Socio-ecological factors shaping mixed-species groups

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ABSTRACT

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Understanding why individuals form groups that are strikingly diverse in their organisation is a central focus in evolutionary ecology. Although mixed-species groups, where members of different species interact and move together, are common across animal taxa, inter-species interactions have often been a point of secondary interest in the study of animal sociality.

Using mixed-species flocks of individually marked tits (Paridae) as a model system, I investigate how individuals make adaptive decisions in their multi-species social environment. First, I investigated the role of social information in facilitating mixed-species groups. I developed a framework that is based on concepts of optimality to link processes of group formation to signalling theory and information use. I found that tits actively produce recruitment calls to form foraging flocks, but social context mediates the strategies for recruiting group members (Chapter 2). Further, I showed that social information about food transmits through heterospecific social connections and that adaptive social learning strategies prevent birds from being trapped in maladaptive behaviour when wrong information is being provided (Chapter 3).

In the second part of my thesis, I addressed whether flock formation is a result of preferential interspecies interactions. I found that active preference for foraging with heterospecifics can enhance social cohesion among individuals, which presumably provides members of mixed-species groups with additional social benefits to single-species grouping (Chapter 4). Separating the influence of spatial environmental patterns, such as resource distribution, from active social preferences is challenging, but comparing observational interaction data to null models using permutations tests, enables to separate the effect of spatial pattern and social preferences. Applying this approach to a large long-term observational data set of heterospecific interactions, I demonstrate that individuals differ consistently in their propensity to associate with heterospecifics (Chapter 5).

The work presented in this thesis demonstrates that individuals consider both their social and non-social environment when making decisions in their natural, multi-species environment. Participation in mixed-species flocks appears to be a complex balance of competition cost and grouping benefits, mediated by both individual phenotype and environmental conditions. The work presented in this thesis supports previous notions that mixed-species flocking is a mutualistic relationship between participating species. This thesis contributes experimental evidence for the importance of positive interactions in community ecology, and justifies recent advances of linking individual behaviour to community processes.

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AUTHOR CONTRIBUTIONS

Main contributors

Friederike Hillemann had independent intellectual input into all aspects of the thesis; carried out experimental data collection over three winters, and contributed to three years of winter and spring data collection as part of the Wytham Tit Project (social association data and long-term population monitoring), analysed data, wrote first drafts, and incorporated co-author comments to produce final versions of all chapters.

Ella F. Cole (co-supervisor and co-author of all data chapters) provided intellectual input and guidance throughout, offered advise on the statistical approach, and gave detailed comments on all chapter drafts.

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Ben C. Sheldon (supervisor and co-author of all data chapters) provided intellectual input and guidance throughout, and gave comments on all chapters.

Additional contributors

Sara C. Keen (co-author of Chapter 2) contributed to data collection, provided input on conceptual design, provided feedback on drafts of chapter 2.

CONTENTS

1

Introduction

SOCIO-ECOLOGICAL FACTORS SHAPING MIXED-SPECIES GROUPS

Foraging in groups

Varying degrees of sociality are found across animal species, and understanding the causes and implications of different forms of social associations has been of great interest to evolutionary and ecological research (Krause & Ruxton 2002; Ward & Webster 2016). An important benefit of grouping is that the proximity to others provides improved access to information about the environment (Dall et al. 2005; Valone 2007). Social information can potentially affect a wide range of fitness-relevant decisions, and has been intensively studied in foraging contexts, as intentionally produced information (e.g., vocal recruitment: Elgar 1986), or unintentionally provided, inadvertent social cues can inform others decision about where to forage (public information: Templeton & Giraldeau 1996; Danchin et al. 2004; Dall et al. 2005). Group foraging further provides anti-predator benefits through several non-exclusive mechanisms, including predator encounter dilution (Hamilton 1971; Bertram 1978), collective vigilance and improved predator detection (Lima 1995), and confusion of targeting predators (Landeau & Terborgh 1986). However, grouping generally increases intra-group competition for limited resources, presenting individuals that forage in groups with a trade-off between predation risk and competition (Giraldeau & Caraco 2000; Verdolin 2006). One behavioural strategy to balance the group-size dependent costs of social foraging is resource partitioning; for example, the temporal use of foraging grounds is predicted by dominance in the brown trout (*Salmo trutta*; Alanärä et al. 2001). Similarly, individuals from mixed-species flocks of North American warblers (*Dendroica spp.)*, use separate feeding zones within trees, thus partitioning a shared resource spatially (MacArthur 1958). Associating with individuals from other species appears to be a wide-spread strategy for reducing the cost of intra-group competition while maintaining relative safety from predators in the group (Morse 1970; Sridhar et al. 2009; Heymann 2011; Dhont 2012; Goodale et al. 2017).

Forms of multi-species associations: Aggregations and cohesive groups

Heterospecific associations can take different forms, from loose aggregations to cohesive groups of individuals that interact and move together. The term 'mixed-species group' has traditionally only been used to specifically refer to groups that form because of active attraction and benefits to members of another species, as opposed to independent accumulation of individuals due to environmental conditions or resources, such as animals gathering at a water hole or for shelter (Hinde 1952; Morse 1970). However, challenging the view that seemingly non-interacting individuals from different species gather independently, interspecific information transfer might influence spatial organisation of individuals, which might lead to the formation of temporary or stable mixed-species groups (Goodale et al. 2010; Schmidt et al. 2010). Throughout this thesis, I follow the terminology suggested in a recent comprehensive discussion on animal mixed-species groups, which acknowledges that the scale of space and time of interactions is important when classifying mixed-species associations (Goodale et al. 2017). Accordingly, I differentiate between mixed-species aggregations, which are usually stationary groupings ultimately formed due to environmental factors, and mixed-species groups, which are groups that are formed and maintained through interspecies interactions.

Analysing mixed-species groups using individual-based approaches

Mixed-species groups are widely prevalent across animal taxa (e.g., fish: Paijmans et al. 2019, mammals: Stensland et al. 2003, birds: Sridhar et al. 2009), although most commonly studied in birds (Goodale et al. 2017). The early literature on mixed-species grouping was mainly of descriptive nature, reporting the composition and size of groups and speculating about the adaptive benefits for participating species and their roles within the group (reviewed in Goodale et al. 2017). About a decade ago, the first quantitative meta-analyses have summarised the literature on forest birds, and concluded that anti-predator benefits and increased foraging efficiency appear to be the main drivers of mixed-species flocks (Sridhar et al. 2009, 2012; Goodale & Beauchamp 2010; Harrison & Whitehouse 2011).

Together, this work has contributed to our understanding of the general, species-level benefits for members of mixed-species groups. However, the question of why species join mixed-species groups has usually considered species averages, thus ignoring the importance of intraspecific variation for social and ecological processes (Drews 1993; Réale et al. 2007; Bolnick et al. 2011; Violle et al. 2012; Hart et al. 2016). It is likely inappropriate to assume that all heterospecific associations provide equal benefits to all members of the same species. Instead, an individual from one species that interacts with different individuals from another species might experience fitness-related outcome of different magnitude or even direction. For example, associating with a smaller, juvenile heterospecific might provide competitive benefits, whereas an adult member of the same species might be a stronger competitor. Thus, individuals may have flexible interaction rules, balancing the cost of competition with social benefits, when deciding who to interact with and who to avoid. Because individuals are inherently different, so should be the groups they form. Our understanding of mixed-species groups might therefore benefit from accounting for differences in individuals' behaviour and preferred interaction pattern.

The social decisions that individuals make scale up to the social structure. It has long been recognised that ecological factors, such as the distribution of resources, and evolutionary processes affect the distribution of individuals, and therefore social interaction pattern and the resulting social structure (Crook 1970; Clutton-Brock 1974; Hinde 1976; Kurvers et al. 2014). A first formal framework for quantifying social interactions, the resulting dyadic relationships, and emerging group social structure was proposed by Hinde (1976). Following from this, biologists have started to apply network thinking to describe various aspects of animal behaviour, based on the core unit of interactions between individuals. Social network approaches have become a useful tool for describing association patterns among individuals, allowing us to describe the social environment for each individual and analyse social processes while accounting for intraspecific variation in behavioural traits (Whitehead 1999, 2008; Croft et al. 2008; Wey et al. 2008; Krause et al. 2015).

It has become increasingly clear that non-random social associations have important consequences for individuals and for population-level processes (Cantor et al. 2019). For example, the number and type of social connections can affect individual survival and reproduction (Schülke et al. 2010; Alberts 2019) and access to resources in foraging contexts (e.g., Aplin et al. 2012; Snijders et al. 2018), and the structure of the network can determine disease or pathogen transmission (Weber et al. 2013; Stroeymeyt et al. 2018). The use of social network analysis in the field of behavioural ecology has continuously increased over the past two decades, with exponential increase in the total number of social network articles over time (Webber & Vander Wal 2019). However, so far only few studies have explored individual-level pattern of heterospecific interactions in mixed-species groups (e.g., Farine et al. 2012; Farine & Milburn 2013). These studies demonstrated that applying social network analysis to mixed-species groups may reveal intraspecific variation in flock participation, raising interesting questions about whether and how individual differences in flocking behaviour affect group-level structure and social processes.

Mixed-species groups as a model for community ecology

Understanding interactions between species is a central goal of ecological research. Animal ecology has classically been mainly concerned with trophic and competitive relationships between species (Elton 1927; Cody 1974; Morin 1999), and the importance of positive interactions between species for the maintenance of ecological networks has only been recognised more recently, although cooperative or mutualistic interactions have been frequently studied in behavioural ecology (e.g., Bshary 2001; Canestrari et al. 2014; Barker et al. 2017). Furthermore, almost all studies that represent species interactions in ecological networks consider interactions between species, i.e. average traits of species (Ings et al. 2009). Species interactions in mixed-species groups include mutualistic, commensalistic, and exploitative relationships (Goodale et al. 2017). As subunits of the whole community, or 'community modules' (Holt 1997), they provide rich opportunities for addressing questions regarding species interactions that are typically addressed in community ecology, such as selective pressures that facilitate coexistence of individuals on the same trophic level. Ultimately, interactions happen at the level of individuals, and analysing inter-

species interactions between individuals, rather than considering species-level averages, allows to shed new light on old questions.

Social information transcends species boundaries and can shape interaction pattern

Improved foraging efficiency and increased predator avoidance have long been considered the main drivers in the evolution of mixed-species groups – a conclusion drawn based on the consistent findings of a number of observational studies (Morse 1977; Sridhar et al. 2009, 2012). Both benefits are often strongly interrelated and can theoretically be obtained from either conspecifics or heterospecifics, as they present general grouping benefits. Additionally, individuals can gain social information benefits from associating with others, i.e. benefits arising from using others' behaviour as a source of information about the environment (e.g., alarm calls or following others that discovered food).

Animals often use information provided by others, both actively communicated signals and inadvertently produces cues (Templeton & Giraldeau 1995; Danchin et al. 2004; Dall et al. 2005), and heterospecifics are often an important source of information (e.g., Sullivan 1984; Goodale & Kotagama 2005; Templeton & Greene 2007; Seppänen et al. 2007; Suzuki 2012). Heterospecific information is, for example, used to decide where to settle (Mönkkönen et al. 1990; Doligez et al. 2002), where to eat (Farine et al. 2015), and predator avoidance (Goodale & Kotagama 2005). It is generally less costly and faster to gain than personal sampling, which involves gathering information through direct, trial-and-error-based interactions with the environment ('personal information'; Galef & Laland 2005; Dall et al. 2005). This is exemplified by individuals trying to find dispersed patchy food resources in ephemeral landscapes. However, foraging patches might be depleted or differ in quality – a suitable foraging patch for one species might not be optimal for another – and using information that is not accurate or not relevant could result in maladaptive foraging. Whether and when to use social information, and from whom, is therefore expected to be a decision considering the potential gains compared to personal information use (Galef & Laland

2005), and can affect interaction pattern among individuals (Goodale et al. 2010; Kulahci & Quinn 2019).

The importance of social information for heterospecific attraction has previously been recognised as a potentially important driver for the formation of mixed-species groups (Seppänen et al. 2007; Goodale et al. 2010). Heterospecifics might provide particularly valuable information that would not be provided by conspecifics (Goodale et al. 2010), for example, if species differ in their sensory capacities, vigilance behaviour, or information gathering methods (e.g., Chittka & Leadbeater 2005; Meise et al. 2018). The relevance of heterospecific information depends on the amount of niche overlap, i.e. whether individuals share the same predators or use similar resources. At the same time, competition for resources is determined by ecological distance. A new framework explaining why individuals interact with heterospecifics or conspecifics captures that the costs and benefits arising from interactions depend on the phenotypic distance between interaction partners (Sridhar & Guttal 2018).

While some individuals may be particularly suitable for providing information, or developing new behaviours through asocial learning ('information producers'), others rather exploit social information ('information scroungers', Barnard & Sibly 1981; Laland 2004). For example, within mixed-species flock that are dominated by birds from the Paridae family (tits or chickadees), some species have been suggested to play an important role in producing information (Farine et al. 2012, 2015; Farine & Lang 2013; Suzuki 2012), whereas nuthatches and woodpeckers benefit from joining the flock as information scroungers (e.g., Morse 1970; Sullivan 1984; Dolby & Grubb 1998). Such asymmetric information flow from producers to seekers can cause disparate dependence between species and influence community structure (Goodale et al. 2010). Understanding who individuals interact with, and why, is therefore an important step in understanding the formation and composition of mixed-species groups.

Study system: Mixed-species flocks of tits

The new focus on inter- and intra-species differences and suggestions to apply bottom-up approaches to communities allows to consider uneven benefits between members of mixed-species groups and to test refined hypotheses on their emergence, composition, and maintenance. Mixed-species flocks dominated by tits, birds from the Paridae family, provide an ideal study system to address these questions, given the detailed knowledge about their ecology and behaviour, as they have long been a model species in ecology and evolution (e.g., Hinde 1952; Gibb 1954; Perrins 1979).

Each chapter presented in this thesis contains a separate section describing relevant details of the particular study design, experimental procedures, and analytical steps. Here, I present an overview of the study system and general data collection. All observational and experimental work for this thesis (Chapters 2-5) was carried out in the context of a large-scale long-term study investigating the social ecology of wild songbirds. Field research took place in Wytham Woods, Oxford, UK (51°46' N, 1°20' W), a 385ha mixed deciduous woodland surrounded by open farmland and pasture (Savill et al. 2010). The University of Oxford's Wytham Tit Project has been studying various aspects of tits' ecology and social behaviour since 1947, with a main research focus on their reproductive ecology. Since then, more than 1200 nest boxes have been installed in Wytham, which are predominately used by blue tits (*Cyanistes caeruleus*), great tits (*Parus major*), but also other hole-nesting species included in this study: coal tits (*Periparus ater*), marsh tits (*Poecile palustris*), and European nuthatch (*Sitta europaea*). Birds get individually ringed as nestlings and breeding adults get caught and identified at nest boxes. Additionally, regular mist-net catching throughout autumn and winter allows marking immigrants and birds that bred in natural cavities. Data on individual characteristics from the breeding season is aligned with data recorded in the winter, when birds are sexed and aged based on plumage characteristics and morphometric information. Each bird is fitted with both a unique BTO (British Trust for Ornithology) metal leg ring, and a plastic leg ring carrying a passive integrated transponder (PIT tag, IB Technologies, UK). PIT tags are small light-weight (<0.1g) battery-free electronic devices that enable automated individual identification by radiofrequency identification (RFID) antennae.

RFID antennae are attached to bird feeders (Dorset ID, Netherlands) that automatically record the identity of each PIT-tagged individual landing and perching on the feeder access hole, providing a time-stamped record of each feeder visit. Applying a machine-learning algorithm to the data stream with spatiotemporal information of PIT-tag detections allows us to describe social relationships among individuals based on co-occurrence in the same flock. A Gaussian mixture model (GMM) clustering algorithm can identify flocks, or 'gathering events', as bursts of feeding activity of different temporal resolution and group size (Psorakis et al. 2012, 2015). Individuals' group membership is assigned based on co-occurrence in the same gathering event using the 'gambit of the group' approach (Whitehead & Dufault 1999; Franks et al. 2010), i.e. assuming that all individuals within a group interact with each other. Dyadic association strengths between individuals is then calculated as the simple ratio index, from 0 (never recorded in the same group), to 1 (always recorded in the same group; Cairns & Schwager 1987).

This system allows us to simultaneously and automatically monitor the behaviour of large numbers of individually-tracked birds from multiple species. Being able to gather detailed data on interactions among individuals from a community of songbirds provides a unique opportunity to study individuals' behaviour in a multi-species context. This will allow us to better understand how individual behaviour contributes to patterns of social associations at the community level, the emergent properties of social structure, and how socio-ecological processes translate to fitness-related outcomes.

In the non-breeding season, tits form mixed-species foraging flocks that are regularly joined by other species, for example nuthatches (Sittidae), tree-creepers (Certhiidae), and woodpeckers (Picidae) (Hinde 1952). Dominance between species and within species is strongly predicted by body size (Morse 1978; Gosler & Carruthers 1999); for example, great tits are dominant to blue tits and marsh tits, and marsh tits are the smallest of the three species and therefore subordinate to both blue tits and great tits, while adults and males are generally dominant to females and juveniles.

Dominant individuals are able to constrain access to resources for subordinates, making the latter more susceptible to interference competition (Ekman 1989; Milligan 2015). Flocks move together as coordinated collectives, but express fission-fusion dynamics that are characterised by high membership turn-over and short-term structural stability (Ekman 1989; Farine et al. 2012, 2014). During winter, tits forage on clumped resources such as beech mast (fallen seed of beech, *Fagus sylvatica*), which are scattered across the environment (Hinde 1952; Perrins 1966). Individuals readily use information provided by conspecifics and heterospecifics while foraging, and information was shown to spread through the population via conspecific and heterospecific social connections (e.g., Aplin et al. 2012, 2013; Farine et al. 2012, 2015; Firth et al. 2015, 2016). While heterospecific information transfer is important for foraging patch discovery, experimental studies in our system found that social attraction (Farine et al. 2014), association strength (Farine et al. 2015), and rate of information transmission (Farine et al. 2015; Firth et al. 2016) is stronger between conspecifics than heterospecifics.

Thesis outline

This thesis presents one of the first cohesive attempts to include heterospecific social interactions in behavioural and community ecology. As outlined above, mixed-species groups provide a great model for investigating how ecological factors, the social environment, and individual differences affect social interactions. The key focus of my thesis is to understand how and why individuals from different species interact with each other to form mixed-species groups, and how environmental factors affect heterospecific interaction pattern. I analysed interaction pattern in mixed-species foraging flocks of tits in undisturbed environments and under experimentally manipulated conditions, to investigate how environmental factors affect individual behaviour and the formation of mixed-species groups.

The first part of my thesis addresses how mixed-species groups are formed, and specifically investigates the role of social information use for establishing foraging flocks. In **Chapter 2**, I study variation in the production of vocal information about novel food resources and used

playback experiments to demonstrate that tits use heterospecific information to find food faster than without calls being produced. I then ask how individuals make adaptive decisions with regard to providing information that attracts others, i.e. how individuals balance the cost of competition with improved anti-predator benefits in groups. I provide a framework that links processes of group formation and social cohesion to signalling, considering concepts of economic decision-making. Using the predictable foraging patterns of songbirds over the course of the day, I quantified individuals' choices about when to vocally recruit others to food, and experimentally evaluate the underlying causes for the observed temporal variation in food-related vocal information.

In **Chapter 3,** I track how different information about novel food patches transmits through the environment via social connections and suggest how social learning strategies can prevent individuals from being trapped in maladaptive behaviour when wrong information is being provided. I address how individuals balance using social cues versus personal experience at different stages in the acquisition process to efficiently navigate their environment while foraging.

The second part of my thesis focuses on how heterospecific attraction contributes to the maintenance of mixed-species groups, despite potentially conflicting interests among members due to individuals experiencing different relative costs and benefits of associating with heterospecifics. I analysed individual grouping decisions under different social and environmental conditions, and discuss consequences for how individual behaviour translates to the social structure of multi-species societies. In **Chapter 4**, I test if mixed-species flocks of tits are formed based on active preference for heterospecific flocking or passive mechanism such as attraction to food and limited opportunities to forage apart due to strong niche overlap. Using an experimental setting that allows to assess active preference for, or avoidance of heterospecifics, I analysed individual flocking decisions under manipulated resource distributions.

In **Chapter 5**, I analysed long-term observational data from mixed-species foraging flocks and analysed whether individuals express consistent social strategies in their heterospecific

environment, i.e. how individuals differ in their propensity to associate with heterospecifics. A challenge when inferring social preferences from observational data is to separate the contribution of individual social choices from spatial environmental effects. I used spatially-controlled randomisations to separate these factors, and identify the importance of individual social strategies.

Finally, in **Chapter 6**, I provide a synthesis of this study. I summarise the goals and key findings of the individual chapters, and their relationships to one another, and discuss the implications of my work for the broader field of behavioural ecology and community ecology.

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2

Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds

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Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds

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Wintering songbirds have been widely shown to make economic foraging decisions to manage the changing balance of risks from predation and starvation over the course of the day. In this study, we ask whether the communication and use of information about food availability differ throughout the day. First, we assessed temporal variation in food-related vocal information produced in foraging flocks of tits (*Paridae*) using audio recordings at radio-frequency identification-equipped feeding stations. Vocal activity was highest in the morning and decreased into the afternoon. This pattern was not explained by there being fewer birds present, as we found that group sizes increased over the course of the day. Next, we experimentally tested the underlying causes for this diurnal calling pattern. We set up bird feeders with or without playback of calls from tits, either in the morning or in the afternoon, and compared latency to feeder discovery, accumulation of flock members, and total number of birds visiting the feeder. Irrespective of time of day, playbacks had a strong effect on all three response measures when compared to silent control trials, demonstrating that tits will readily use vocal information to improve food detection throughout the day. Thus, the diurnal pattern of foraging behaviour did not appear to affect use and production of food-related vocalizations. Instead, we suggest that, as the day progresses and foraging group sizes increase, the costs of producing calls at the food source (e.g. competition and attraction of predators) outweigh the benefits of recruiting group members (i.e. adding individuals to large groups only marginally increases safety in numbers), causing the observed decrease in vocal activity into the afternoon. Our findings imply that individuals make economic social adjustments based on conditions of their social environment when deciding to vocally recruit group members.

