance, be generated by female efforts to increase within-brood diversity (Yasui 1998) or the existence of competing behavioral strategies that are most vulnerable to cuckoldry by one another. As this scenario requires no overall difference in trait values between the males that gain EPP and those that are cuckold (Fig. 2D, E), it may be difficult to detect, despite its ability to underestimate heritability by almost 20% (proportionally—Fig. S2). Such underestimation is significantly larger than compared with the findings of Charmantier and Reale (2005), who concluded traits with heritability of 0.4 in large pedigrees with 10% EPP rates are underestimated by 0.8–6.6%.

Finally, males could be cuckolded by those most similar to themselves if, for instance, EPP was nonadaptive (Forstmeier et al. 2014) and females simply maintained their mating preferences over both social and genetic mate choices. This scenario could also arise if particular phenotypes were associated with both the loss, and gain, of paternity through EPP. For example, in our study system, great tits with "bold" personalities suffered increased cuckoldry but gained more EPP (Patrick et al. 2012). Encouragingly, this scenario decreases the underestimation of heritability by the social pedigree, as the genetic father is similar to the social father. Therefore, here, the social pedigree can be used more reliably than expected under random EPP. It is also

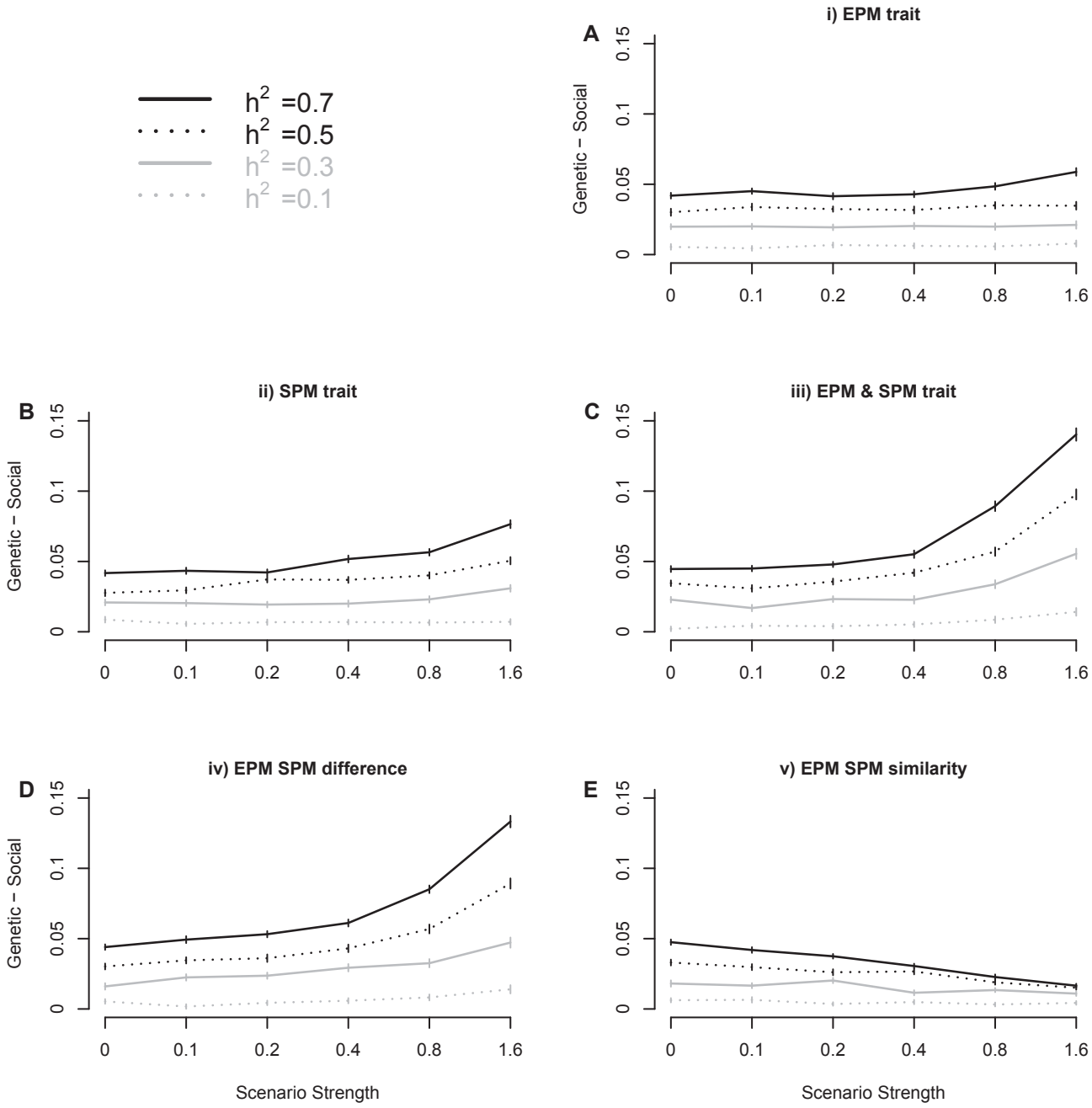


Figure 3. **Total difference between the heritability estimates using the genetic pedigree in comparison to the social pedigree. Titles illustrate EPP scenario: (A) EPM trait increases EPP, (B) social father trait decreases cuckoldry, (C) combination of i and ii, (D) difference between EPM and social father increases cuckoldry, and (E) difference between EPM and social father decreases cuckoldry, (see Methods for details). Vertical lines indicate standard error whereas mid-point represents the mean. Difference is expressed as difference from input heritability and proportion difference (%) is shown in Figs. S1 and S2, respectively. The *x*-axis shows the strength of the scenario (i.e., strength of relationship between the trait and EPP) which refers to β from equation (6). This is analogous to a linear standardized selection gradient for scenarios [i], [ii], and [iii] (Supporting Information).**

notable that the underestimation of heritability for traits with low (10%) heritability does not appear to increase under any scenario (Fig. 3). Thus, traits with low heritability (e.g., fitness components) appear unlikely to be greatly underestimated through using social pedigrees.

The error rate resulting from EPP in the great tit social pedigree used in this study (12.5%) is very close to the average EPP rate of socially monogamous bird species (~11%, Griffith et al. 2002); therefore these findings may be reasonably applicable to a large number of systems. Although the analytical model provided