1. Introduction

Many species demonstrate strong temporal behavioural patterns over the course of the day in response to environmental changes such as photoperiod, temperature, food availability, and predation risk [1–3]. Energy management and diurnal foraging patterns depend on an individual's current physiological state, as well as their past and anticipated state [4,5]. For example, foraging activity throughout the day in small wintering songbirds is influenced by the inherent trade-off between risk of starvation and risk of predation; birds must gain enough fat during the day to survive through the night, but this is balanced by the increased predation risks

associated with weight gain and impaired mobility [6–8]. Birds' diurnal changes in body fat, which can be used as a proxy for foraging activity, generally show a sharp increase in mass during early morning hours, to compensate for overnight body fat loss, and another increase in body mass during the hours immediately before roosting [6,7]. The hypothesis that wintering songbirds should delay accumulating fat during the day to lower predation risk suggests that their foraging tactics, and thus their behaviour, should change as their primary concern shifts from avoiding predators to surviving the night ahead. In accordance with this suggestion, birds from winter foraging flocks appear to apply different foraging strategies over the course of the day, prioritizing the detection of food patches in the morning, and exploiting these known patches later in the day, when the cost of exploration is high relative to foraging on a previously identified food source [9].

When searching for food sources, animals can use information generated by the behaviour of others ('social information'), which is usually less costly and faster to acquire than information about the distribution of resources through direct, trial-and-error-based interactions with the environment ('personal information'; [10,11]). However, social information can be less reliable than personal information and might result in sub-optimal behaviour, especially in rapidly changing environments [12–15]. Thus, predictions derived from theoretical models and empirical studies suggest that individuals should rely on social information when personal information cannot be gathered reliably and at a low cost [13,16]. On the other hand, when both types of information are available but in conflict, personal information should be preferred and conflicting social information ignored ([14,17]; but see [18] and [19] for examples of conformist social learning). If availability and reliability of personal information improves with time, owing to accumulated personal experience, animals should reduce their reliance on social information and instead rely on personal information later in the day. Whether the use of food-related social information has such temporal components, shifting over the course of a day in relation to foraging strategies, has yet to be explored.

A parallel decision that some animals appear to make when foraging is whether to actively produce information about the presence of food for others. In many species, vocalizations given upon food discovery attract conspecific and heterospecific foragers, functioning as a form of social recruitment [20]. Recruiting others to a food source provides a range of potential benefits to the caller, including reduced predation risk [21,22], increased inclusive fitness via kin selection [23,24], increased mating opportunities [25,26], or the ability to cooperatively defend the resource [27,28]. However, these benefits diminish with an increase in competition as group size increases, and studies have suggested that individuals make different decisions based on whether recruiting others will lead to an increase in competition [29]. Moreover, calling is a conspicuous behaviour that facilitates prey detection and localization for predators [30,31]. For example, sparrowhawks, *Accipiter nisus*, attacked stuffed models of crested tits, *Parus cristatus*, significantly more often when presented along with playbacks of the species' long-distance calls, compared to when the model was displayed without playbacks [32].

Given these considerations, we expect that the extent to which individuals produce vocalizations which attract group members to a food source ('recruitment calls'), depends not only on levels of competition and predation risk, but also on how the social environment mediates the trade-off between these factors. To understand the interaction between these components, we outline an economic framework that predicts under which social conditions individuals should and should not produce such recruitment calls. First, a solitary forager is expected to produce recruitment calls because it conveys large benefits with regard to relative predation risk, at a comparably small cost of competition: recruiting just one individual will halve the risk of predation, while competition will not be greatly increased if the food resource is shareable. Further, the probability of being heard by another individual or group is high (because there are $N-1$ potential listeners, where N is the local population size), whereas the probability of a predator attack is low (for the same reason, that there are $N-1$ other individuals located elsewhere that could be detected). By contrast, the propensity to vocally recruit group members to a food source should reduce with an increase in foraging group size. An individual that forages in a large group would receive only a slight increase in anti-predator benefits by recruiting an additional group member (because $1/N$ is non-linear, and $1/(N+1)$ is only marginally larger than $1/N$ when N is $\gg 1$), but might suffer from a disproportionate increase in the within-group competition for food. The exact relationship between group size and competition between group members depends on the shareability of the food, while the costs and benefits associated with an increase in foraging group size also depend on an individual's position within the group; access to food and anti-predator effects are higher for dominant individuals in the centre of the group [33–36]. In table 1 we outline the relative costs and benefits of making recruitment calls under different social conditions, allowing us to make predictions about when recruitment calling is expected. Using this framework, we predict that individuals will produce recruitment calls when foraging in a larger group (relative to the current group size) yields a net benefit to the caller.

Here, we propose, and experimentally test, two hypotheses that may lead to temporal variation in the production and use of food-related acoustic information. The 'economic hypothesis' assumes that individuals experience a shift in the costs and benefits of calling owing to a change in group size (as outlined in table 1), which causes a producer-driven reduction of vocal information with increasing foraging group size. Accordingly, if group sizes increase throughout the day, it becomes less beneficial to recruit additional individuals to the foraging group, and consequently fewer calls will be produced later in the day. Alternatively, the 'foraging strategies hypothesis' assumes that a switch in foraging strategies over the course of the day (as demonstrated in [9]) causes individuals to change from using social information in the morning (to find food) to ignoring social information in the afternoon (once personal information about the environment has been accumulated). This hypothesis predicts that call production is reduced in the afternoon as it is no longer effective at recruiting others.

In this study, we test these competing hypotheses using data from mixed-species foraging flocks of tits (*Paridae*). First, we establish how calling patterns in mixed tit flocks vary throughout the day using audio recordings at feeding stations. Next, we explore the underlying causes of temporal variation in calling behaviour. To do so, we set up bird feeders with or without a playback of calls from tit species, either in the

Table 1. Cost–benefit considerations for recruitment calling. (Framework highlighting the shifting costs and benefits associated with competition and safety from predators. When costs are lower than benefits (e.g. when alone or in a small group), individuals should make recruitment calls. By contrast, when individuals are in large groups, adding more individuals to the group will increase competition but provide fewer added benefits, in which case an individual should not recruit. Classification of effects as high or low should be considered in relation to other scenarios.)

potential caller's social context	effect of additional group member (GM)	cost–benefit balance for recruitment calling
alone	very high probability attracting GM	cost $\ll$ benefit
	low competition between GM	
	very high value regarding predation risk	
	low probability of predator attack	
small group	high probability attracting GM	cost = benefit
	increasing competition between GM	
	low value regarding predation risk	
	low probability of predator attack	
large group	low probability attracting GM	cost > benefit
	high competition between GM	
	low value regarding predation risk	
	high probability of predator attack	

morning or in the afternoon, and measured latency until discovery and number of birds visiting the feeder. Given our knowledge of the daily patterns of foraging in wintering songbirds, we can predict that the decisions to produce information about food should also differ throughout the day, mirroring changes in birds' foraging behaviour and social environment. Under the economic hypothesis, we would expect that individuals vocalize less in the afternoon, when group sizes are large and vocalizations might attract predators, but that listeners will respond to experimentally presented calls irrespective of time of day. Under the foraging strategy hypothesis, we would predict that flock members can be attracted by calls given in the morning but not in the afternoon, resulting in a listener-driven reduction in calling over the course of the day.

2. Methods

(a) Study system

The study was conducted in Wytham Woods, Oxford, UK (51°46′ N, 1°20′ W), on a wild population of individually tagged Parid species (blue tit, *Cyanistes caeruleus*; great tit, *Parus major*; marsh tit, *Poecile palustris*). Birds were tagged either as nestlings or as adults, when caught at nest-boxes, or using mist-nets in winter (percentage of the population being tagged was estimated at *ca* 70–80% for the winter seasons 2011–2014: [37]). Each bird was fitted with a unique British Trust for Ornithology (BTO) metal leg ring, and a plastic leg ring carrying a passive integrated transponder (PIT tag, IB Technologies, UK). PIT tags can be read by radio-frequency identification (RFID) antennas attached to bird feeders (Dorset ID, Netherlands), providing a timestamp of feeder visits.

Tits in this population are almost always found in mixed-species flocks [38,39], and information is readily transferred across species [40,41]. Thus, we analyse our data at the community level. However, we also report analyses of species-level patterns in the electronic supplementary material for two main reasons: first, because marsh tits are food-caching birds, they could express different behavioural strategies to blue tits and great tits (cf. [42]). Second, not all species are equally represented in the population, with great tits being most numerous across all experimental sites in this study (mean $\pm$ s.d.: 50.1 $\pm$ 14.2%), followed by blue tits (36.0 $\pm$ 10.6%), whereas marsh tits (14.0 $\pm$ 10.3%) are scarcer despite being found throughout the woodland.

(b) Measuring diurnal variation in vocalizations at feeding stations

Over the course of two winters, we ran 18 independent feeder discovery trials at unique sites across the study area (10 trials in February to March 2016, eight trials in February to March 2017). At each site, we deployed feeding stations after sunset on the evening before the trial to ensure natural discovery of the novel feeder the next morning (following [9,40,43]). Feeders were filled with sunflower seeds, and RFID antennas automatically recorded the time and identity of PIT-tagged birds for each feeder visit. We recorded vocalizations at each feeder throughout the length of the trial, i.e. from sunrise to sunset, using small voice recorders with omnidirectional microphones (VN-741 PC Digital Voice Recorder, Olympus, Japan) attached to the feeder.

(c) Playback experiments

(i) Experimental procedure

We conducted playback experiments and control trials at 12 sites during the non-breeding season in February and March 2017. The discovery and experimental sites were distinct, widely distributed across the study area (separated by $\geq$200 m), and had never previously had feeders present. We used a fully balanced experimental design, with each site used for four conditions in random order: playback morning (AM), control AM, playback afternoon (PM), control PM. Morning experiments were run from 08.30 onwards, and afternoon experiments from 14.30. Playbacks were broadcast at 72 $\pm$ 3 dB (measured with a Maplin, UK, ST-85C sound level meter at 1 m distance), using a loudspeaker (Road Rocker™, Ion Audio LLC., USA) connected to a Raspberry Pi (Raspberry Pi Foundation, UK), and set up on a platform of 2 m height, approximately 3 m from the feeder. By running control trials using a silent dummy loudspeaker, we account for potential effects on feeder discovery owing to differing activity levels, foraging strategies, or flock sizes in the morning and the afternoon (see [9]). For each trial, we temporarily deployed a bird feeder providing sunflower seeds, and recorded latency

until feeder discovery and number of birds visiting. Feeder visits of PIT-tagged birds (time and identity) were recorded automatically through RFID antennas attached to the feeder, and trials were additionally video recorded. Trials started with the delayed, automated onset of the playback, or after an equal delay in the control trials, when the experimenter finished setting up the equipment and left the site. While setting up the experiment, no bird could be seen or heard at the experimental site. Each trial lasted for 120 min and feeders were removed quickly afterwards. We waited a minimum of two days (mean ± s.d.: 4.6 ± 2.09 days) after a feeder was discovered before conducting the next trial at that given site.

(ii) Stimulus design

Previous work in our system showed that any of the species (blue tits, great tits, and marsh tits) can be the first to discover food sources [9,39,41,44]. Therefore, we created mixed-species stimuli by combining chirp calls of blue tits, chaffinch-like chirp calls of great tits, and chick-a-dee-like dä/D calls of marsh tits (classification and naming of call types following [45], figure 2). Audio files and spectrograms of the call types can be found in the electronic supplementary material, figure S4.

Food-recruitment calls have been described for closely related species (black-capped chickadees, *Parus atricapillus*: [46]; Carolina chickadees, *Poecile carolinensis*: [47]; willow tits, *Poecile montanus*: [48]), but there is no evidence that the species concerned in our study make distinct food-related recruitment calls. However, their calls adapt across a variety of social contexts, including flock movement and foraging [45,49], and specifically the number of notes included in a call appears to provide context-dependent information. For example, dä/D calls of marsh tits given in predator demonstration trials have more notes than dä/D calls recorded during foraging [45]. For the playback stimuli, we used calls that consisted of mean ± standard deviation (s.d.): 3.1 ± 1.3 notes, reflecting the characteristics of calls naturally occurring in a foraging context for this population (mean number of chirp notes in blue tit and great tit calls: 2.4 ± 1.7 s.d., mean number of dä/D-notes in marsh tit calls: 2.6 ± 1.8 s.d.; analysis of 577 chirp calls and 65 dä/D calls recorded at feeding stations during the first phase of this study; see the electronic supplementary material, table S1 for mean number of notes per call recorded during predator presentation experiments, data from [45]).

We selected calls from high-quality recordings of natural calling sequences that were published under a Creative Commons license on www.xeno-canto.org, an online archive of bird calls and birdsongs. For editing the recordings and generating stimulus files, we used Audacity® recording and editing software [50]. Recordings were bandpass-filtered to reduce low-frequency background noise, and we normalized volume levels to peak-amplitude. We created twelve unique 10 min stimuli (one for each experimental site), by combining four calls from each species in randomized order. The stimulus was presented twice during an experimental session, once at the start of the trial, and once one hour after the onset of the first presentation. For a schematic of the stimuli see the electronic supplementary material, figure S1.

(d) Data analysis

(i) Audio recording at feeding stations

Recordings were manually inspected for calls from tits using sound analysis program PRAAT [51]. We only considered calls given within very close proximity to the feeder and immediately before or after a bird landed on the feeder (which was detectable because landing on the feeder was audible on the recording). Following Carlson *et al*. [45], we classified call types based on structural differences that are clearly visible in the spectrograms. We summarized the number of calls given for each hour of daylight, the number of individual birds visiting the feeder during that hour, and the total number of feeder visits per hour for each site, and calculated mean values and standard errors for all measures across all trials ($n = 18$). We then compared the number of calls made per visit for each hour of the day using the same permutation test as Farine & Lang [9]. We first calculated the difference between the mean calls per visit for morning hours (before 12.00) to the mean calls per visit for afternoon hours (after 12.00). We then compared this observed difference to a distribution of 10 000 differences generated by randomizing the 'hour' column in our dataset (restricted within trial). The observed difference was significant if it was larger than 95% of the differences generated by the randomized datasets [52].

(ii) Playback experiment

Feeders were usually discovered within one hour of deployment in the majority of trials (in 38 of 48 trials; in 7 of 48 trials the feeder remained undiscovered during the 2 h deployment). Thus, we analysed behavioural responses to the experimental treatments during the first hour of the trial. We measured latency to feeder discovery, initial recruitment (number of individuals logged at the feeder within the first two minutes of discovery), and total number of unique individuals (using PIT-tag data) that visited the feeder over the course of the trial (60 min). Latency to feeder discovery was measured as the time elapsed between the onset of the trial and the first recorded visit to the feeder. Video recordings were used to ensure we had accurate estimates of the time that the first bird recorded automatically was indeed the first individual taking a seed across all trials. When no bird visited the feeder within the first hour of the trial ($n = 10$), we censored the latency by setting it to 60 min. Owing to technical problems with the automated logging of tagged birds in five trials, we used a restricted dataset ($n = 43$) for analysing the number of birds visiting the feeder, both during the initial recruitment and the 60 min trial.

The balanced design of the playback experiment allowed us to test our hypothesis regarding the use of social information across the day, by contrasting responses to the same social stimulus in two contexts (morning/AM and afternoon/PM). To estimate the effect of time of day (AM, PM) and experimental treatment (playback, control) on the three response measures, we used generalized linear mixed models (GLMMs) with gamma distribution to overcome over-dispersion in skewed latency data [53], and Poisson error distribution in models with count values (i.e. number of birds). As the effect of playbacks might have been different for morning and afternoon trials, we included an interaction term (time of day * treatment) as fixed effect. However, for simplification of the final models, we removed nonsignificant interactions [54]. We included trial order (i.e. experimental day, 1–4) as a main effect to account for any habituation over the course of the trials. To factor in non-independence of repeated trials at the same site, we included experimental site as a random effect in all models. We additionally conducted all three models analysing birds' response measures separately for each species, using the same methods as described above on species-specific subsets of the data. All tests were two-tailed and significance levels set at 0.05, and models were fitted in R (v. 3.1.2; [55]) using the glmer function in the lme4 package [56].

3. Results

(a) Diurnal patterns of vocal and foraging activity at feeding stations

Feeders were usually discovered within the first hours after sunrise (median [first quartile, third quartile]: 27 [13.5, 60.8]

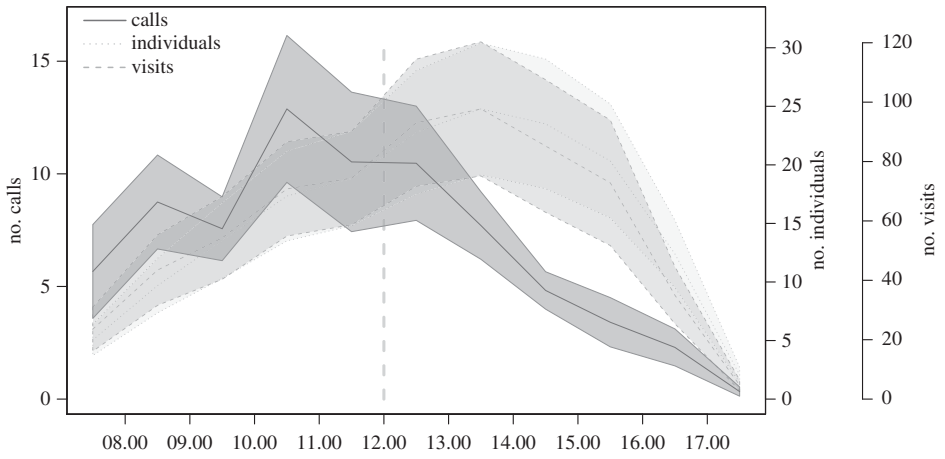

Figure 1. Diurnal patterns at feeders. Mean number of calls given per hour (solid line), and mean number of individuals and feeder visits recorded at a feeder (dotted and dashed line respectively). Shaded areas are standard errors of means, across all 18 sites. Data on number of calls show a clear divergence with number of visits after 12.00 (vertical line).

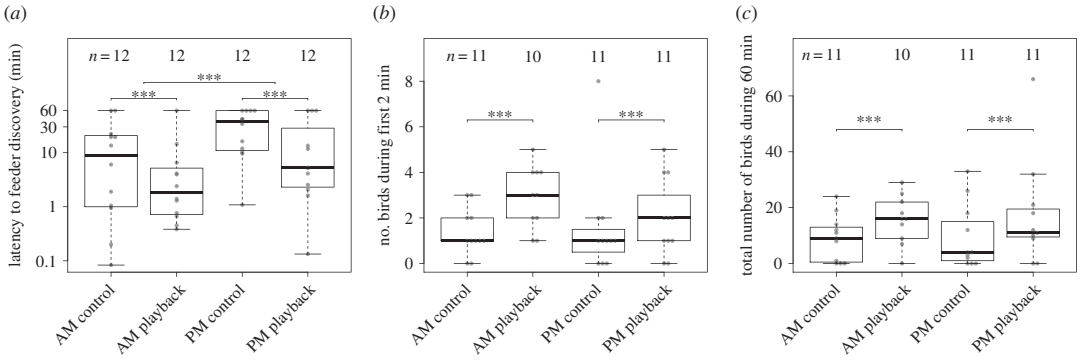

Figure 2. Responses to the four experimental treatments: (*a*) latency to feeder discovery (note log scale), (*b*) initial recruitment, and (*c*) number of birds visiting during the first hour of the trial. Boxplots show the median and interquartile range (IQR), whiskers represent 1.5 × IQR. Dots represent individual trials, number of trials included in the analysis is given for each experimental treatment respectively. Starred bars indicate significant differences (p-values <0.001) between treatments based on outcomes of the GLMMs.

minutes after sunrise; times for sunrise were extracted from www.timeanddate.com). Vocal activity at these feeders was highest during the morning hours and then decreased throughout the day, whereas the number of individuals and the number of feeder visits increased into the afternoon, peaking at about 13.00, and then decreasing into the evening, presumably as individuals departed for roosting in the evening (figure 1). We found that birds made significantly more calls per visit in the morning hours than in the afternoon hours (PM-AM: −0.24, $P_{rand}< 0.001$, 95% range of differences from randomized data: −0.11, 0.10; see also the electronic supplementary material, figure S2). We provide additional details on the diurnal patterns of vocal activity in the electronic supplementary material, including temporal pattern and spectrograms of the main call types recorded (electronic supplementary material, figures S2–S4). Although we ran 18 replicates within the same woodland (10 trials in 2016, eight trials in 2017), the majority of individuals were observed at only one trial (electronic supplementary material, figure S5).

(b) Experimental test of the hypotheses

(i) Latency to feeder discovery

Feeders were discovered significantly more quickly in the playback treatment than in control trials (table 2); compared to the control, latency to feeder discovery was on average five times shorter with a playback in morning trials (AM control median: 9.8 min, IQR: 19.81 min; AM playback median: 1.9 min, IQR: 4.60 min; figure 2*a*), and about seven times shorter in afternoon trials (PM control median: 37.85 min, IQR: 48.94 min; PM playback median: 5.25 min, IQR: 34.42 min; figure 2*a*). Irrespective of playback treatment, time to discovery was generally shorter when feeders were deployed in the morning than in the afternoon (table 2). The chronological order of trials had a comparatively low, reversed, effect on the latency: latencies were longest in first trials and shorter when birds had previously used a feeder at that site (table 2), and the effect size was approximately half that of the experimental treatment variables.

Table 2. Results of generalized linear mixed models. (Summary of estimated effects on the three response variables describing feeder discoveries, by the fixed effects of time of day (PM relative to AM), treatment (playback relative to silent control), and order of trial at a given site (1st, 2nd, 3rd, or 4th). Experimental site was included as a random term in all models. The degrees of freedom (d.f.), coefficient, standard error (s.e.), *z*-statistic and standard *p*-value are provided.)

	response variable			
fixed factors	d.f.	coefficient ± s.e.	*z*	*p*
latency first bird				
intercept	1	8.03 ± 0.45	17.92	<0.001
time of day	1	1.03 ± 0.30	3.40	<0.001
treatment	1	−1.17 ± 0.31	−3.74	<0.001
order of trial	1	−0.59 ± 0.13	−4.58	<0.001
initial recruitment				
intercept	1	1.25 ± 0.23	5.41	<0.001
time of day	1	−0.09 ± 0.09	−0.97	0.33
treatment	1	0.52 ± 0.09	5.80	<0.001
order of trial	1	0.31 ± 0.04	7.51	<0.001
number of birds				
intercept	1	1.16 ± 0.28	4.18	<0.001
time of day	1	−0.09 ± 0.09	−1.06	0.29
treatment	1	0.53 ± 0.09	5.88	<0.001
order of trial	1	0.31 ± 0.04	7.37	<0.001

(ii) Initial recruitment

The number of individuals that visited the feeder in the first 2 min after discovery was significantly greater for the playback treatment than for the control treatment (table 2; figure 2*b*), but initial group sizes did not differ between feeders discovered in the morning and those discovered in the afternoon (table 2). Over the course of the experiment, when multiple trials had been conducted at a given site, more individuals were recorded in the first 2 min period, as indicated by a positive effect of trial order (table 2).

(iii) Number of birds

The total number of unique individuals recorded at a feeder over the first hour of the trial was significantly higher in playback trials than in control trials (table 2; figure 2*c*). This pattern was unaffected by time of the day, i.e. the number of unique individuals did not differ significantly between morning and afternoon trials (table 2). Order of trials on the number of unique individuals again had comparatively small effect: subsequent trials had higher numbers of individuals visiting the feeder than first trials (table 2). Despite running four treatments in each of the 12 replicated sites, nearly 80% of all individuals were only ever detected at a single site (electronic supplementary material, figure S5).

(iv) Species-level patterns

Species-level analyses of the responses to playbacks revealed nearly identical results to the composite results (electronic supplementary material table S2 and figure S6). In all three species, the direction of the effect of treatment had the same direction with similar effect sizes. Because the marsh tit population was much smaller, owing to their lower relative abundance in the population, the effect sizes for the number of recruits (initial and total) are lower than for blue tits and great tits, although the difference may be less than expected given the difference in population sizes. The effect of time of day on latency to arrive appears to be stronger for blue tits than for other species.

4. Discussion

We present data revealing diurnal dynamics of vocal behaviour and foraging activity in wintering mixed-species foraging flocks of tits, and experimentally test predictions from two hypotheses about the underlying causes. By recording vocalizations given at feeding stations over the course of the day, we find clear temporal variation in call rate; vocal activity was highest in the morning and decreased in the early afternoon. By contrast, group size continued to increase until late in the day. In the second part of the study we experimentally evaluate the recruitment function of these calls, and whether their value changes over the course of the day. Our playback experiment shows that social information results in a faster discovery of resources and rapid accumulation of individuals at food patches. This suggests that calls given at the feeders indeed have a recruitment function similar to food-associated vocalizations in other species (reviewed in [20]), including closely related Parid species [46–48]. However, by using a balanced experimental design, our results also show that birds use social information about novel food patches equally throughout the day. Thus, our data support the economic hypothesis, which predicts that individuals reduce calling in the afternoon owing to the reduced benefits of recruitment, and not the foraging strategies hypothesis, which suggests that birds stop calling in the afternoon because social information is ignored.

The notion that birds will reduce their propensity to recruit flock members with increasing group size has been reported in other avian species on a much smaller timescale, analysing changes in calling behaviour as flocks establish at bird feeders. Calling rate at feeders was found to be inversely proportional to foraging flock size in house sparrows, *Passer domesticus* [29] and willow tits [48], and in Carolina chickadees, chick-a-dee calls given by the first bird to arrive at a new food source contain more D-notes and were found to attract conspecifics faster than calls of the subsequent individuals [47]. Spider monkeys, *Ateles geoffroyi*, adjust their food calling not only to the number of conspecifics present but to their social status, and thus manipulate the size and social composition of foraging subgroups [57]. Together, these studies provide additional support for the economic hypothesis for recruitment, suggesting that the decisions to make recruitment signals are subject to the social environment, and specifically group size.

Our balanced playback experiments enabled us to directly compare birds' responses to standardized stimuli at different times of the day, and allowed us to contrast the economic hypothesis against an alternative hypothesis that could generate similar patterns of calling that are related to individuals' foraging strategies over the course of the day. Previous work (e.g. [9]) suggested that wintering songbirds have different foraging strategies in the morning and afternoon, and also reported an increase in flock size over the course of the day. Using experimental playbacks of recruitment calls, our current study demonstrates that tits will readily use vocal information to improve food detection at all times of the day: playing calls from blue tits, great tits, and marsh tits near bird feeders significantly reduced the latency to feeder discovery, facilitated recruitment of flock members, and increased the total number of birds attracted to food patches irrespective of the time of the day. The positive effect of broadcasting vocalizations on the recruitment of flock members was evident on the significantly higher number of individuals discovering the food source in the first 2 min after the original discovery, suggesting that it operates as an effective mechanism for increasing group size. By contrast, our results do not support the hypothesis that vocalizations are ignored in the afternoon owing to a switch in foraging strategies. The species-level analyses revealed almost identical results to the pooled analyses; all species recruited significantly faster under playback treatments in both the morning and in the afternoon (electronic supplementary material, figure S6). Thus, our experimental data support the framework we laid out in which individuals should make economic decisions (table 1).

Under the economic hypothesis, one reason for not making recruitment calls in the afternoon is that there are fewer potential flock members available to recruit in the local environment. While we found similar effects of the playback on the three response variables in the afternoon as in the morning, the latencies to feeder discovery were generally longer in afternoon trials, in both control and playback trials. This is likely to be because of individuals accumulating at alternative food sources over the course of the day (*sensu* [44]), resulting in a general decrease in movement between food patches later in the day (a pattern observed by [9]). However, as we have no indication that tits ignore vocalizations in the afternoon (as would be expected under the foraging strategies hypothesis), our findings suggest that recruitment calling could be less efficient at eliciting a response in the afternoon owing to a reduced pool of potential recruits. Thus, irrespective of the current group size, the benefits of recruiting, i.e. attracting group members, will be reduced relative to the risk of attracting a predator.

Many animals make signals in a social context, and recruitment calling is particularly interesting as it could be an important mechanism in underpinning fission–fusion dynamics, since individuals' decisions about when to recruit others has implications for group formation. However, it is not always clear what mechanisms underlie the decision to make a signal or not. We laid out a simple framework (table 1) that uses the concepts of optimality to make predictions about when recruitment calls should be made. This framework considers group size, and the impact of group size on competition and predation. Such an approach is powerful because the predictions can be tested relatively easily, and it provides a useful baseline on which future theoretical models can be built.

Ethics. This study was conducted in accordance with the Guidelines for the treatment of animals in behavioural research and teaching of the Association for the Study of Animal Behaviour [58]. Experimental playback procedures were conducted completely non-invasively. All handling and ringing of birds was conducted by experienced ringers, licensed by the BTO, and approved by the Local Ethical Review Panel of the University of Oxford.

Data accessibility. Data and code used for analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.21b52d0 [59].

Competing interests. We declare we have no competing interests.

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SUPPLEMENTARY INFORMATION

Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds

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Composition of playback stimuli

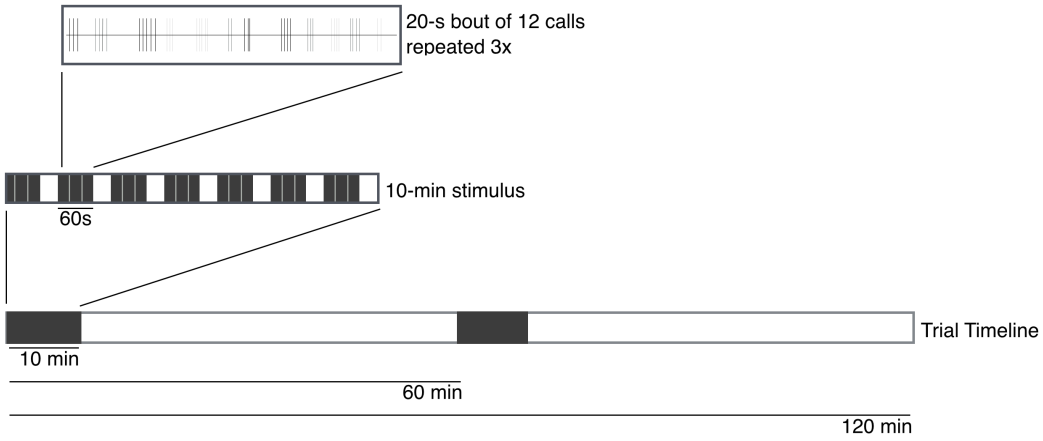

Figure S1. Schematic timeline of playback trials. For each stimulus, we combined four calls from each of the three species to a 20-s calling sequence with a random succession of calls. This 20-s sequences was repeated three times, creating a one-minute bout of calls. Separated by 30-s periods of white noise, the one-minute bout was repeated seven times to create a 10-min stimulus. White areas represent silent periods.

Vocal behaviour at feeders: call rate

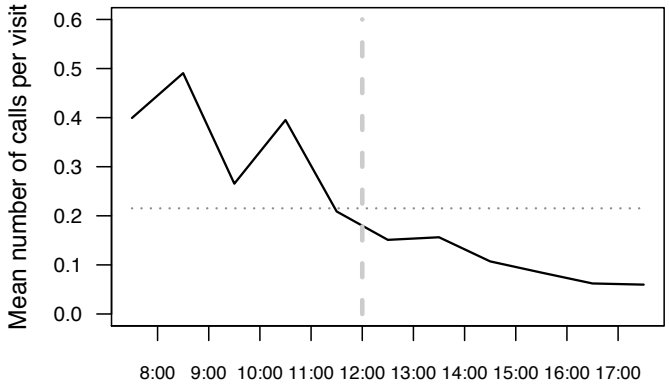

Figure S2. Hourly call rates measured as number of calls per feeder visit. The mean number of calls per visit declined throughout the day. The black line is the observed calling rate (n=18 trials), the dotted horizontal line is the expected calling rate. The calling rate before 11:00 h is always higher than the random rate and the mean value in all afternoon hours.

Vocal behaviour at feeders: number of notes and number of feeder visits

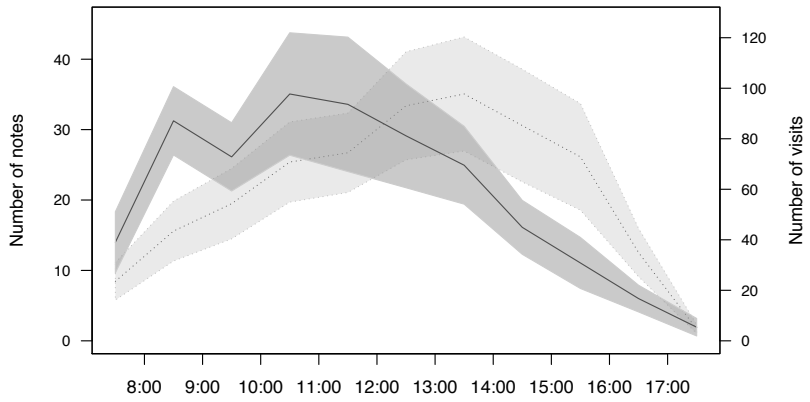

Figure S3. Diurnal patterns at feeders. Vocal activity at the feeder measured as sum of notes of all calls (solid line), and foraging activity measured as hourly mean number of feeder visits (dotted line); shaded areas are standard errors of respective means, n=18 trials. Production of acoustic information decreases into the afternoon, both when measured as number of calls (Figure 2 in the main text) and number of notes per hour.

Vocal behaviour at feeders: call type pattern

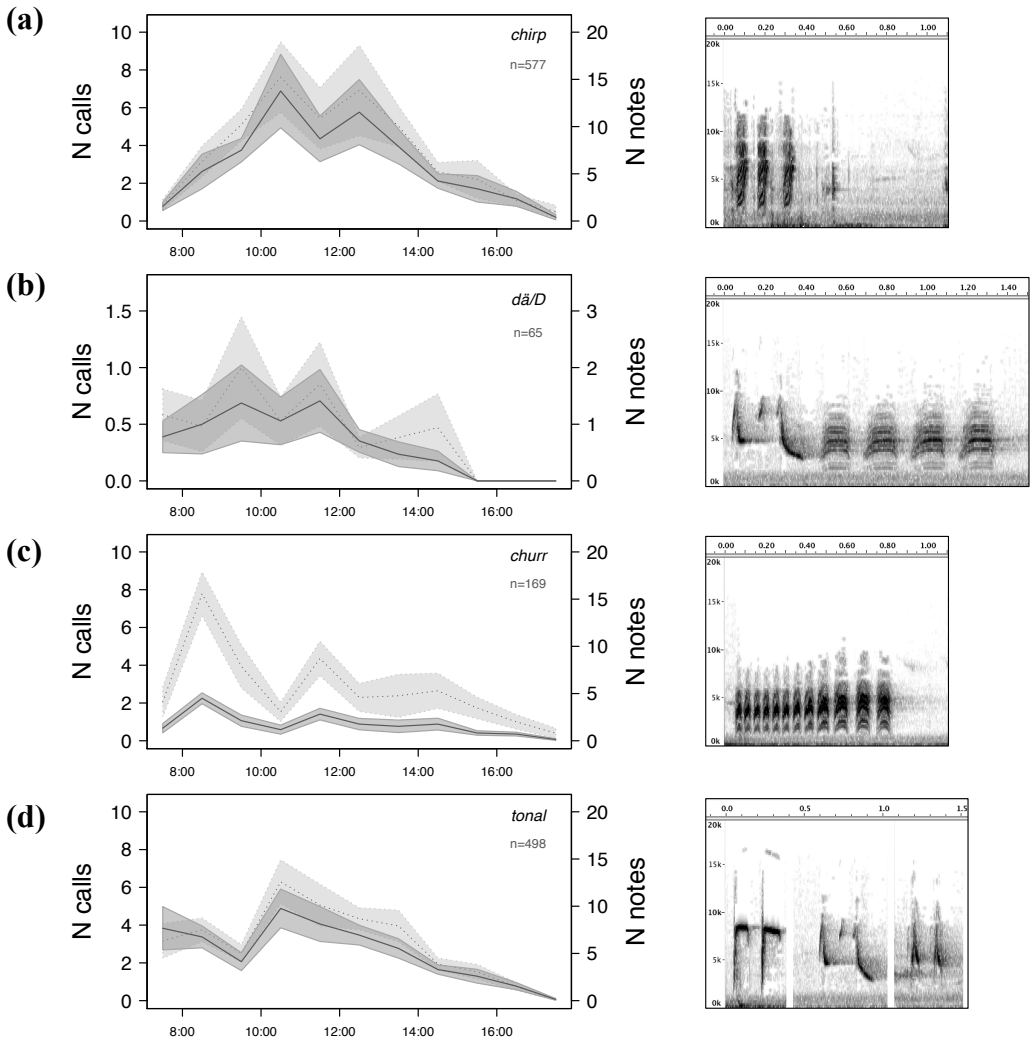

Figure S4. Main call types recorded at feeding stations: temporal pattern and spectrograms. Mean number of calls (solid line) and notes (dotted line) recorded per hour and standard errors (shaded area) across all 18 trials for (a) *chirp* calls, (b) *dä/D*-calls, (c) *churr* calls, and (d) calls only consisting of tonal elements. Total number of calls recorded: 577 *chirp* calls, 65 *dä/D* calls, 169 *churr* calls, 498 *tonal* calls. For classification and naming of call types, we followed a recent overview of call types in British tits (Carlson et al. 2017). An audio file with example calls of each call type is available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.21b52d0.

For each plot, the y-axes are in a ratio of 1:2 (number of calls: number of notes). Only the *churr* call, which was not used in the playback, shows a marked variation in number of notes per call throughout the day: *churr* calls given in the early morning hours had more notes than *churr* calls given in the afternoon.

Number of notes in chirp and dä/D calls (data from Carlson et al. 2017)

Table S1: Number of notes per *chirp* and *dä/D* call in different contexts. Mean number of *chirp* notes and mean number of *dä/D* notes in blue tit, great tit, and marsh tit calls, given with standard errors and sample sizes in brackets, recorded during presentation of robotic stuffed taxidermy mounts. Data underlying Carlson, N. V., Healy, S. D., & Templeton, C. N. 2017. A comparative study of how British tits encode predator threat in their mobbing calls. Animal Behaviour, 125, 77-92, DOI: 10.1016/j.anbehav.2017.01.011, and was kindly provided by Nora Carlson.

	Blue tit *chirp* calls	**Great tit *chirp* calls**	**Marsh tit *dä/D* calls**
Non-threat control (Grey partridge, *Perdix perdix*)	1.72 ± 0.15 (124 calls, 41 trials)	0.59 ± 0.10 (36 calls, 35 trials)	0.85 ± 0.30 (12 calls, 7 trials)
High-threat predator (Sparrowhawk, *Accipiter nisus*)	0.50 ± 0.04 (191 calls, 43 trials)	0.04 ± 0.01 (24 calls, 42 trials)	5.22 ± 0.33 (158 calls, 9 trials)

Independence of trials

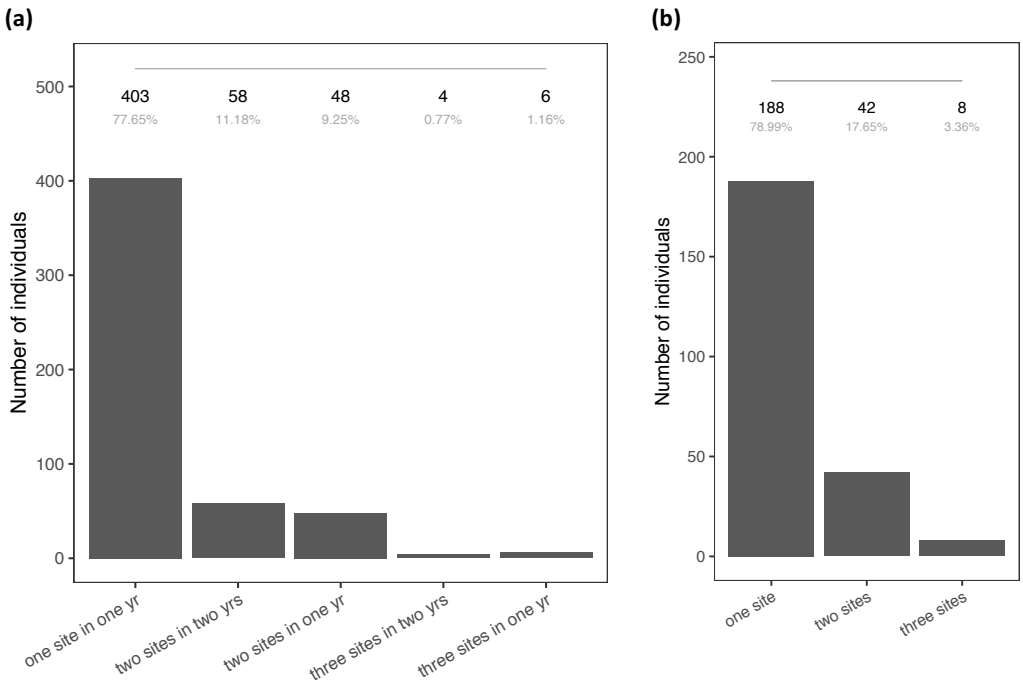

Figure S5. Number of individuals that were recorded at one or multiple sites in (a) feeder discovery trials and (b) playback experiments. Feeder discovery trials were conducted at 18 unique sites, in two consecutive winters (10 sites in early 2016 and 8 sites in early 2017). In (a), bars represent the number of individuals that were recorded at only one site, at two sites but once in 2016 and once 2017, at two sites within the same year, or three times in total. The playback experiment was conducted at twelve sites across the woods. In (b), bars represent the number of individuals that were recorded at either one, two, or three different sites. The total number of individuals recorded in the experiment is indicated by the grey line above the bars, black numbers give the total number of individuals recorded per category, percentages are given in grey.

The majority of individuals were recorded at only one site for both feeder discovery trials and playback experiments. Across the 18 feeder discovery trials, most individuals were recorded either at only one site throughout the study, or at two sites in total but only one in 2016 and 2017 each (89%, or 461 of 519 unique individuals recorded in total fall into these two categories). Across the 12 sites used for the playback experiment, most individuals were recorded at only one site (79%, or 188 of 238 individuals recorded in total). From those individuals that visited more than one playback site, only about half of the birds experienced the same condition twice (24 of the 50 birds that were recorded at more than one site; number of), and no individual experienced the same experimental condition more than twice.

Response to playbacks: species-level pattern

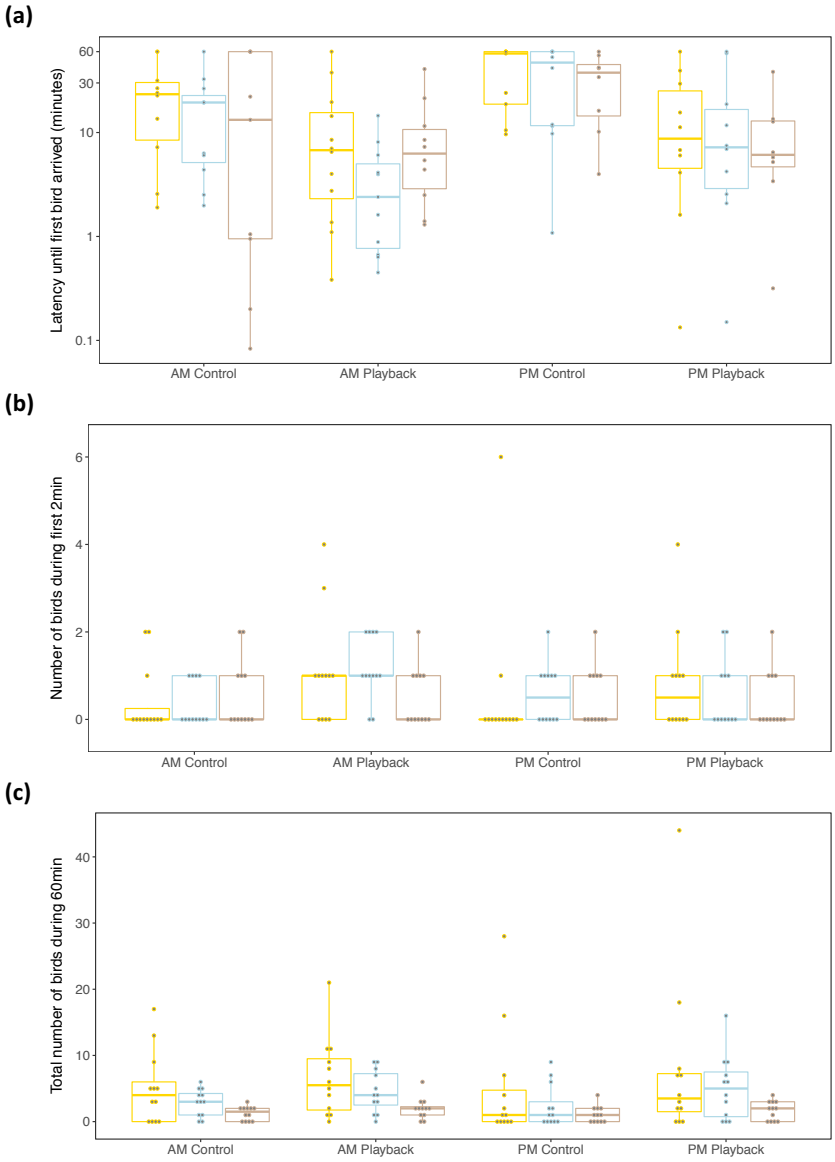

Figure S6. Response to the four experimental treatments, measured as (a) latency to feeder discovery (note log scale), (b) recruitment to feeder, and (c) number of birds visiting during the one-hour long trial. Data points from individual trials, with boxplots showing median and interquartile range (IQR), and whiskers represent 1.5 x IQR. Results are presented for the four experimental treatment conditions, and separately for each species, as indicated by colours (yellow: great tit, blue: blue tit, brown: marsh tit).