(eq. 4) allows consideration of a large range of EPP rates, the empirically parameterized simulation approach does not. Therefore, applying the same methodology to other pedigrees would now be beneficial to confirm that the general patterns are also consistent under more extreme rates of EPP. This may be facilitated through open-source pedigree permutation software, such as *Pedantics* (Morrissey et al. 2007; Morrissey and Wilson 2010), as well as the R code provided here (Supporting Information). Furthermore, although random pedigree errors may have similar effects on genetic variances and covariances, they may have a larger influence on estimates of parental and indirect genetic effects (Morrissey et al. 2007). Indeed, the influence of nonrandom pedigree error on other quantitative genetic parameters remains largely unknown, yet it has the potential to influence estimates of inbreeding (Reid et al. 2014), genetic correlations and covariances (Berenos et al. 2014), and indirect effects, for example, if males alter their behavior in different ways in response to EPP (Eliassen and Kokko 2008). The analytical model (eq. 4) could potentially be expanded to incorporate these other quantitative genetic parameters. Similarly, particular caution should also be taken when utilizing multiple measures that could be subject to pedigree error (Reid et al. 2014), as in the case of estimating the response to selection of a trait that is associated with EPP, where both heritability and selection could be underestimated. Finally, although the biases we report are small, it is possible that comparative/meta-analytic studies of heritability may systematically bias certain comparisons. For example, when testing differences in heritability between sexually and nonsexually selected traits (Alatalo et al. 1997), the possibility that the effects are driven by biases in estimation should be acknowledged.

In conclusion, although pedigree errors in wild populations only result in minor underestimation of heritability of particular traits (Keller et al. 2001; Charmantier and Reale 2005; Berenos et al. 2014), an association with EPP may influence this. However, traits of low heritability appear to be relatively unaffected by this, and, even for traits with higher heritability, the social pedigree remains adequate in all but the most extreme scenarios. This demonstrates the general utility of social pedigrees under most circumstances, although further consideration of multiple systems and various quantitative genetic parameters is now needed to guide our level of assurance in utilizing long-term social pedigrees in understanding evolutionary processes.

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DATA ARCHIVING

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.7nb81.

LITERATURE CITED

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