Table S2. Results of GLMMs analysing the response to playback trials separately for each species. Estimated effects of fixed factors (time of day: PM relative to AM, treatment: playback relative to silent control, and order of trial at a given site: 1st, 2nd, 3rd, or 4th) on the three measures describing the response to playback trials. Experimental site was included as a random term in all models. Model outputs provided are: degrees of freedom (df), coefficient and standard error (SE), z-statistic, and standard P-value. Significant terms (P-value < 0.05) are indicated in bold.

Species	Response Variable ~ Fixed Factors	df	Coefficient ± SE	*z*	*P*
Great Tit	Latency First Bird				
	Time of Day	1	0.42 ± 0.31	1.36	0.172
	Treatment	**1**	**-0.92 ± 0.32**	**-2.89**	**0.004**
	Order of Trial	**1**	**-0.32 ± 0.14**	**-2.22**	**0.026**
	Recruitment				
	Time of Day	1	-0.20 ± 0.36	-0.56	0.572
	Treatment	**1**	**0.76 ± 0.37**	**2.06**	**0.039**
	Order of Trial	**1**	**0.38 ± 0.17**	**2.26**	**0.024**
	Number of Birds				
	Time of Day	1	0.03 ± 0.12	0.23	0.815
	Treatment	**1**	**0.52 ± 0.12**	**4.22**	**< 0.001**
	Order of Trial	**1**	**0.35 ± 0.06**	**6.22**	**< 0.001**
Blue Tit	Latency First Bird				
	Time of Day	**1**	**1.02 ± 0.28**	**3.59**	**< 0.001**
	Treatment	**1**	**-1.39 ± 0.27**	**-5.13**	**< 0.001**
	Order of Trial	**1**	**-0.33 ± 0.13**	**-2.52**	**0.011**
	Recruitment				
	Time of Day	1	-0.25 ± 0.36	-0.70	0.481
	Treatment	1	0.65 ± 0.37	1.74	0.082
	Order of Trial	1	0.18 ± 0.16	1.10	0.270
	Number of Birds				
	Time of Day	1	0.00 ± 0.15	0.20	0.984
	Treatment	**1**	**0.60 ± 0.15**	**3.85**	**< 0.001**
	Order of Trial	**1**	**0.21 ± 0.07**	**3.12**	**0.002**
Marsh Tit	Latency First Bird				
	Time of Day	1	0.22 ± 0.39	0.56	0.576
	Treatment	**1**	**-1.00 ± 0.39**	**-2.60**	**0.009**
	Order of Trial	1	-0.18 ± 0.19	-0.96	0.338
	Recruitment				
	Time of Day	1	-0.16 ± 0.41	-0.39	0.696
	Treatment	1	-0.20 ± 0.42	-0.49	0.623
	Order of Trial	**1**	**0.38 ± 0.19**	**1.98**	**0.047**
	Number of Birds				
	Time of Day	1	-0.16 ± 0.24	-0.70	0.486
	Treatment	1	0.44 ± 0.24	1.82	0.069
	Order of Trial	**1**	**0.22 ± 0.11**	**2.04**	**0.041**

The three species show similar behavioural responses to the four experimental treatments. Compared to silent control trials, feeders were discovered earlier and by more individuals during playback trials, and the effect of playback was independent of time of the day (AM or PM). Note that the three species differ in their relative abundance across the population, and different numbers of individuals per species were recorded at experimental sites: mean number of great tits: 24.4 ± 7.4 SE individuals, blue tits: 14.8 ± 2.9 SE individuals, marsh tits: 6 ± 0.9 SE individuals. Too few observations of the less abundant species might not allow to properly investigate effects on number of individuals.

3

Information use in foraging flocks of songbirds – no evidence for social transmission of patch quality

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Information use in foraging flocks of songbirds – no evidence for social transmission of patch quality

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HIGHLIGHTS

- Songbirds used social information to find food.
- Social connections predicted patch discovery, i.e. order of arrival of individuals.
- Upon discovery, individuals gathered personal information about patch quality.
- Social and personal information is used at different phases while foraging.
- The relative costs of social and personal information predict information use.

ABSTRACT

Animals use behavioural cues from others to make decisions in a variety of contexts. There is growing evidence, from a range of taxa, that information about the locations of food patches can spread through a population via social connections. However, it is not known whether information about the quality of potential food sources transmits similarly. We studied foraging behaviour in a population of wild songbirds with known social associations, and tested whether flock members use social information about the profitability of patches to inform their foraging decisions. We provided artificial patches (ephemeral bird feeders) that appeared identical but were either profitable (contained food) or unprofitable (contained no food). If information about patch profitability spreads via social associations, we predicted that empty feeders would only be sampled by individuals that are less connected to each other than expected by chance. In contrast, we found that individuals recorded at empty feeders were more closely associated with each other than predicted by a null model simulating random arrival of individuals, mirroring pattern of

increased connectedness among individuals recorded at full feeders. We then simulated arrival under network-based diffusion of information, and demonstrate that the observed pattern at both full and empty feeders matches predictions derived from this post-hoc model. Our results suggest that foraging songbirds only use social cues about the location of potential food sources, but not their profitability. These findings agree with the hypothesis that individuals balance the relative economic costs of using different information, where the costs of personally sampling a patch upon arrival is low relative to the cost of searching for patches. This study extends previous work on information spread through animal social networks, by suggesting important links between how individuals use information at different stages of the acquisition process and the emerging population-level patterns of patch use.

Keywords: collective animal behaviour, economic decision-making, group foraging, local enhancement, Paridae, social information, social network

INTRODUCTION

Animals can learn about their environment by observing others. Socially-acquired information involves any information gained through social processes, whether extracted from actively produced signals, or (inadvertent) cues provided by others' behaviour and its consequences (Danchin et al. 2004; Smidt et al. 2010). Use of social information has been demonstrated in a wide variety of contexts including habitat choice (Forsman et al. 1998), assessing predation risk (Dawson & Chittka 2014), finding food (Tóth et al. 2017), and learning which food to avoid (Van de Waal et al. 2013; Thorogood et al. 2018). Social information about the availability of food is particularly valuable in unpredictable ephemeral environments (Baude et al. 2008; Boyd et al. 2016) when acquiring personal information about the environment can be costly in terms of time and energy (Valone & Templeton 2002; Kendal et al. 2005). Models assuming perfect information-sharing among group members suggest that groups have a higher searching efficiency than individuals, resulting in improved patch-finding rate with increased group size, and that groups are more efficient in patch assessment, reducing the time spent in unprofitable patches (e.g., Clark &

Mangel 1986; Ranta et al. 1993). However, information acquired through personal experience can be more accurate, or relevant, than social information. For example, individuals can differ in their preferences or needs with regard to resource quality, and observing one individual choose, or reject, a patch could yield incorrect information to the observer. Using social information could also represent an ecological trap (Schlaepfer et al. 2002)—if many patches are unprofitable, it could cause individuals to spend more time finding food. Thus, when faced with a trade-off between gathering more accurate (personal) information or cheaper (social) information, foragers should use social information when personal information cannot be gathered reliably at a low cost, and otherwise rely on personal experience (Kendal et al. 2005; Galef 2009; Czaczkes et al. 2019).

Studies across a range of taxa have found that information about the location of food patches spreads through a population via social connections, i.e. individuals are more likely to discover novel resources that are widely dispersed throughout the landscape when they are socially connected to knowledgeable conspecifics or heterospecifics (e.g., Aplin et al. 2012; Webster et al. 2013; Farine et al. 2015a; Jones et al. 2017; Tóth et al. 2017). Further, birds foraging within patches have been found to move to areas of the patch containing the largest proportion of the flock (Farine et al. 2014). Together, these results suggest that songbirds use social information both when finding patches, and when deciding where to forage within a patch. However, it is not always clear what cues animals are responding to, or whether information is being transmitted between individuals, because different social and asocial mechanisms can lead to similar pattern of apparent spread of information.

Identifying what information individuals acquire and use is important for understanding social influences on foraging (Galef & Giraldeau 2001). For example, it may not be immediately obvious whether individuals arriving at a new resource discovered the patch together (i.e., simultaneously), or whether information is being transferred from individuals that are knowledgeable of the availability of resources to naïve individuals. To differentiate the effect of collective movement from social transmission of information about the patch location, some studies have compared the

order in which individuals arrived at foraging patches with the order of arrival at control patches (Atton et al. 2012), while others adjusted their analysis to exclude individuals that arrived within a short period of time when estimating information transmission rates (e.g., Aplin et al. 2012, Farine et al. 2015a, Firth et al. 2010). Similarly, individuals might use personal or social information to assess the quality or profitability of foraging patches. There is mixed evidence on whether individuals determine foraging patch quality from the behaviour of others; the use of social information in this context has been reported for European starlings, (*Sturnus vulagaris*, Templeton & Giraldeau 1995), red crossbills, (*Loxia curvirostra*, Smith et al. 1999), and three-spined sticklebacks (*Gasterosteus aculeatus*, Coolen et al. 2003), but there was no evidence this was the case in studies of European blackbirds (*Turdus merula*, Smith et al. 2001) or nine-spined sticklebacks (*Pungitius pungitius*, Coolen et al. 2003). Further, it is not known whether information about patch quality transmits via social connections, in a similar fashion to the way information about the location of foraging patches has been shown to spread through populations.

Here, we study foraging behaviour in mixed-species flocks of tits to test whether individuals use social information when assessing foraging patches. Tits and other species from the Paridae family provide a good system for information diffusion experiments, because they readily use social information in foraging contexts, from finding food (e.g., Sasvári1979; Farine et al. 2015a; Firth et al. 2016; Hillemann et al. 2019a), to learning innovative foraging techniques (Aplin et al. 2013, 2015) and avoidance of unpalatable prey (Thorogood et al. 2018). Further, it has been shown that information does not spread between individuals at random but can be predicted by their connections in the population-level social network (Aplin et al. 2012; Farine et al. 2015a; Firth et al. 2016). We expand these previous studies on social foraging in songbirds by contrasting pattern of information spread for patches that varied in profitability, to test whether songbirds use social information about whether a patch contains food or not. We provided artificial patches (bird feeders) that appeared identical but were either empty or stocked with seed, and calculated the connectedness of individuals arriving at each feeder using the edge strength from independently-

recorded social association network data. We then compared the order in which birds discovered these feeders with a null model simulating random arrival of birds, to test two distinct hypotheses.

The first hypothesis is that, additionally to information about patch location, birds also acquire social information about patch profitability by attending to the behaviour of others. If individuals gain information from their close associates that the patch was not rewarding (here, absence of food), we expect them to not sample the patch themselves. Thus, under this hypothesis, we predict that individuals sampling empty feeders will be less connected to those that had previously visited the feeder ('knowledgeable individuals', hereafter) than would be expected by the random arrival model, because closely-associated individuals are more likely to learn from each other (e.g., Coussi-Korbel & Fragaszy 1995). At profitable feeders, on the other hand, we expect that arriving birds should be more connected to the knowledgeable individuals in their social network than predicted by the null model.

The alternative hypothesis is that birds acquire only information about the location of potential resources, but not their quality. Individuals may not obtain the relevant social information to assess whether a patch is profitable, or they may not use it. Under this hypothesis, individuals discovering a potential patch are therefore expected to sample it regardless of its quality. Thus, we expect that the connectedness of arriving individuals should be higher than predicted by the random arrival model, regardless of whether the feeder is full or empty. In other words, the results should reflect the same social effects on patch discovery that have been shown in other studies (Aplin et al. 2012; Farine et al. 2015a; Firth et al. 2016).

METHODS

Study system

We studied a population of individually tagged songbirds in Wytham Woods in Oxfordshire, UK (51°46' N, 1°20' W), consisting of blue tits (*Cyanistes caeruleus*), great tits (*Parus major*), marsh tits (*Poecile palustris*), and Eurasian nuthatches (*Sitta europaea*). Tits in this population move and

forage in mixed-species flocks during the non-breeding season (Hinde 1952; Farine et. al 2012, 2014, 2015a), with blue tits and great tits being the most abundant species, that together accounted for more than 90 % of the bird recorded in this study. Birds were each fitted with a unique British Trust for Ornithology (BTO) metal leg ring as nestlings or as adults, either when caught at nest boxes during the breeding season or in mist nets during the winter. Additionally, birds were fitted with a plastic leg ring carrying a passive integrated transponder (PIT) tag (IB Technologies, UK), that can be read by radio-frequency identification (RFID) antennae.

Social association data

Following the same protocol as previous studies on our system (e.g., Aplin et al. 2012, Farine et al. 2015b, Hillemann et al. 2019b), we quantified social associations of individuals based on co-occurrence in foraging groups. Feeder visits (time and location) by PIT-tagged birds were recorded at automated feeding stations with RFID antennae (Dorset ID, Netherlands), that were spread in a grid of 250 x 250 m across the study area (56 sampling sites in the first season, and 54 sites in second season). These feeding stations were accessible for a two-day sampling periods per week over multiple consecutive weeks in January and February (first season: eight sampling periods, second season: six sampling periods), thus providing a data stream detailing the spatio-temporal distribution of birds. To identify gathering events, or flocks, we used a Gaussian mixture model (GMM) that was designed to detect periods of high activity (Psorakis et al. 2012, 2015). The GMM approach is a clustering algorithm that can identify groups of different sizes and temporal resolution, without the need to set arbitrary time resolution parameter (e.g., fixed time windows). For detecting groups, we used the gmmevents function in the asnipe package (Farine 2013) in R (v. 3.4.4; R Development Core Team 2018).

To calculate a 'local' network for each experimental site, we used subsets of the population-scale social association data. For each trial, we included data collected at the four logging stations closest to the experimental site, and during the four two-day sampling periods closest to the feeder discovery trial. GMM models were applied to the data from each feeder on each day, and we

aggregated data from all of the flocks into one group-by-individual matrix for each of the local networks. Social association was assumed based on co-presence in the same gathering event, and association strengths for each dyad was calculated as the simple ratio index, which ranges from 0 (never recorded in the same foraging flock) to 1 (always recorded in the same foraging flock). Social networks were constructed using the asnipe R package (Farine 2013).

Patch-discovery experiment

We conducted patch discovery trials at 18 different sites (10 sites in February - March 2016, 8 sites in February - March 2017). Each foraging patch consisted of a bird feeder that was either stocked with unhusked sunflower seeds or completely empty, and covered with an opaque tube (grey PVC pipe; see Fig. S1 for a photo of an experimental feeder). Feeders were placed close to vegetation, providing observation perches, but because of the opaque covering they required birds to perch on one of the feeder's two access holes to inspect the state of the food (or to take a seed). These two access holes were fitted with RFID antennae (scanning rate: 16 Hz) that recorded the identity and order of all PIT-tagged birds landing on them (one record per individual in each 15-s interval). Similar feeders are regularly used across the study area, for behavioural research relating to social associations of wintering songbirds, or for catching and marking individuals using mist nets throughout the non-breeding season.

Experimental sites in the same year were separated by at least 350 meters, and 88% of the individuals (N = 538) recorded throughout the experiment were either only ever recorded at one experimental site, or at only one site in each of the two years (supplementary material, Fig. S2). We implemented a fully balanced design, presenting both treatments (full and empty feeder) at each site. This design allowed us to balance potentially confounding factors such as variation in the local density of birds and habitat structure. The order of trials was pseudo-randomised, and we left a minimum of 3 days between consecutive trials at a given site (average ± standard deviation: 10.3 ± 7.2 day). We deployed feeders after sunset on the evening before the trial to ensure natural patch discovery the next morning. Discovery trials lasted one day, and feeders were removed

immediately after the end of the trial. Data from full-feeder trials were previously published in Hillemann et al. 2019a, in the context of analysing diurnal foraging patterns.

Modelling the spread of information about food availability

For each trial, we recorded the order of arrival of k individuals, with k being the total number of tagged birds that discovered the patch. Birds were classified as knowledgeable after their first visit was detected at the patch. For each arriving bird, we calculated its mean edge strength to knowledgeable individuals, using the independently collected social association data (i.e. the local network). We then compared the observed pattern of patch discovery to a null model simulating random arrival of individuals by selecting k individuals at random from the local network. A random discovery pattern is expected if individuals are not using social cues, but instead discover and sample the food source independently. We ran 1000 repetitions of this simulation, and compared the observed social connectivity between knowledgeable individuals to the model prediction.

Since birds that were recorded at the feeders were more connected than predicted by the null model in both treatments (full and empty feeders), we then developed a network-derived transmission model, the 'affiliative model', to test whether the observed pattern of arrival at the feeders could be explained by social associations. For each site, we randomly selected one individual from the local network to make the initial discovery, then randomly chose one of its associates as the second individual to arrive at the feeder. For each subsequently arriving bird, we randomly chose an individual from the growing number of associates to knowledgeable individuals. We repeated this process until k individuals were selected. Values obtained from 1000 repetitions of this simulation were again qualitatively compared to the observed pattern. Running these random-arrival simulations and network-derived simulations allowed us to quantify how the strength of connections between new discoverers and knowledgeable birds was expected to increase as the pool of information grows in a local population, under different mechanisms of information use.

Ethical Note

This work was conducted as part of a large ongoing research project on Parid social behaviour at Wytham Woods. All work was subject to review by the local ethical review committee of the Department of Zoology, University of Oxford. Birds were caught, ringed, and PIT-tagged by experienced ringers under BTO licences.

RESULTS

All of the full feeders (n=18 out of 18 trials) and all but three of the empty feeders (n=15 out of 18 trials) were discovered. Compared to full feeders, empty feeders were discovered by fewer individuals, and were visited less often throughout the length of the trial (Fig. 1). Empty feeders were only visited by few individuals in the early-morning hours, whereas birds accumulated at full feeders throughout the morning (Fig. 1a). The average number of unique birds visiting empty feeders was 10.2 ± 2.3 standard error mean (SEM; n=15), compared to 36.1 ± 6.8 SEM at full feeders (n = 18). Empty feeders were on average visited 25.5 ± 6.2 SEM times across the whole duration of each trial (median per capita number of visits [and first and third quantile]: 1 [1,3]), whereas the average number of visits to full feeders was 645.2 ± 146.0 SEM (median per capita number of visits: 12 [6,25].

At empty feeders, knowledgeable individuals were more connected to each other than predicted by the null model of random arrival (Fig. 2). For both feeder types, new individuals arriving at a feeder had a much higher edge strength to those birds that had already experienced the profitability of the patch, relative to the same number of individuals drawn randomly from the local population. The affiliative model, which simulates network-derived pattern of discovery, accurately predicted the observed connections among individuals arriving at either feeder (empty or full), with average values of edge strength to knowledgeable individuals falling within the 95% range of the values obtained from the affiliative model simulations.

DISCUSSION

By providing artificial patches that differed in their profitability, we found that non-rewarding patches were visited less often, and by fewer individuals, than patches that contained food. However, our results do not support the hypothesis that individuals acquire and use social information to assess the profitability of potential patches. Our prediction was, that empty patches should have been sampled only by individuals that are less connected to each other than the same number of randomly chosen individuals from the local population. Instead, we found that individuals arriving at empty feeders were more connected to each other than expected by chance. These results closely matched the patterns observed at independent trials presenting full feeders. Thus, we find no evidence that tits use social information to assess the profitability, or quality, of foraging patches.

From our data, we cannot conclude whether social information about patches not being profitable is (i) not available to other foragers, (ii) is not collected, or (iii) if foraging individuals actively forgo social information about patch quality (i.e., information is available but not used). We expect that individuals should observe different behavioural cues from others experiencing a full versus an empty patch (e.g., leaving with or without carrying a seed in their bill; see Fig. S1 for a photo of a bird carrying a seed). However, individuals may not have had the opportunity to carefully observe potentially subtle differences in others' behaviour, but instead sample personal experience about the patch immediately upon arrival. Alternatively, individuals may ignore the presented information (i.e., observe others return after unsuccessful feeder visits) in favour of sampling potentially more relevant and reliable personal information.

Using personal information to evaluate the quality of patches supports existing theory on economic decisions relating to social information use strategies. A number of theoretical models and empirical studies have suggested that personal and social information are not weighed equally, and that the relative use of social and personal information should depend upon the costs involved with acquiring and using each (e.g., Valone & Templeton 2002; Kendal et al. 2005; Hillemann et al.

2019a). Whereas personal exploration and trial-and-error sampling of the environment can be relatively costly, the cost of gathering personal information about the quality of a patch upon arrival is much smaller (Kendal et al. 2005; Galef 2009). Our results align with the predictions of this theory. Wintering songbirds seem to balance the costs of using personal versus social information during foraging by using social information to find potential resource locations, but not when evaluating the quality of a patch (which suggests that they then rely on personal information).

An economic view on when animals should use social versus personal information is consistent with recent findings about conformist transmission in our population (Aplin et al. 2015a). Conformity occurs where individuals ignore personal information, or forgo sampling it, and instead match their choices with the majority behaviour in the population (e.g., Kendal et al. 2004; Van de Waal et a. 2013; Aplin et al. 2015b). Behavioural conformism, such as visiting a patch together even if it is unprofitable, has been suggested to facilitate greater cohesion at the pair-level (Firth et al. 2016), and group-level (Aplin et al. 2014). The potential loss of contact with flock members and loss of anti-predator benefits associated with social foraging (e.g., Lima 1995) could select for social information use strategies that contribute to maintaining group cohesion above other factors. Formation of, and moving together in, foraging flocks is important for small songbirds such as tits, as it improves protection from predators. Further, during the winter, tits depend on dispersed, clumped food resources such as beech mast (the seeds of beech, *Fagus sylvatica*; Hinde 1952). Using social information to find potentially rich resources significantly reduces the time to patch discovery (e.g., Hillemann et al. 2019a), and this benefit may outweigh the costs of occasionally getting incorrect information.

Although birds appeared to use information similarly when discovering full versus empty feeders, we found that the number of individuals that visited feeders in the different conditions differed consistently. On average, 3.5-times more individuals arrived at full feeders than at empty feeders. The differences in the number of arrivals in the two conditions highlights how beneficial group-level properties—in this case having more individuals discover profitable than non-profitable food

sources—can emerge as a result of the strong social reinforcement in patch use by species such as tits (Aplin et al. 2014; Farine et al. 2014). Our data also suggest that birds visited empty patches because they acquired 'wrong' information from observing others, demonstrating that social information use can also be costly, or represent an ecological trap (Schlaepfer et al. 2002), hindering effective foraging by causing large numbers of birds in a population to sample potentially suboptimal patches before acquiring personal information. However, we observed that individuals departed from a patch once they updated their personal information. Of those birds that did visit the empty feeder more than once, about a third of all repeated visits were made within 1 minutes of the first arrival, presumably reflecting an extended exploration of the feeder, such as inspection of both access holes. Others made repeated visits several hours after the initial visit, which could represent a strategy of updating personal information. By departing patches rapidly, birds reduced the time available for others to also acquire incorrect social information, thus minimising the opportunities for social reinforcement of incorrect information. We also know that birds in our population are unlikely to become trapped by incorrect information. A previous study of information transfer in our population that used puzzle-boxes that gave low rewards for common solutions and high rewards for uncommon solutions found that populations did not get trapped by their conformist choices or their personal information. Instead, populations could switch to high reward solutions as a result of the dynamic structure of the social network they live in (Aplin et al. 2017). Work in fish has also suggested that social interactions among individuals can facilitate 'collective sensing', or the fine-scale tracking of environmental features without requiring any group-level control (Berdahl et al. 2012). How social information use among individuals translates to group-level, or population-level, movement and patch use decisions in habitats of varying qualities is an exciting area for future research.

Our study extends previous work on information use in a foraging context (e.g., Aplin et al. 2012) to test how individuals use social cues at different stages when navigating their environment. We build on previous approaches using populations with known social structure to track the acquisition of social information (Duboscq et al. 2016), such as studies using network-based diffusion analysis

(Franz & Nunn 2009, Hoppitt et al. 2010). In our study, we used simulations to test for the expected patterns of connections between new arrivals and previous discoverers for each experimental trial. These models allowed us to evaluate alternative hypotheses about social information use at different steps in the acquisition process. Our hypothesis was that information about the lack of food transmits through social connections, as has been established for transmission of information about the presence of food (e.g., Aplin et al. 2012; Firth et al. 2016). However, our empirical data was better explained by a simulation for an alternative hypothesis, that information about patch locations, but not patch quality, spread through the local social networks. Despite this, the behaviour of birds in response to acquiring personal information (i.e. to avoid empty patches) prevented large-scale spread of incorrect information. Thus, our study adds to the growing evidence for the importance of social information, and that information use does not necessarily represent an ecological trap, where suboptimal behaviour spreads through the population, even if individuals sometimes acquire wrong information.

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FIGURES

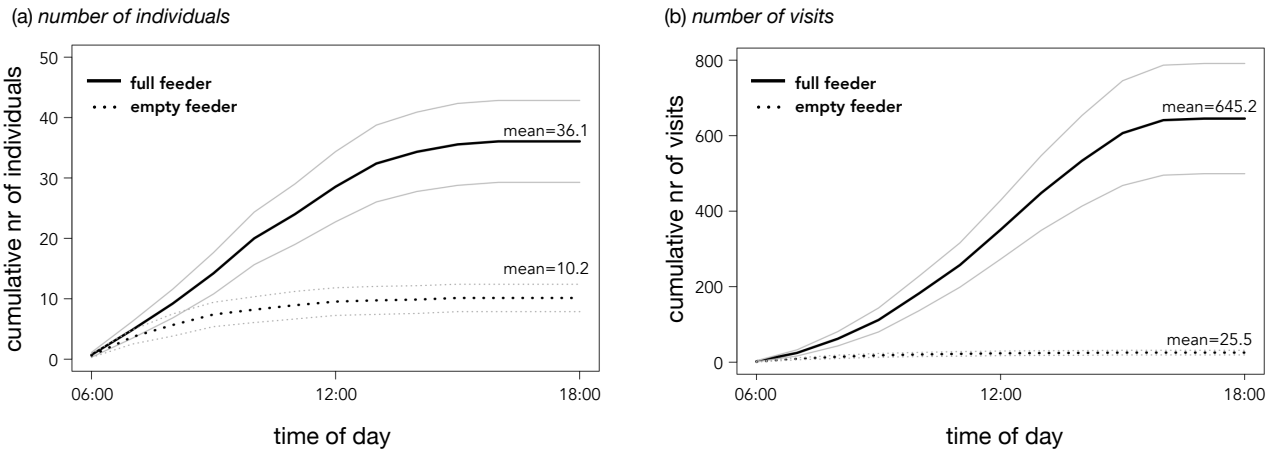
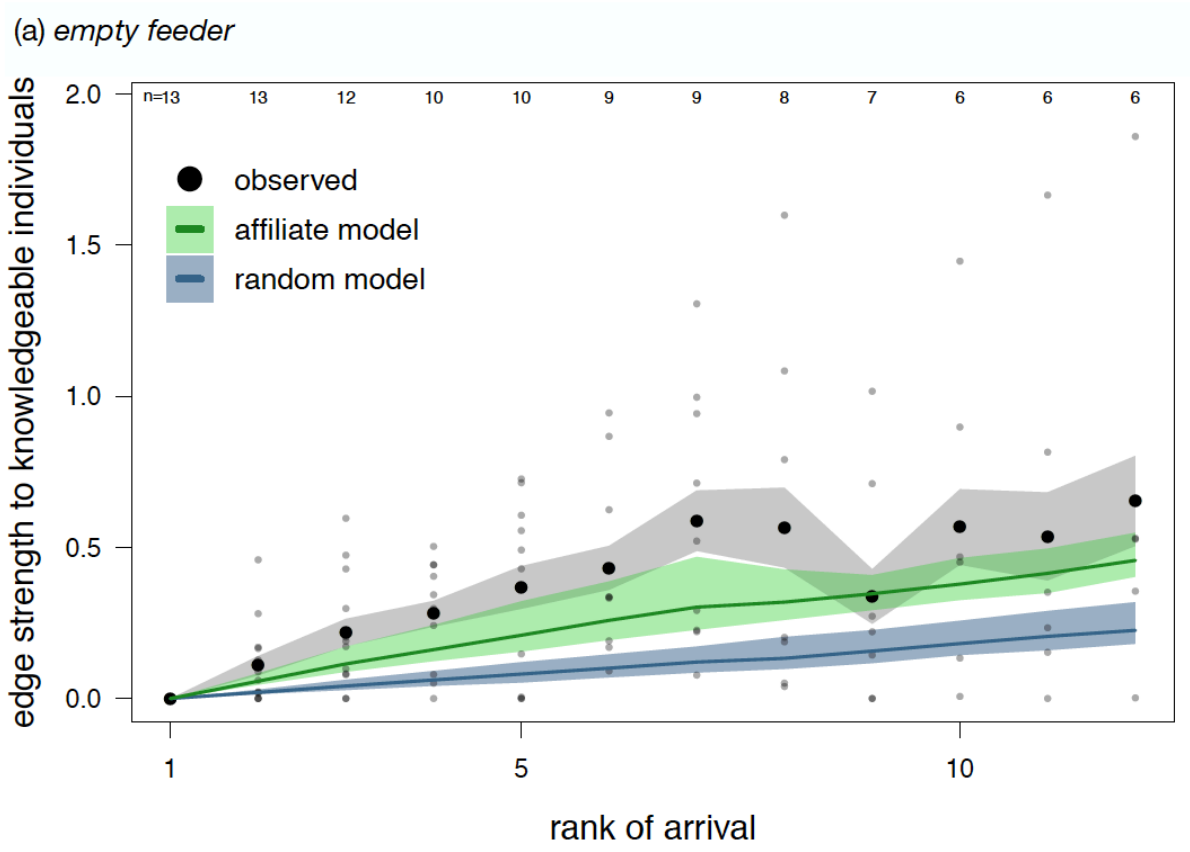


Figure 1: Cumulative number of (a) individuals visiting, and (b) feeder visits at full (continuous line) and empty feeders (dashed line) per hour of the day. Bold lines represent mean values across all trials in which the feeder was visited by at least one individual (18 full-feeder discovery trials and 15 empty-feeder trials, out of 18 trials conducted for each condition), and thin lines show standard errors of the mean. The total number of individuals visiting full feeders was on average 3.5-times higher than the number of birds visiting empty feeders, and full feeders were on average visited 25-times more than empty feeders.


(a) empty feeder
n=13 13 12 10 10 9 9 8 7 6 6 6
observed
affiliate model
random model
edge strength to knowledgeable individuals
2.0
1.5
1.0
0.5
0.0
1
5
10
rank of arrival

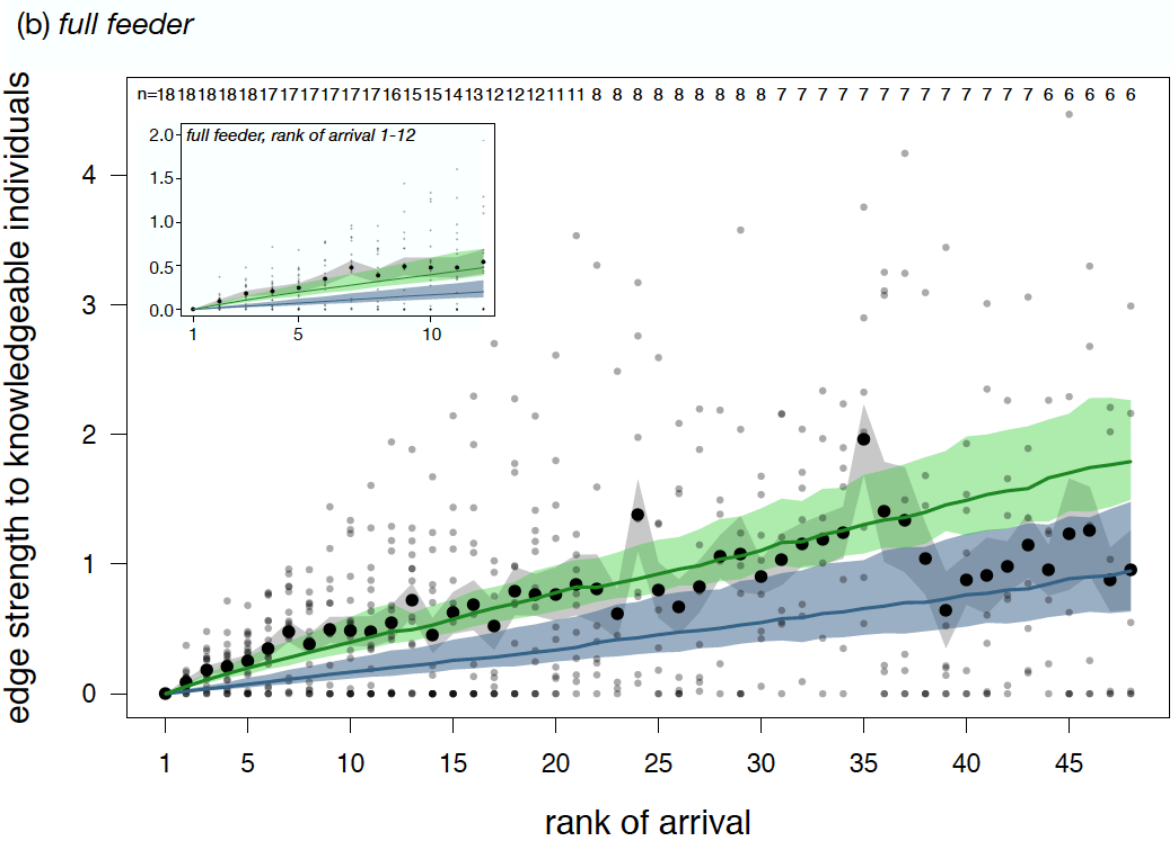

(b) full feeder
n=18181818181717171717171615151413121212111 8 8 8 8 8 8 8 8 7 7 7 7 7 7 7 7 7 7 7 6 6 6 6 6
full feeder, rank of arrival 1-12
edge strength to knowledgeable individuals
4
3
2
1
0
1
5
10
15
20
25
30
35
40
45
rank of arrival

Figure 2: Mean edge strength of arriving individuals to birds that have already visited (a) empty feeders, or (b) full feeders. Small grey dots show observed data from single trials, larger black dots show mean values over all trials, and grey-shaded areas represent the mean ± SEM of the observed data (number of trials is given at the top margin of the plot). Only trials in which at least two individuals visited the feeder were included, and the plots only show up to the k-th rank of arrival that was observed in at least six trials (rank 1-12 for empty feeder trials, rank 1-48 for full feeder trials; the smaller frame in (b) shows only ranks 1-12 for full feeder trials). Blue and green and blue lines are means of expected values according to 1000 simulations of the random and affiliate model, and shaded areas represent the 95 % ranges of the simulated data, respectively. Perfect transmission of social information about patch quality would result in a straight line along 0 for empty feeders (i.e., only unconnected individuals visiting the unprofitable patch). Instead, individuals' arrival to a feeder –empty or full– was strongly predicted by social connections suggesting that only information about the location of a potential resource is being transmitted socially, and not information about the quality of the patch. The drop in average connectedness to knowledgeable individuals, after the arrival of ca 35 to 40 individuals, indicates new independent discovery events. The average number of birds visiting full feeders was 36.1 ± 6.8 (mean ± SEM, n = 18), and 10.2 ± 2.3 at empty feeders (mean ± SEM, n = 15).

SUPPLEMENTARY MATERIAL

Information use in foraging flocks of songbirds - no evidence for social transmission of patch quality

Hillemann F, Cole EC, Sheldon BC, & Farine DR

Bird feeders as artificial patches

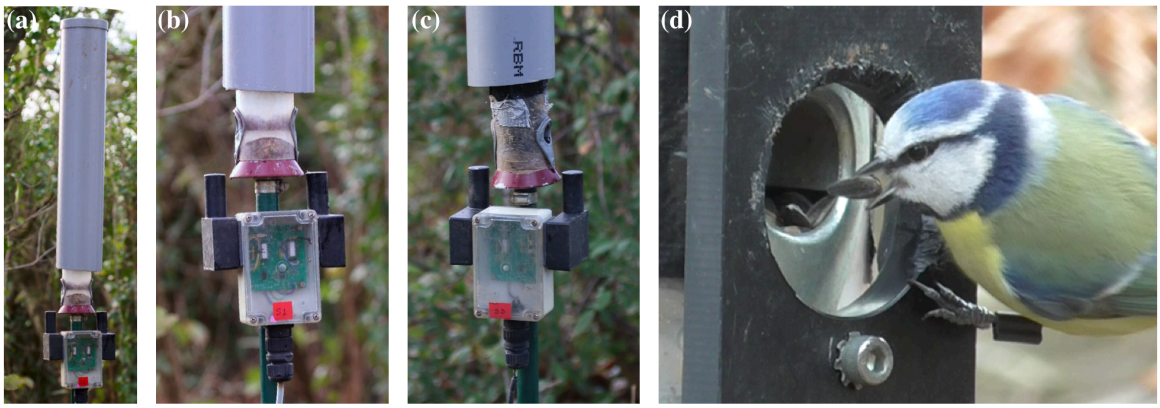


Figure S1. Experimental feeders. Automated feeding stations were covered with an opaque tube and either presented empty (a-b), or filled with unhusked sunflower seeds (c). RFID antennae in front of the access holes recorded the identity of PIT-tagged birds perching to inspect the feeder or take a seed. A PIT-tagged blue tit takes a sunflower seed from a similar feeder in our system (d).

Independence of trials

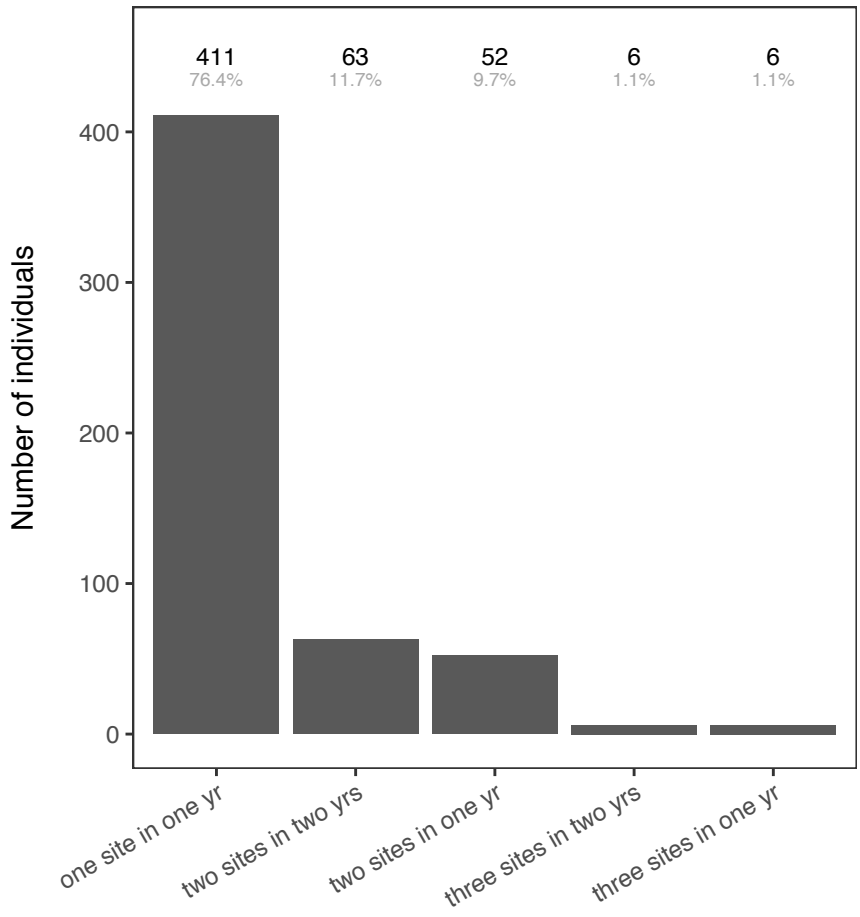


Figure S2. Number of individuals that were recorded at one or multiple experimental sites. Discovery trials with artificial patches that varied in their profitability (full and empty bird feeders) were conducted at 18 unique sites spread across the study area, and in two consecutive winters (10 sites in early 2016 and 8 sites in early 2017). Within the same year, experimental sites were separated by at least 350 meters. Represented are the number of individuals that were recorded at only one site, or at multiple sites (because they were recorded at neighbouring sites either in different years, or within the same year). Black numbers at the upper margin of the plot give the total number of individuals recorded per category, percentages are given in grey. Of all the 538 birds included in our study, 474 individuals (or 88%) were either only ever recorded at one experimental site throughout the study, or at only one site in each of the two years.

4

Active preference for foraging with heterospecifics? An experimental study on mixed-species flocks of songbirds

Active preference for foraging with heterospecifics? An experimental study on mixed-species flocks of songbirds

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ABSTRACT

Mixed-species groups are common across animal taxa and provide a unique opportunity for studying trade-offs in social decisions. However, interspecific social behaviour has often been a point of secondary interest in the study of animal sociality, and the role of heterospecific social preferences for shaping mixed-species groups is not well understood. Here, we test if mixed-species foraging flocks of tits (Paridae spp.) form via active preference for heterospecifics or passive mechanisms (limited opportunities to forage apart). We created a competitive foraging patch and used an experimental feeding array that gave birds the option to partition out the resource by species. We subsequently analysed individual foraging decisions of more than 400 PIT-tagged birds from three species, and compared probabilities for choosing to forage together with heterospecifics. In all species, individuals actively preferred foraging in larger mixed-species flocks, despite the expected increase in competition for the shared resource. Our data show that individuals maintain cohesion with heterospecifics even when given the opportunity to forage separately, suggesting that mixed-species grouping provides benefits that compensate the costs of resource sharing.

Keywords: group foraging, interspecific competition, mixed-species groups, niche differentiation, Paridae, resource sharing

INTRODUCTION

Understanding interactions between species is a central aim of ecology. Discussions of selective pressures that structure animal communities have traditionally focussed on trophic and competitive relationships (Cody 1974; Morin 1999), but the significance of beneficial, or facilitative, interactions has been increasingly acknowledged more recently (Stachowicz 2001). In particular, heterospecific information, for example about resource availability or habitat quality, facilitates temporary or stable associations between members of potentially competing species, and can affect the composition or structure of communities (Mönkkönen & Forsman 2002; Goodale et al. 2010; Parejo & Avilés 2016; Orr et al 2019). However, interspecies interactions are dynamic, with different costs and benefits arising under changing environmental conditions or species abundances (Bronstein 1994; Poisot et al. 2015). Despite recent theoretical advances and simulation studies that have considered multiple interactions in ecological networks, we have little knowledge about how the dynamic nature of interspecies interactions relates to community composition and stability (Garcia-Callejas et al. 2018).

A good model for addressing these and other questions in community ecology are mixed-species groups, which represent subunits of the community, or 'community modules' (Holt 1997; Goodale et al. 2010). Multi-species associations are ubiquitous across taxa and contexts, and include loose assemblages of individuals gathered at clumped resources as well as groups of individuals that move together and interact for unilateral or mutualistic benefits, such as increased foraging efficiency, predator avoidance, and social information benefits (Morse 1977; Sridhar et al. 2009; Goodale et al. 2017). When choosing interaction partners, individuals face trade-offs because those species that provide ecologically relevant information are likely to be strong competitors due to overlapping niches. Uneven benefits from different potential interaction partners can affect species interaction patterns (e.g. Meise et al. 2018), and asymmetric relative benefits within heterospecific dyads, for example due to dominance, might explain inter- and intraspecific differences in the propensity to associate with heterospecifics (Sasvari 1992; Hino 2000, 2005; Cameron et al. 2019; Hillemann et al. 2019b). A recent review of the benefits and ecological context of heterospecific

sociality highlighted parallels with social behaviour among conspecifics, and concluded that social benefits and choice of interaction partners should be considered as a continuous function of ecological similarity (Sridhar & Guttal 2018).

Among the most widely studied examples of mixed-species associations are avian mixed-species foraging groups (Harrison & Whitehouse 2011; Sridhar et al. 2009). Two fundamentally different mechanism have been suggested to facilitate the formation of groups that consist of ecologically close potential competitors: niche segregation and niche conversion. Classic niche differentiation theory suggests that sympatric species can coexist because they exploit different resources or differ in the way they use the same resource (Lack 1971), such as birds using separate feeding zones within trees, as described for flocks of North American warblers, *Dendroica spp.* (MacArthur 1958) and flocks dominated by members of the Paridae family (Morse 1970; Lack 1971). Niche segregation could be the result of past or ongoing interspecific competition and social dominance effects, and there is some evidence from removal and introduction experiments for competition-driven niche shifts in the presence of heterospecifics (Morse 1974; reviewed in Dhondt 2012). However, a more recent large-scale analysis found that mixed-species flocks consist of species that are ecologically more similar than would be expected if competition alone was driving associations patterns (Sridhar et al. 2012). In contrast to predictions arising from competition theory, several species have been described to actively converge when in mixed-species groups, i.e. changing their behaviour to decrease, instead of increase, their ecological distance to heterospecifics (e.g., Valburg 1992; Hino 2000; Zou et al. 2011; Farine & Milburn 2013). Conversion with heterospecifics can facilitate the consumption of specific resources; for example, Common Bush-Tanagers, *Chlorospinguso phthalmicus*, switch from frugivory to consuming more insects when flocking with insectivores, possibly as a result of increased protection against predators that allows changes to foraging tactics (Valburg 1992). Individuals might accept a potential increase in competition when joining and converging with heterospecifics, when doing so provides anti-predator benefits that outweigh the costs of sub-optimal foraging (Hino 2000; Farine & Milburn 2013).

Here, we study mixed-species flocks of closely related and ecologically similar species of tits (Paridae). Tits usually move and forage in mixed-species flocks with fission-fusion dynamics outside the breeding season, and depend on scattered, clumped resources such as beech mast (fallen seed of beech, *Fagus sylvatica*) during winter (Hinde 1952; Perrins 1966; Farine et al. 2012, 2014). Their common main predator is the Eurasian sparrowhawk, *Accipiter nisus* (Newton 1986), and group foraging can reduce the risk of predation for individuals. However, dominant individuals are able to constrain access to resources for subordinates (Lack 1971; Ekman 1989; Milligan et al. 2017), and local competition and body-size mediated dominance relationships within and between species have been suggested to drive differences in resource use; for example, larger species forage more at ground level or closer to the tree trunk than lighter species that forage among smaller, and more exposed, branches and twigs (Betts 1955).

We consider two alternative explanations for the formation and maintenance of parid mixed-species foraging flocks: The first hypothesis suggests that flocks form passively, as a result of strong niche overlap, leading to attraction to the same clumped resources and limited opportunity to forage apart. Alternatively, mixed-species flocks might form as a result of active preference for heterospecific flocking, for benefits that could not be gained from foraging in single-species groups. For example, heterospecifics can provide valuable information if they differ in their information gathering methods or abilities (e.g., Chittka & Leadbeater 2005; Meise et al. 2018), and individuals of less abundant species may be able to reduce their predation risk by forming larger groups with heterospecifics. We analyse individual grouping decisions under manipulated ecological conditions using an experimental design that allows to assess active preference for, or avoidance of heterospecifics. We designed experimental foraging patches that allowed individuals to partition out a resource by species, and analysed the relative preference for foraging with heterospecifics, or at feeders that restrict access to members of one species. If mixed-species flocks form as a result of extensive niche overlap, and limited resource availability restricts individuals' ability to forage separately, we expected that individuals should forage away from other species to reduce competition-related costs of foraging together at a shared resource. However, individuals

are expected to incur uneven competitive costs while foraging with heterospecifics, and species may differ in their preference for associating with conspecifics or heterospecifics as a result of different, dominance-dependent social tactics. For example, individuals from a subordinate species might avoid joining dominant species, while dominant individuals might actively follow subdominants to exploit information or resources they provide (Jolles et al. 2013; Lee & Cowlishaw 2017).

METHODS

Study System

We studied a large population of individually-tagged wild songbirds in Wytham Woods, Oxfordshire, U.K. (51°46'N, 01°20'W). Blue tits (*Cyanistes caeruleus*), great tits, (*Parus major*), and marsh tits, (*Poecile palustris*), were fitted with unique British Trust for Ornithology (BTO) metal leg band, and a plastic leg carrying a passive integrated transponder (PIT tag, IB Technologies, UK). Birds were ringed as nestlings or breeding adults trapped at nest-boxes, and regular catching sessions using mist-nets targeted immigrants throughout the non-breeding season.

Data Collection

Our experiment consists of six independent replicates, conducted over two winters: four replicates in 2016/17 and two replicates in 2017/18. Within any one year, sites were separated by at least 700m to reduce the likelihood of individuals moving between sites. In each trial, we deployed experimental foraging patches of four sunflower seed feeding stations, placed in a square of 50x50m. Feeders were within the auditory and visual range of the birds, but the distance hindered social cohesion between individuals feeding at different feeders (Farine et al. 2014). Radio-frequency identification (RFID) antennae at the feeders automatically recorded individuals' within-patch choices as time-stamped feeder visits of PIT-tagged birds. Access to feeders was controlled by a selectively locking mechanism, that was programmed to unlock only for specific individuals, based on their PIT-tag codes (see Firth & Sheldon 2015 for details on the 'selective feeder'

mechanics). Feeders remained unlocked for two seconds, allowing another individual to gain access to the feeder by 'scrounging', i.e. closely following an individual that had successful unlocked the device (Firth et al. 2015). Feeder visits of PIT-tagged birds were automatically classified and recorded as 'access allowed' or 'access denied', depending on whether the individual was granted access at the respective feeder, or 'scrounge', when an individual arrived within 2 seconds of an allowed individual leaving the feeder, i.e. when the device was still unlocked. These feeders have previously been successfully used to impose segregation in our study population (Firth & Sheldon 2015; Firth et al. 2015, 2016). In the pre-experimental phase (5 days), all four feeders granted access to any PIT-tagged bird. The pre-experimental phase was followed by two days in which none of the feeders was accessible. During the experimental phase (5 days), access to the feeders was based on individuals' species identity: three of the four feeders allowed access to only either blue tits, great tits, or marsh tits ('species-specific feeders'), and the fourth feeder granted access to any PIT-tagged bird ('any-tag feeder').

Data Analysis: Social attraction to heterospecifics

To analyse feeder preferences, i.e. which feeder individuals decided to visit, we included any feeder record regardless of whether the individual was granted or denied access, or gained access through scrounging. For each species, we classified feeders as either granting access (i.e. the any-tag feeder and its appropriate species-specific feeder), or denying access (those two species-specific feeders that allowed access to individuals from the other two species, respectively). We analysed individuals' relative preference for foraging in mixed-species groups or with conspecifics, by comparing how individuals distributed their visits between the two access-granting feeders and calculating the proportion of all visits made to the any-tag feeder and the species-specific feeder.

We compared the patterns of feeder use in the experimental period with the pattern in the pre-experimental phase. The distribution of visits in the pre-experimental phase provides information about individuals' preferences in the absence of any selective access rules. These data therefore provide a null model of expected feeder visitation pattern that controls for potential spatial within-

patch preferences for feeders due to differences in the local vegetation structure and other uncontrolled aspects. In the pre-experimental phase, feeders were classified as granting access to a given species, or any-tag feeder, based on their access plan in the experimental phase.

We used generalised linear mixed models (GLMMs) with binomial distribution and logit link function to model the proportional feeder use for each study species in the pre-experimental phase and the experimental phase. The response term in both models was the probability for foraging at the any-tag feeder. We fitted an interaction term day*species, to test for a temporal component in the birds' response to the treatment over the course of the experiment, and to consider potential differences between species in the preference for visiting the any-tag feeder. However, we removed the interaction from the models as it was non-significant in both analyses, and we report the reduced model including day and species as main effects (Engqvist 2005). To account for pseudoreplication from repeated measures, we included experimental site and individual as a random effect in both models. Model fitting was conducted in R (v. 3.1.2) using the glmer function in the lme4 package (Bates et al. 2015).

RESULTS

We analysed within-patch foraging decisions of 206 blue tits, 204 great tits, and 31 marsh tits across the 6 replicates. To assess an effect of the experimental manipulation on feeder visitation patterns, we calculated bird densities and species compositions at feeders, and individuals' probabilities of visiting a feeder that allowed access to heterospecifics. The preference for the any-tag feeder was increased in the experimental phase, while individuals decreased their average number of daily feeder visits to the other, species-specific feeders (Fig. 1). The introduction of selective locking mechanism during the experimental phase caused a change in the species composition at feeders, with blue tit and great tit species-specific feeders becoming more homogeneous when access was limited to individuals of one species only (Fig. 2). However, for marsh tits, the any-tag and the species-specific feeder did not notably differ in their ratio of conspecific to heterospecific visitors in the experimental phase. Marsh tits are much less abundant

than blue tits and great tits, and are generally expected to be found in more heterogeneous groups with a higher relative number of heterospecifics to conspecifics.

There was no effect of day on the probability of visiting the any-tag feeder in the pre-experimental phase (estimate ± SE = -0.05 ± 0.03, z = -1.38, p = 0.168), but day had a significant positive effect on the birds' probability to visit the any-tag feeder in the experimental phase (estimate ± SE = 0.50 ± 0.08, z = 6.01, p < 0.001). When given the opportunity, i.e. in the experimental phase, members of all three species increasingly foraged at the any-tag feeder that allowed access to any PIT-tagged bird (Fig. 3). However, the GLMMs' main factor species had an effect on the probability to visit the any-tag feeder in both the pre-experimental and experimental phase: great tits and marsh tits differed significantly from blue tits in their feeder visitation pattern before the experimental manipulation (great tit probability of visiting any-tag feeder: estimate ± SE = -1.23 ± 0.24, z = -5.06, p <0.001; marsh tits, estimate ± SE = -1.71 ± 0.50, z = -3.40, p < 0.001), and during the experimental phase (great tit, estimate ± SE = 1.17 ± 0.23, z = 5.08, p <0.001; marsh tit, estimate ± SE = 0.89 ± 0.45, z = 1.96, p = 0.05).

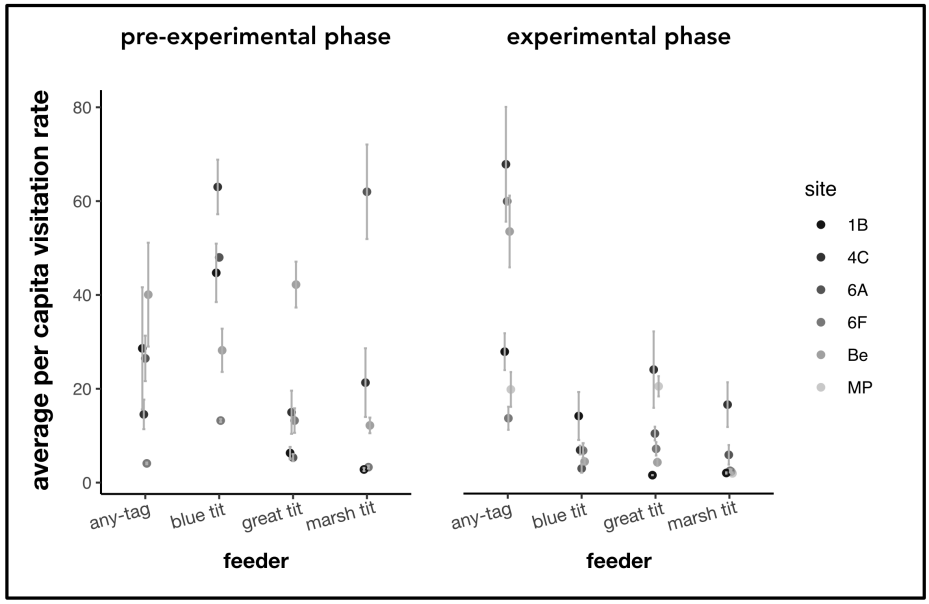

Fig. 1: The mean number of feeder visits per individual recorded at a given feeder in the quad. In the pre-experimental phase, feeders were classified as granting access to a given species (any-tag feeder), or granting access to members of one species based on their access plan in the

experimental phase. Individual daily mean values and 95% range are given, summarising all data from all sites throughout each experimental phase, respectively. Data from the pre-experimental phase, where all feeders allowed access to any PIT-tagged bird, provide a null model of expected feeder visitation pattern in the absence of any experimental, selective access rules. In the experimental phase, birds shifted their preference to the any-tag feeder, and away from species-specific selective feeders.

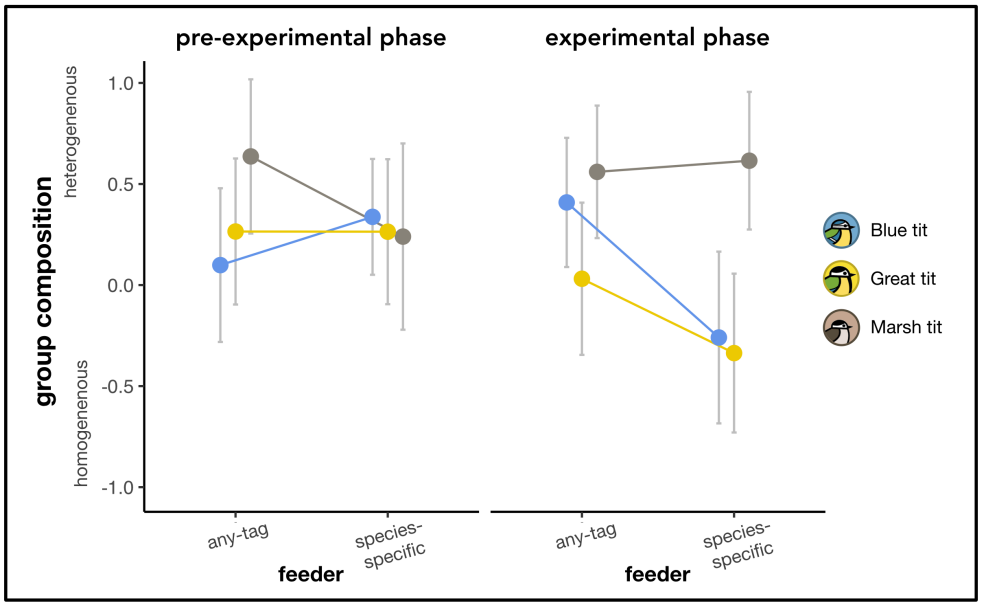

Fig. 2: A measure of group composition indicates whether birds visiting a feeder were predominantely conspecifics or heterospecifics. The ratio of heterospecific to conspecific group members was calculated for each species seperately, both at the unselective (any-tag) feeder and the focal species' specific selective feeder, using a similar formula as for the external-internal (E-I) index (Krackhardt & Stern 1988): the number of conspecifics visiting a feeder was subtracted from the number of heterospecifics, and this was divided by the total number of birds recorded at a given feeder. Positive values indicate heterogeneous groups, and negative values indicate that the focal individual was in a group with more conspecific than heterospecific members. Mean values and 95% range were calculated for all individuals across all sites. Unselective (any-tag) feeders had a higher ratio of heterospecifics to conspecifics in the experimental phase, but only for blue tits and great tits. Marsh tits are much less abundant throughout the study area and are generally expected to forage in more heterogeneous groups, which consist mainly of individuals from other species.

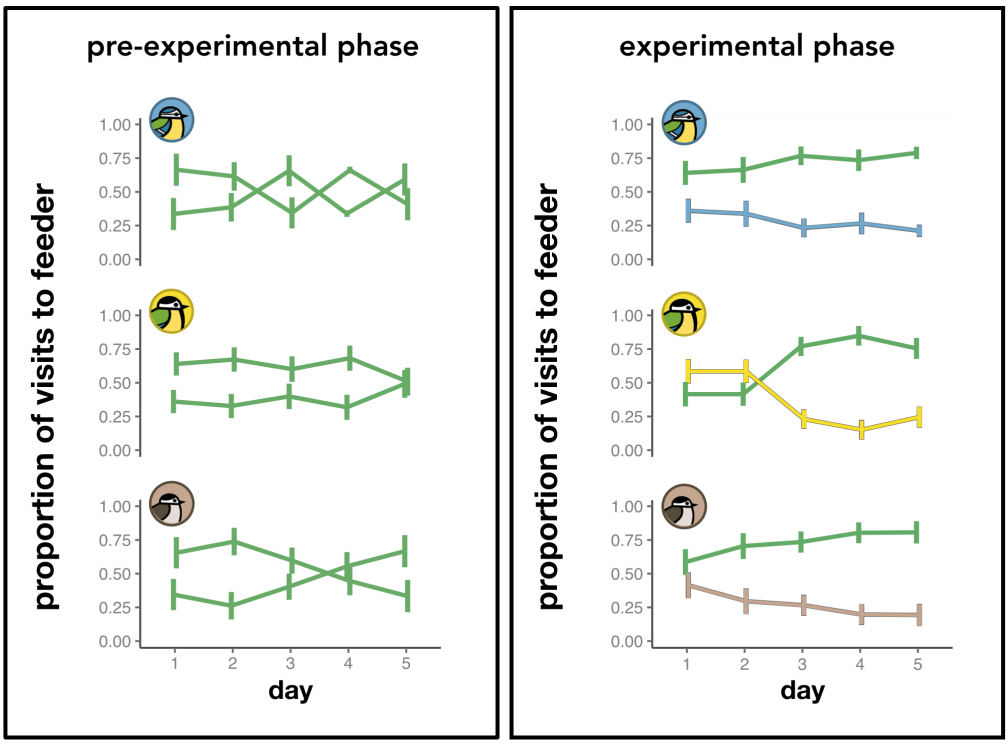

Fig. 3: Proportion of visits to the feeder that allowed any PIT-tagged bird (green) and visits to species-specific feeders (blue: blue tit, yellow: great tit, brown: marsh tit). Mean values and Standard Errors over all experimental trials are given for the n-th day of each phase of the experiment, respectively. Birds show no clear pattern of feeder preference in the pre-experimental phase, but birds of all three species increased their probability of visiting the any-tag feeder throughout the experimental phase.

DISCUSSION

We present data on heterospecific grouping under experimentally manipulated foraging conditions in mixed-species flocks of songbirds. We created foraging patches of clumped resources that individuals could access either together with, or away from heterospecifics, and compared individuals' choices for the those options. Individuals from the three parid species actively preferred foraging in larger multi-species flocks over foraging at smaller, more homogenous feeders, where only members of their own species could access the food freely. Our findings are in contrast to the prediction that these flocks of ecologically similar species result from competition-driven constraints in niche use – if inter-species competition is the key force shaping the foraging behaviour in tit flocks, individuals were expected to shift their behaviour to their preferred

monospecific foraging niche in the absence of heterospecifics (Morse 1970; Dolby & Grubb 1998). Instead, our data suggest an active preference for foraging with heterospecifics, even when given the opportunity to partition out the resource by species, and despite the expected increase in competition when foraging in larger groups.

In our experiment, the preference for foraging at the multi-species feeder had a strong temporal component for all species, with the probability to forage at the any-tag feeder increasing over the course of the experimental period, reaching up to 0.8 at the end of the experimental period, whereas fewer visits were made to the feeder that only allowed access to any one species, respectively. The observed pattern might result from a combination of conformist social learning and individual reinforcement, two mutually not exclusive explanations. In the experimental phase, each individual had access to two of the four feeders within the patch, and when choosing where to forage, individuals could copy others' choices instead of individually sampling the environment. The feeder visitation rate was much higher at the any-tag feeder than at the other feeders during the experimental phase, and there is ample evidence that tits use social information to find food (Aplin et al. 2012, Farine et al. 2015a; Firth et al. 2016; Hillemann et al. 2019a, b), and, within patches, individuals move towards the largest proportion of the flock (Farine et al. 2014). When deciding between alternative options, great tits have been shown to exhibit a conformist bias, i.e. individuals are more likely to adopt the majority behaviour (Aplin et al. 2015, 2017). Together, these processes can have a cumulative effect on the probability of observing individuals visit the feeder that allowed access to any PIT-tagged bird, and individuals' preference for foraging at that feeder.

As outlined above, heterospecific attraction is not necessarily needed to explain the preference for mixed-species grouping in our study. Besides conformist behaviour and individual reinforcement, general grouping benefits could account for the observed feeder choice pattern. Foraging in larger groups increases foraging efficiency via shared vigilance (Lima 1995), and might improve the nutritional condition of joining species (Dolby & Grubb 1998), which is particularly important in for small-bodied birds in harsh winter environments. Further, predation by sparrowhawks is one of

the main factors of mortality in tits (Suhonen 1993; Vedder et al. 2014), and reduced per-captia predation risk when flocking in larger groups might outweigh the potential costs of increased competition, regardless of the composition of the groups. Tits were previously shown to avoid foraging with few individuals, and actively move towards the larger proportions of the flock when moving between clumped resources (Farine et al. 2014). Maintaining social cohesion with both conspecifics and heterospecifics while foraging is an important factor affecting individual decisions, and multiple studies in avian species, including on our own system, have found that foragers may accept reduced food intake rates to maintain cohesion with flock members (Delestrade 1999; Vasquez & Kacelnik 2000; Farine & Milburn 2013; Farine et al. 2014; Firth et al. 2015; Evans & Morand-Ferron 2019). The relative preferences for heterospecific associations might depend on local environmental conditions, because the relative costs and benefits of the species interactions fluctuate in space and time (Bronstein 1994). For example, fish preferentially associated with conspecific over heterospecific shoals when predation risk was low, but preferred shoaling with more vulnerable heterospecifics under increased predation risk (Mathis & Chivers 2003).

When deciding whether and who to join during foraging, individuals have to trade-off reduced predation risk with increased competition when foraging in larger groups. Foraging in mixed-species groups can be a strategy to mitigate the costs of competition, because reduced niche overlap between heterospecifics can relax within-group competition, compared to single-species group of the same size (Barnard & Thompson 1985). Associating with heterospecifics can also provide additive benefits to grouping with conspecifics only, allowing individuals to forage in larger groups. For example, grouping with species that are more vulnerable prey or preferred by common predators provides additional anti-predator benefits to monospecific groups (Fitzgibbon 1990; Mathis & Chivers 2003). Individuals might further maximise the benefits from mixed-species grouping, by selectively associating with subdominant species. Whether dominance relationships between species affected flocking decisions in our experiment could be investigated by analysing active following, i.e. whether individuals' preferentially chose one heterospecific

feeder over the other heterospecific feeder for scrounging attempts. Given the known dominance relationships between species of tits, there are clear hypothesis over the directionality of scrounging. In tits, dominance and susceptibility to interference is strongly predicted by body size (Morse 1978; Ekman 1989; Milligan 2015). Great tits are dominant over the two smaller species and are expected to be less selective when deciding who to associate with, whereas blue tits are expected to preferentially visit the species-specific feeder that grants access to the smaller marsh tits, to reduce competition and increase their probability for successful scrounging.

Whereas interspecific competition for nest sites has been suggested to be an important evolutionary force structuring avian communities by niche segregation (Dhont 2012), competition for limited resources outside the breeding season might not be the strongest factor shaping mixed-species foraging flocks of small wintering songbirds. Instead, our data show that members of parid mixed-species flocks maintain cohesion with heterospecifics flock members when foraging at clumped resources, even when given the opportunity to forage separately. In our study, members of parid mixed-species flocks maintain cohesion with heterospecifics flock members, suggesting that multi-species grouping provides benefits that compensate the costs of resource sharing. Our results therefore contribute to the notion that positive interspecies interactions play an important role in the formation and maintenance of biological communities.

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5

Wild songbirds exhibit consistent individual differences in interspecific social behaviour

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Wild songbirds exhibit consistent individual differences in interspecific social behaviour

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ABSTRACT

1. Natural populations and communities consist of individuals that differ in their phenotypes. There is increasing evidence in community ecology that consistent intraspecific variation in behaviour changes the outcome of ecological interactions.
2. Differences in intra- and interspecific interactions are expected to play a major role in determining patterns of species coexistence and community structure. However, the question of whether individuals vary in their propensity to associate with heterospecifics has been neglected.
3. We used social network analysis to characterise pattern of heterospecific associations in wild mixed-species flocks of songbirds, and assessed whether individuals adopt consistent social strategies in their broader, heterospecific, social environment. We quantified heterospecific foraging associations using data from a large automatically monitored PIT-tagged population of birds, involving more than 300 000 observations of flock membership, collected over three winters, for two tit species (Paridae), blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*.
4. We assessed individual consistency in interspecific social preferences over both short-term (week-to-week) and longer-term (year-to-year) timescales for a total of 4610 individuals, and found that blue tits and great tits exhibited marked and consistent intraspecific differences in heterospecific social phenotypes in terms of both absolute and relative number of associates. Further, we found that these consistent differences were significantly greater than expected from spatial and temporal differences in population densities.

5. Heterospecific associations represent a major component of the social environment for many species, and our results show that individuals vary consistently in their social decisions with respect to heterospecifics. These findings provide support for the notion that intraspecific trait variation contributes to patterns at community and ecosystem levels.

Keywords: *Cyanistes caeruleus*, mixed-species group, Paridae, *Parus major*, repeatability, social behaviour, social network analysis, social phenotype

INTRODUCTION

The social environment is an important component of individuals' lives. How individuals interact with conspecifics has been shown to have implications for their susceptibility to disease (Silk et al. 2018), access to resources (Aplin et al. 2012), and reproductive success and survival (Alberts 2019). Many potential mechanisms might mediate a sociality-fitness link, including access to resources, agonistic support, and anti-predator benefits (Ostner & Schülke 2018). While much of our current understanding of the costs and benefits of group living results from research on single-species groups (Krause & Ruxton 2002), social groups can take many different forms, and frequently include individuals from different species (Goodale et al. 2017). Mixed-species groups are widespread across animal communities (amphibians: Glos et al. 2007, birds: Sridhar et al. 2009, fish: Paijmans et al. 2019, mammals: Stensland et al. 2003), and offer opportunities for studying causes of social behaviour in the absence of kin selection or mate choice, i.e. direct grouping benefits as drivers of social behaviour (e.g., Farine et al. 2015a). Many of the key processes thought important for group-living in single-species contexts have been suggested to also apply to the formation of mixed-species groups (Dhondt 2012, Sridhar & Guttal 2018). For example, both grouping and use of heterospecific social information have been shown to provide anti-predator benefits (Magrath et al. 2015; Meise et al. 2018; Goodale et al. 2019) and foraging benefits (Dolby & Grubb 1998; Farine et al. 2015a) to members of mixed-species groups. In turn, interactions with heterospecifics could influence the positions of individuals within their social networks, and

thereby contribute to ecological and evolutionary processes arising via the social environment (see Cantor et al. 2019 for a review).

Ecological research on species coexistence has traditionally focussed on averaged differences between species, thus ignoring the importance of intraspecific variation among individuals for species interactions (Bolnick et al. 2011; Violle et al. 2012; Hart et al. 2016). However, it has become increasingly apparent that individual-level processes are of vital importance for understanding community dynamics and other emerging properties of individual interactions. To study social behaviour in mixed-species groups, Farine et al. (2012) suggested shifting from a species-level perspective to treating interactions between individuals as the basic unit of analysis (*sensu* Hinde 1976). Such a bottom-up approach accounts for the effect of inter-individual differences in behavioural or morphological traits and has long been applied to study sociality in single-species groups, thus providing a theoretical and analytical basis for analysing heterospecific sociality. Social Network Analysis (SNA) has become an important method for quantifying individuals' social decisions (such as partner choice), interaction pattern among individuals, and the emerging social structure of groups and populations (Cantor et al. 2019). To our knowledge, only two studies have analysed dyadic interactions to explore the role of individual-level decisions in shaping heterospecific groups and both focus on within-species variation in measures of social behaviour (Farine et al. 2012; Farine & Milburn 2013). These studies show that a bottom-up approach is useful when exploring hypotheses regarding individual variation in heterospecific association propensity. Yet, neither of these studies explored whether individuals differ consistently in their propensity to associate with heterospecifics.

Considering individuals' social decisions in a broader, multi-species context will allow a better understanding of the link between individual-level decisions, fitness-related outcomes, and the structure of mixed-species social communities (Farine et al. 2012). For example, how individuals are positioned within their social environment can predict their reproductive success (Formica et al. 2011; Farine & Sheldon 2015). Specifically, the propensity for great tits, *Parus major*, to acquire a

breeding territory has been shown to be higher, not only for birds that dispersed into the population earlier, but also when individuals dispersed early relative to their competitors (Farine & Sheldon 2015). For selection to act via the social environment, individuals must vary consistently in their social environment (McDonald et al. 2017). Hence, a key first step in relating fitness consequences to social network position is to understand the distribution and consistency of individual variation in behaviour by characterising individual interaction patterns and social phenotypes. Consistency in social behaviour is often assumed, but only a few studies have shown that individuals can express consistent social phenotypes, by repeatedly measuring and comparing their behaviour over larger time spans (Blumstein et al. 2013; Jacoby et al. 2014; Aplin et al. 2015; Menz et al. 2017; O'Brien et al. 2018). Whether individuals also express consistent social strategies in a multi-species context is yet to be explored.

In this study, we test whether individual members of wintering mixed-species flocks of songbirds have consistent interspecific social preferences. Over three winters, we recorded associations among two tit species (Paridae) fitted with individual passive integrated transponder (PIT) tags, recorded by a grid of automated feeding stations fitted with radio frequency identification (RFID) antennae. This large-scale observational study provided a unique opportunity to assess individual consistency in interspecific social preferences over both short-term (week-to-week) and longer-term (year-to-year) timescales. We used SNA to quantify measures of gregariousness and heterospecific flocking propensity for 2775 individual blue tits and 1835 great tits, observed over three years, and then assessed the individual consistency of these traits using repeatability analyses. We then used network randomisation approaches (Farine 2017) to calculate repeatability estimates after accounting for spatio-temporal differences in the distribution, and thus broad social environments, among individuals. By comparing the two sets of repeatability estimates, we were able to separate consistency in social decision making from consistency in behaviour caused by spatial factors.

METHODS

Study system

This study was conducted from December 2011 to March 2014, in the context of a long-term research project studying the social behaviour of tits in Wytham Woods, Oxfordshire, U.K. (51°46'N, 01°20'W). Blue tits and great tits, as well as some coal tits (*Parus ater*), marsh tits, (*Poecile palustris*), and European nuthatches (*Sitta europaea*), were individually tagged with a unique British Trust for Ornithology (BTO) metal leg band, and a plastic leg ring carrying a passive integrated transponder (PIT tag, IB Technologies, UK). Birds were ringed as nestlings or as adults caught at nest-boxes during the breeding season, or using mist-nets in winter. Sex and age (first year/adult) were identified using plumage coloration or breeding records. The proportion of the population being tagged was very high, estimated over 90% for the first year of the study (see Aplin et al. 2013 for a formal analysis).

Tits form mixed-species foraging flocks with fission-fusion dynamics outside the breeding season, which mainly consist of Parid species, but can be joined by nuthatches, treecreepers, and woodpeckers (Hinde 1952; Ekman 1989). In this study, we consider heterospecific interactions between blue tits and great tits, the most abundant species in this population, that together account for 90.6 ± 0.8 % (mean ± SEM) of individuals recorded across the three winters under study.

Data collection

We collected data on social behaviour of individual birds by recording their visits to feeding stations equipped with radio-frequency identification (RFID) antennae (Dorset ID, Netherlands). A total of 65 sunflower-seed bird feeders with two access points were deployed throughout the study area in an even grid of approximately 250 x 250 m (see Supplementary Material Figure S1). These feeding stations opened automatically before sunrise and shut down after dusk on Saturday and Sunday (hereafter *weekends*), and remained closed on weekdays. Each time a PIT-tagged bird visited the feeder, the identity of the bird detected by the RFID antenna would be logged automatically onto the RFID logger, and we downloaded these data from each feeder weekly. Data

for this study was collected during three separate seasons of 14 weekends each, over three winters: 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). These time periods correspond to those used to assess individual differences social phenotypes of great tits in a single-species context (by Aplin et al. 2015). Number of individuals observed in each season is given in Table 1.

Detecting groups

We followed the same protocol as previous studies on this system (e.g., Aplin et al. 2013, 2015; Farine et al. 2012, 2015) to process the datastream of spatiotemporal detections of PIT-tagged birds at feeders. We used a Gaussian mixture model (GMM) to identify gathering events, or flocks (Psorakis et al. 2012). The GMM works by identifying short-term bursts of activity of individuals repeatedly visiting a feeder. When birds visit a feeder, they briefly perch to collect a seed that they then take to nearby vegetation to process (see Supplementary Material Video S1). These visits generate temporal waves in the number of detections that the GMM identifies. The advantage of the GMM approach is that it can identify flocks of differing sizes, and modelling shows that the resulting networks are more robust than other approaches (Psorakis et al. 2015). We applied this method to the data at each feeder on each day, and aggregated data from all of the flocks into one group by individual matrix for each of the 42 weekends in our study period. Detection of groups was done using the gmmevents function in the asnipe package (Farine 2013) in R v.3.4.4 (R Core Team, 2012)

Constructing social networks

Dyadic association strength was calculated using the simple ratio index. The simple ratio index generates a value between 0 and 1, which represents the probability of observing two individuals together given that at least one individual was in a given flock (Hoppitt & Farine 2017). This represents an unbiased estimate of the proportion of times two individuals spend together (Whitehead 1995). We combined association strengths for each dyad for each weekend to produce a social network. We generated 42 weekend social networks. In addition, we combined data on

flock membership over whole winters to produce one social network for each season (3 winter). Social networks were constructed using the asnipe package (Farine 2013) in R v.3.4.4 (R Core Team, 2012).

Measures of social phenotype

We calculated the following individual-level measures of social behaviour for great tits and blue tits: i) measures of gregariousness: unweighted degree (total number of associates of any species), weighted degree (overall association strength for all species interactions), and average foraging group size, and ii) a relative measure of heterospecific flocking propensity that is independent from an individual's gregariousness: a variant of the 'external-internal' (E-I) index (Krackhardt & Stern 1988). The E-I index quantifies the relationship between links in two exclusive categories and was originally proposed for friendship links to organisational subunits (i.e., external: friendship links between subunits, internal: friendship links within subunits). Analogously, we calculated the E-I index by subtracting the number of ties to conspecifics from the number of heterospecific associations, and dividing this by the total number of associations. Values range from 1 to -1, with 1 specifying that the focal only associates with heterospecifics, -1 indicating strong homophily (focal individual only has ties to conspecifics); the index will be zero if links are distributed equally between conspecifics and heterospecifics.

Repeatability Analysis

We calculated the proportion of phenotypic trait variation that can be attributed to inter-individual variation, where repeated samples corresponded to replicated networks. To assess consistency in social phenotypes over short and long time periods, we calculated within-year (week-to-week) and between-year repeatability in measures of great tit and blue tit behaviour. Our approach to analysing repeatability of heterospecific social behaviour follows methods previously used to calculate individual differences in the social phenotypes of great tits in a single-species context (Aplin et al. 2015). We calculated repeatability scores using linear mixed-effects models, as the proportion of variance that can be explained by the individual random effect (intra-class correlation

coefficient, ICC; Nakagawa & Schielzeth 2010). Our models accounted for the global population size and network density of the sampling period (weekend or season, respectively). For all models, with the exception of the E-I index, we square-rooted the response variables to conform to normality. We estimated a 95% range confidence intervals of the repeatability scores using restricted maximum likelihood Markov chain Monte Carlo sampling, using the R package MCMCglmm with default priors (Hadfield 2010).

Comparing observed repeatability results to null expectations

As is often the case for social networks, we can expect strong influences of i) resource distribution and other spatial features on group formation (Farine & Sheldon 2019), and ii) local population density (Farine et al. 2015b), on social metrics. We therefore used network randomisation approaches (Farine 2017) to control for the spatio-temporal distribution of individuals to isolate the social component of individuals' decisions from environmental factors. We designed a null model that randomised identities in each step (1000 randomisations in total), but controlled for the spatio-temporal distribution of individuals and species identity. Within each network, we randomly swapped identities among individuals (node permutations), but restricted swaps to be between individuals of the same species that had the majority of their visits recorded at the same feeding station during the period of data collection for that network (i.e. only swap identities between individuals that had the same primary feeder). Such restricted node permutations were necessary in order to maintain the total amount of variance in the model constant when applied to randomised datasets by maintaining a consistent social network structure, while randomising the link within individuals across different networks. We estimated the repeatability values for each of the 1000 resulting randomised networks using the same mixed-model approach described above. From the distribution of null repeatability values, we extracted the 95% confidence intervals for repeatability estimates to represent the expected range of individual behaviour without social preferences, i.e. the repeatability arising from their spatiotemporal occurrence only. To calculate what proportion of the repeatability was accounted for by the permuted data, we divided the mean of the randomised estimates by the observed repeatability estimate.

Ethical Note

This work was part of an ongoing long-term research project at Wytham Woods, which was approved by the local ethical review panel at the Department of Zoology, University of Oxford. All catching, handling, and ringing of birds was conducted by experienced BTO licence holders.

RESULTS

We quantified heterospecific associations in 342 510 observations of flock membership, or grouping events, recorded over three years. Great tits were on average observed in 13.57 ± 10.26 (mean ± SD) sampling periods (weekends), and blue tits in 11.37 ± 10.03 sampling periods, across the three years. The majority of birds were recorded in one winter only (1876 blue tits and 1270 great tits), but 629 blue tits and 356 great tits were observed in two years, and 270 blue tits and 209 great tits were recorded in all three years of data collection.

Blue tits and great tits exhibited considerable intraspecific variation in measures of social behaviour (see Table1). On average, individuals had an annual total of 120 associates, but some individuals were recorded foraging with more than 600 other individuals in one year. Birds also varied markedly in the average strength to their associations, with some individuals being three-times more strongly connected to their associates than the population's mean edge strength. Blue tits and great tits were on average seen with ten other group members, but some individuals' annual mean foraging group sizes reached up to 40. The relative number of heterospecific to conspecific group members (E-I index) also varied considerably for individuals, with some preferentially associating with conspecifics (negative values of E-I index) and others preferentially associating with heterospecifics (positive values of E-I index). Table 1 summarises the spread of inter-individual differences in measures of social behaviour, and provides number of individuals included in each year.

Individuals from both species were significantly repeatable in their heterospecific social behaviour on both short (week-to-week) and long (year-to-year) timescales (Figure 1, Table S1). Across the

three years of the study, the average week-to-week repeatability scores ranged from 0.49 to 0.62 for heterospecific degree, from 0.43 to 0.61 for heterospecific edge strength, from 0.45 to 0.63 for heterospecific average foraging group size, and from 0.38 to 0.51 for E-I index. Table S1 in the Supplementary Material lists repeatability scores separately for blue tits and great tits. Year-to-year repeatability estimates were similar to, or slightly higher than within-year scores for degree, edge strength, and group size, but the between-year consistency in relative number of conspecific and heterospecific associates (E-I index) was moderately low for both blue tits and great tits, with R=0.38 and R=0.25, respectively.

All repeatability scores were significantly higher than expected by chance. The observed repeatability values were outside the 95% range of estimates calculated from 1000 permuted datasets for each measure, despite the spatially constrained null model sometimes explaining a large share of individuals' repeatability scores (see Table S1 in the Supplementary Material). For example, where individuals foraged explained 85-90% of blue tits' week-to-week consistency in average group size, whereas the permuted data only accounted for about 50% of the week-to-week repeatability in blue tits' association strength. In both blue tits and great tits, the proportion of the individual week-to-week repeatability that can be explained by the spatio-temporal distribution of birds was largest for group size, slightly lower for E-I index, and smallest for degree and edge strength. In other words, how individuals are distributed in space and time contributed relatively more to the consistency in measures of social behaviour for some phenotypes than for others. The repeatability estimates for degree, edge weight, and group size were usually higher when considering year-to-year repeatability, compared to week-to-week repeatability. In contrast, the year-to-year repeatability of individuals' relative number of conspecific to heterospecific group members was lower than its short-term consistency, from week-to-week.

DISCUSSION

We show that individual great tits and blue tits differ consistently in their propensity to associate with heterospecifics. In part, the repeatability in heterospecific associations was driven by spatial

variation in population densities and grouping tendencies, with 40-90% of the within-year variation and 20-80% of the between-year repeatability in individual behaviour explained by the spatio-temporal distribution of individuals. These high values suggest that individuals may be making decisions about heterospecific associations as a parameter of their habitat choice. Further, we identified a significant social component to the consistency in measures of heterospecific social behaviour over and above the variation explained by space alone, suggesting that individuals make choices about who to associate with on a flock-by-flock basis, or over timescales of minutes. Our results demonstrate that social phenotypes translate into the heterospecific social environment, with individuals showing marked inter-individual variation in overall gregariousness, and connectedness to heterospecifics in multi-species networks. Given the growing evidence for the effects of individuals' social environment on modulating evolutionary and ecological processes (Cantor et al. 2019), the importance of decisions about the heterospecific social associations could be widely under-appreciated.

While blue tits and great tits were consistent in measures of their heterospecific social behaviour over both short (weekend-to-weekend) and long (year-to-year) timescales, repeatability scores for degree, edge weight, and group size tended to be higher when measured across years, compared to within years. Similarly, between-year repeatability estimates of great tit social phenotypes in a single-species context were higher than their within-year estimates (Aplin et al. 2015). Annual averages of behavioural measures might provide a more accurate description of individual phenotypes than parameters extracted from weekend-long social networks. It is also possible that more consistent individuals have a higher probability of year-to-year survival. These hypotheses are not mutually exclusive and require further investigation.

Direct comparisons of repeatability values, for example between great tits and blue tits, or between different years, are not straightforward, because the calculation of between-individual variance will depend on population sizes of both species, and therefore opportunities to associate with conspecifics and heterospecifics. Yet, compared to repeatability of different behaviours observed in

other studies (reviewed in Bell et al. 2009), blue tits and great tits showed a high consistency in their heterospecific social behaviour. For example, repeatability scores reported for migration, mate preference, and parental behaviours were on average less than 0.3, whereas week-to-week repeatability values observed in this study ranged from 0.4 to 0.6. Consistent individual differences in social network position were previously shown in only a few populations where social behaviour was studied in a conspecific context (e.g., Jacoby et al. 2014; Menz et al. 2017; O'Brien et al. 2018), including a study on our system, which noted inter-individual differences and reported similar repeatability in great tit social strategies (group size: R = 0.43-0.64, degree: R = 0.46-0.61, association strength: R = 0.41-0.64) in a single-species context (Aplin et al. 2015). Here, we extend findings of studies on single-species systems by showing that individuals vary in their heterospecific social associations in much the same way as was previously reported within species.

A major ecological and evolutionary question is how social groups form. While we found that individual-level repeatability was significantly larger than expected by chance, the null distribution of repeatability values (from the spatially-constrained permuted datasets) were also consistently larger than 0, and within the range of what are considered moderate to high repeatability values for behaviour (Bell et al. 2009). Different metrics of individuals' heterospecific social phenotypes can thus be explained by differences in spatial choices and within-location social choices to varying relative amounts. Our results suggest that social choices explain a relatively larger proportion of measures of sociability that represent the outcome of repeated measures of associations among the same individuals (e.g., average association strength), while the distribution of individuals, or their choice of location, explains relatively more of the measures that represent cumulative observations (e.g., E-I index). The high levels of repeatability in measures represented by cumulative observations suggest that individuals may be choosing these environments via larger-scale social decisions, such as those involving the decision of where to disperse. Studies on dispersal have found that the presence (Doligez et al. 2002) and behaviour (Seppänen & Forsman 2007) of heterospecifics can play a major role in shaping individual-level dispersal and habitat choice

decisions. Thus, the social environment that individuals experience depends on social choices made at different temporal and spatial scales.

Our findings open up many new questions regarding the evolutionary ecology of behaviour in natural populations. Heterospecific associations might have long-term impacts on individual fitness-related traits, going beyond the immediate drivers arising from foraging and anti-predator benefits. For example, a recent analysis on our study system suggest that great tit breeding performance is affected by their heterospecific breeding neighbourhoods (Roth 2019). How differences in individual association pattern can shape the local structure of populations is demonstrated by carry-over effects of social behaviour. For example, associations among wild zebra finches, *Taeniopygia guttata* during the nesting period predict pattern of interactions in subsequent years (Brandl et al. 2019), while winter social networks among great tits translate to breeding neighbourhoods during spring (Firth & Sheldon 2016). The patterns of local structure arising from interactions among individuals can then translate into local communities, and, in turn, these communities can generate repeatable hierarchical social structures (Farine & Sheldon 2019). Thus, carry-over effects of social structure arising from heterospecific social associations warrants much greater attention.

Our study contributes to the emerging picture that a bottom-up approach integrating the different components, or scales, of social decision-making is needed to gain full understanding of how social communities are formed and maintained. Individuals are not only considering conspecifics when making decisions about which groups to join, but also heterospecifics. This insight opens opportunities to address new questions, such as whether non-random social associations form between individuals of different species, how these emerge and are maintained, and their consequences across different ecological and evolutionary processes. Future work should also explore the underlying causes and fitness consequences of individual differences in the propensity to associate with heterospecifics, and test how such processes can influence the evolution of social groups.

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AUTHOR CONTRIBUTIONS STATEMENT

All authors conceived the idea of the study, FH and DRF analysed the data; FH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code used for analyses will be available from the figshare repository.

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TABLES AND FIGURES

Table 1. Number of individual great tits and blue tits included in each winter data collection period, and spread of metrics of social behaviour. Annual mean values across all individuals are provided, and 1st and 3rd quartile in brackets.

		Blue tit	Great tit
N individuals	2011-12	1631	1085
	2012-13	1306	813
	2013-14	1154	842
Degree	2011-12	131.2 [71.0, 183.0]	169.9 [106.0, 226.0]
	2012-13	101.9 [49.0, 145.0]	115.1 [65.0, 158.0]
	2013-14	93.6 [50.5, 133.0]	111.3 [62.0, 156.0]
Strength	2011-12	3.8 [1.2, 5.8]	5.0 [3.4, 6.8]
	2012-13	3.2 [0.9, 5.1]	4.2 [1.9, 6.2]
	2013-14	2.9 [1.1, 4.4]	3.4 [1.7, 5.0]
Group size	2011-12	11.6 [9.0, 14.0]	11.6 [9.5, 13.8]
	2012-13	10.3 [6.9, 13.2]	9.9 [6.9, 13.0]
	2013-14	8.8 [6.1, 11.1]	8.7 [6.2, 10.9]
E-I index	2011-12	-0.05 [-0.18, 0.68]	-0.06 [-0.20, 0.07]
	2012-13	-0.10 [-0.24, 0.04]	0.02 [-0.10, 0.13]
	2013-14	-0.06 [-0.19, 0.08]	-0.05 [-0.19, 0.10]

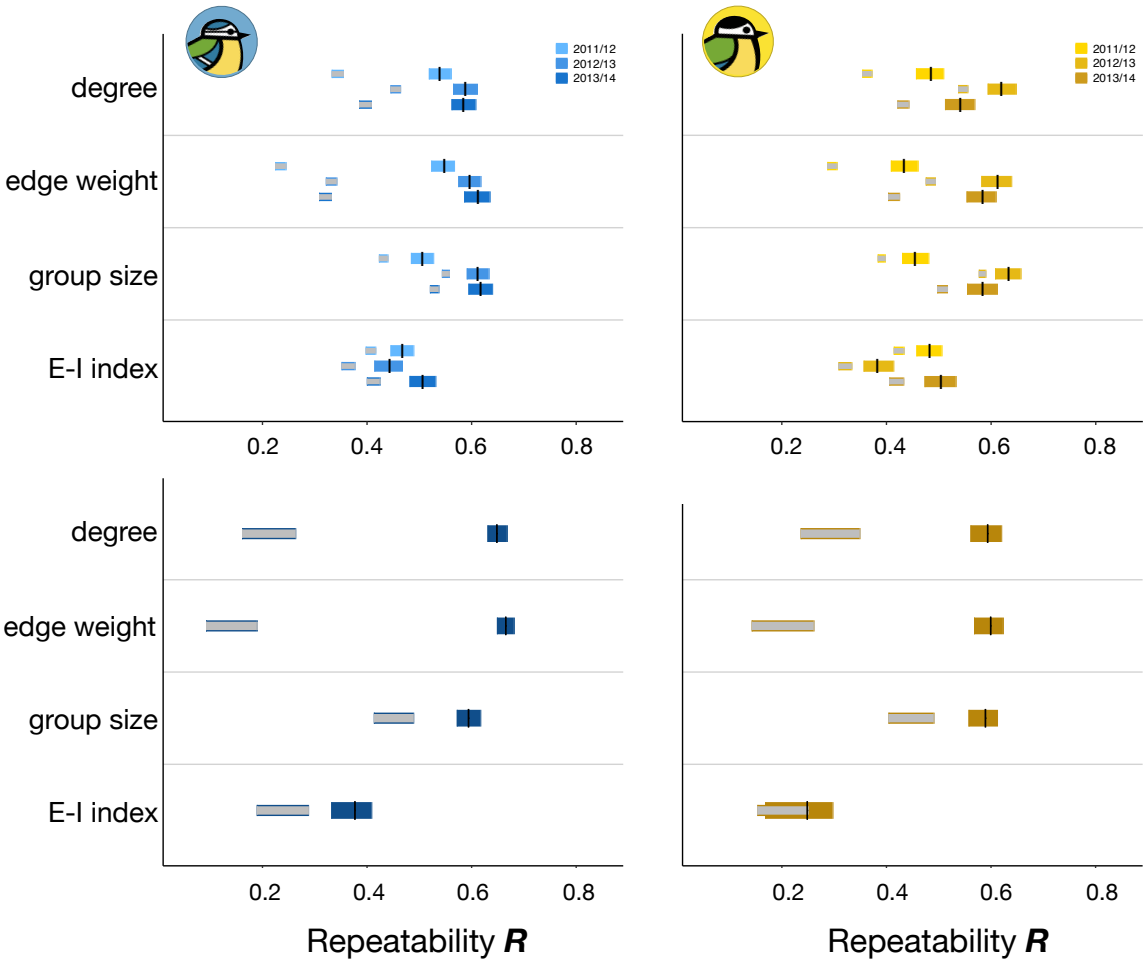


Fig. 1: Repeatability scores for week-to-week (top row) and between-year (bottom row) heterospecific social behaviour in blue tits (left) and great tits (right). Black lines show the R score estimates, and yellow or blue bars indicating the 95% range, which was obtained using restricted maximum likelihood Markov chain Monte Carlo sampling. Grey bars represent the 95% range of the repeatability values calculated from 1000 spatially-controlled data randomisations. All measures of social behaviour were significantly repeatable (confidence intervals do not overlap with zero; $p < 0.001$ in all cases), and observed values are significantly higher than the repeatability scores from the randomised data ($p = 0.027$ for E-I index between-year repeatability in great tits, and $p < 0.001$ elsewhere). Underlying data can be found in Table S1 in the Supplementary Material.

SUPPLEMENTARY MATERIAL

Table S1: Repeatability scores (R_{obs}) and 95% range of confidence, as per restricted maximum likelihood Markov chain Monte Carlo sampling, for degree (total number of associations), edge weight (association strength), average group size, and E-I index. All measures are significantly repeatable and observed values are significantly higher than expected repeatability scores (R_{ran}) from 1000 permutations of the data ($p = 0.027$ for E-I index between-year repeatability in great tits, and $p < 0.001$ elsewhere). The spatially constrained null model accounts for different proportions of the within-individual consistency in heterospecific social behaviour.

Species	Metric	Season	R_{obs} [$R_{obs,low}$ - $R_{obs,up}$]	[$R_{ran,low}$ - $R_{ran,up}$]	$R_{ran,mean}/R_{obs}$
Blue tit	**Degree**	2011-12	0.54 [0.52-0.56]	[0.33-0.35]	63.66 %
		2012-13	0.59 [0.56-0.61]	[0.44-0.46]	77.20 %
		2013-14	0.58 [0.56-0.61]	[0.38-0.41]	67.83 %
		year-to-year	0.65 [0.63-0.67]	[0.16-0.27]	32.67 %
	Edge weight	2011-12	0.55 [0.52-0.57]	[0.22-0.24]	42.79 %
		2012-13	0.60 [0.57-0.62]	[0.32-0.34]	55.57 %
		2013-14	0.61 [0.59-0.63]	[0.31-0.33]	52.20 %
		year-to-year	0.67 [0.65-0.68]	[0.09-0.19]	21.14 %
	Group size	2011-12	0.51 [0.48-0.53]	[0.42-0.44]	85.27 %
		2012-13	0.61 [0.59-0.63]	[0.54-0.56]	89.91 %
		2013-14	0.62 [0.59-0.64]	[0.52-0.54]	85.62 %
		year-to-year	0.59 [0.57-0.61]	[0.41-0.49]	75.86 %
	E-I index	2011-12	0.47 [0.44-0.49]	[0.40-0.42]	87.05 %
		2012-13	0.44 [0.41-0.47]	[0.35-0.38]	82.10 %
		2013-14	0.51 [0.48-0.53]	[0.40-0.42]	81.38 %
		year-to-year	0.38 [0.33-0.41]	[0.19-0.29]	63.20 %
Great tit	**Degree**	2011-12	0.49 [0.46-0.51]	[0.35-0.37]	74.78 %
		2012-13	0.62 [0.59-0.65]	[0.54-0.55]	88.11 %
		2013-14	0.54 [0.51-0.57]	[0.42-0.44]	79.76 %
		year-to-year	0.59 [0.56-0.62]	[0.23-0.34]	49.23 %
	Edge weight	2011-12	0.43 [0.41-0.46]	[0.29-0.30]	68.27 %
		2012-13	0.61 [0.58-0.64]	[0.48-0.49]	78.98 %
		2013-14	0.58 [0.55-0.61]	[0.40-0.42]	70.87 %
		year-to-year	0.60 [0.57-0.62]	[0.14-0.26]	33.61 %
	Group size	2011-12	0.45 [0.43-0.48]	[0.38-0.40]	85.86 %
		2012-13	0.63 [0.61-0.66]	[0.58-0.59]	92.06 %
		2013-14	0.58 [0.55-0.61]	[0.50-0.52]	86.74 %
		year-to-year	0.59 [0.56-0.61]	[0.40-0.49]	75.85 %
	E-I index	2011-12	0.48 [0.46-0.51]	[0.41-0.43]	87.73 %
		2012-13	0.38 [0.36-0.41]	[0.31-0.33]	83.89 %
		2013-14	0.50 [0.47-0.53]	[0.41-0.43]	83.05 %
		year-to-year	0.25 [0.19-0.30]	[0.15-0.25]	80.94 %

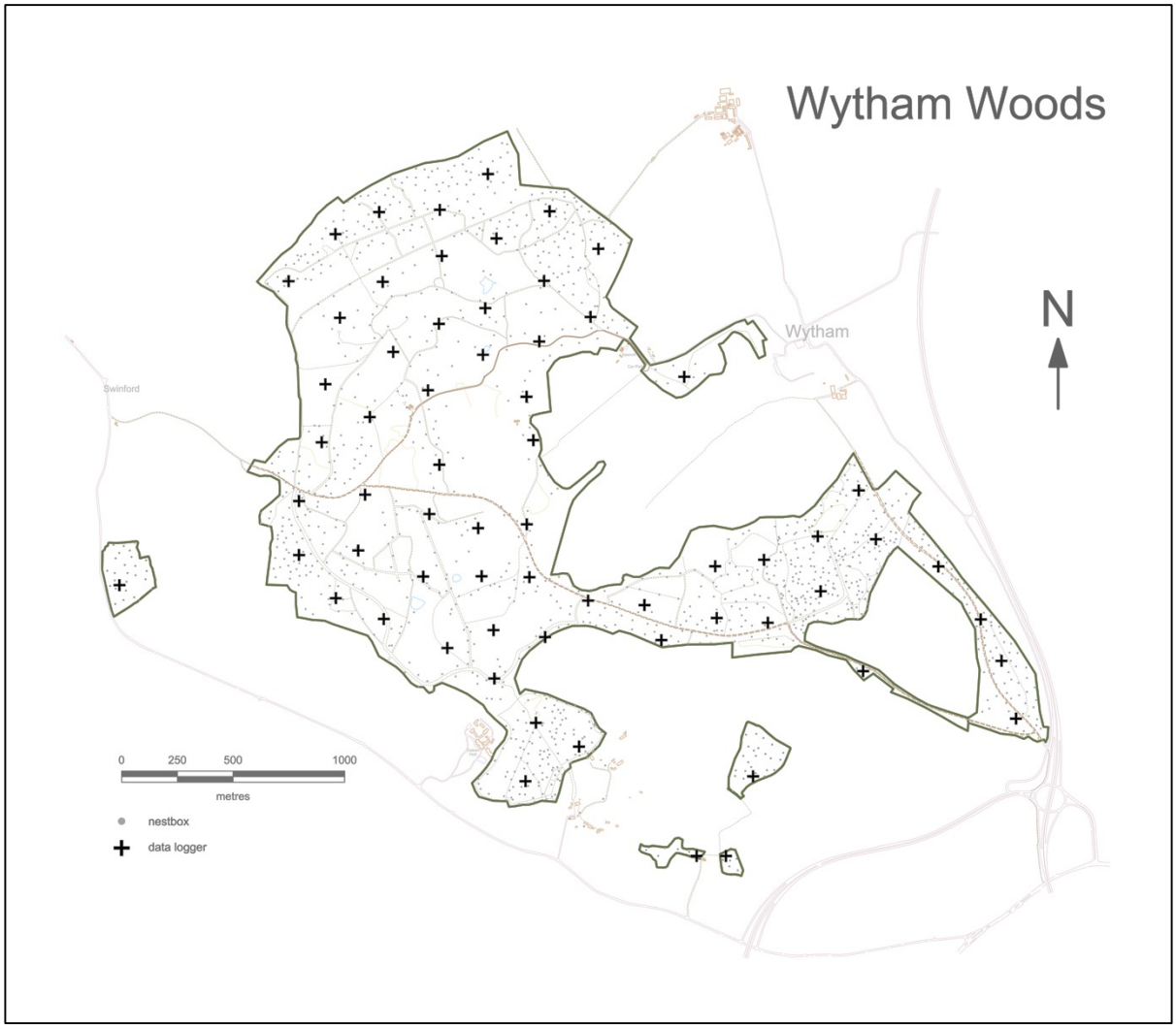
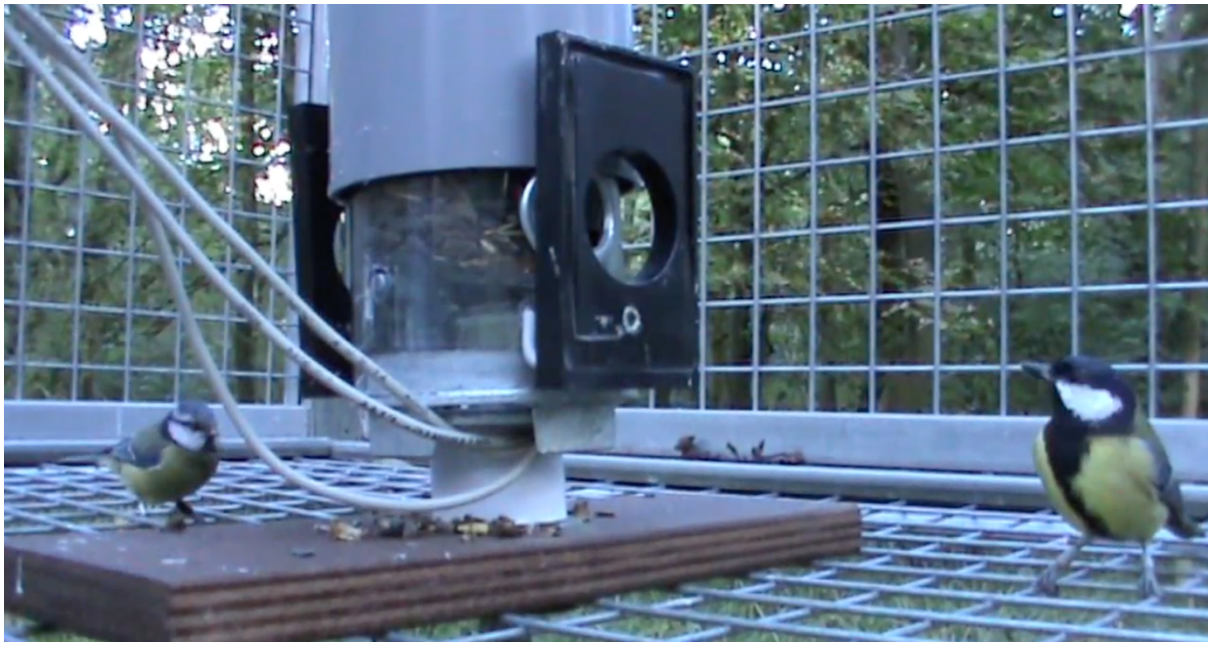


Figure S1: Map of the study site, Wytham Woods (Oxfordshire, UK). Black crosses show the location of the 65 automated RFID feeding stations, which record feeder visits of PIT-tagged birds. These data loggers are distributed in a grid of each approximately 250 x 250 m, and open and close simultaneously on two days per week during the winter months, thus providing a snapshot of the spatio-temporal distribution of birds.



Video V1: Link to Video demonstrating the collection of social association data at automated feeding station. Birds (Paridae spp.) with PIT-tags moulded into plastic rings on their legs perch on the RFID antennae when taking a seed from one of the feeder's two access holes, and typically process the unhusked seeds in the nearby vegetation.

6

General Discussion

THESIS AIMS AND MOTIVATION

This thesis addresses questions at the interplay of behavioural and community ecology, with the primary goal of relating individual decisions in a dynamic environment, with changing social and ecological conditions, to the formation and maintenance of mixed-species flocks of songbirds. Mixed-species groups are widespread across animal taxa and contexts, and heterospecific associations often represent a major component of individuals' social environments. Yet, the majority of research on animal sociality concerns interactions between individuals of the same species, and the evolutionary ecology of interspecies sociality has rarely been investigated using existing analytical frameworks (Sridhar & Guttal 2018). Only a small number of studies on mixed-species flocks have so far applied theoretical approaches and methodological tools that are well-established for studying social behaviour in single-species contexts, specifically social network analysis (e.g., Farine et al. 2012, 2015). Social network analysis allows to determine how social interaction pattern are mediated by individual traits, and using it to investigate social processes within multi-species environments thus follows recent developments in ecology, recognising the importance of individual differences for interspecies interactions and community processes (Ings et al. 2009; Bolnick et al. 2011; Farine et al. 2012). Adopting this individual-based approach, I analysed social association data in a large multi-species community of wild songbirds, with the aim to assess how trade-offs in heterospecific environments determine interaction rules (i.e., whether to use social information, who to interact with) and translate to emergent community-level structure. Further motivated by a lack of experimental work testing hypotheses about the drivers of mixed-species grouping, I used a combined observational and experimental approach to investigate heterospecific attraction under different ecological and social conditions. I specifically focussed on the role of social information use and optimal decision-making in foraging contexts.

GENERAL DISCUSSION

The role of social information in forming MSG

A key benefits of group living is improved access to social information. Acquiring heterospecific social information may facilitate more effective exploration and exploitation of new food resources (Farine et al. 2015; Freeberg et al. 2017; Schakner et al. 2017). Navigating ephemeral environments and finding dispersed clumped resources is essential for survival for wintering songbirds, and using social information can improve individuals' time to discover new patches (Chapter 2 and 3). Upon discovery of food, individuals benefit from reduced per-capita predation risk (Hamilton 1971; Pulliam 1973; Lima 1995). Such anti-predator benefits of grouping have been suggested to be the main reason why individuals, across many taxa, give food-related vocalisations that attract others (Elgar 1986; Suzuki 2012; Clay et al. 2012). By actively recruiting others and increasing their foraging group size, individuals can increase their relative safety from predators. However, this trades off with individuals' access to resources, and because the mathematical relationships of the costs and benefits associated with group size are non-linear, the effects of an additional group member are not always equal but depend on the current group size (Giraldeau & Caraco 2010; Chapter 2). I developed a theoretical framework based on principles of economic optimality to make predictions about when recruitment calls should be made. First, I quantified individuals' choices about when to recruit others to food and found a strong temporal pattern of call production, with the number of calls produced being negatively correlated with foraging flock size at the patch. Then, using the predictable foraging patterns of tits over the course of the day, I experimentally evaluated the underlying causes for the observed temporal variation in food-related vocal information. The results of this study suggest that, as the day progresses and foraging group sizes increase, the costs of producing calls at the food source (e.g. competition and attraction of predators) outweigh the benefits of recruiting group members (e.g. adding individuals to large groups only marginally increase safety in numbers). Although producing calls that attract others, i.e. potential competitors, to a food source may represent a detrimental strategy, I suggest that the social context mediates strategies for recruiting group members, and individuals balance competition and grouping benefits when deciding when to produce recruitment calls. Furthermore,

the results from this study contribute experimental evidence to signalling theory, which predicts that signalling interactions are beneficial to both the sender and receiver (Zahavi 1975, 1987). My framework therefore formally links processes of group formation and social cohesion to signalling theory.

Understanding how individuals with potentially different interests form mixed-species foraging groups was one of the aims of my study. In Chapter 2 and 3, I demonstrate that active production and spread of social information promotes formation of mixed-species flocks, and that use of heterospecific information allows foragers to quickly discover novel food sources. However, theory predicts that if too few individuals in the population gather personal information, this can result in informational cascades of maladaptive information and behaviour spreading through the population (Giraldeau et al. 2002; Rieucau & Giraldeau 2011). Instead, I found that selective information use prevents individuals and groups from being trapped in maladaptive behaviour, suggesting that information use is regulated by adaptive strategies which prevent suboptimal choices (Laland 2004). In conclusion, I show that social context has consequences for both the production (Chapter 2) and transmission of social information (Chapter 3) in mixed-species flocks of tits.

While I quantified the production of information about food at the group level, it is theoretically possible to analyse effects of the social environment on call production in more detail, for example by relating individual characteristic of the caller to the composition of the audience group. Primate studies on production of food-related calls have found that callers flexibly adjust their calling behaviour to their audience, and specifically the presence of dominant individuals in the group (Chapman & Lefebvre 1990; Di Bietetti 2005). While it is well established that social structure determines emergent group properties, such as information spread between individuals, a reversed causal relationship is also possible, where the provision and transmission of information affects association pattern (Cantor & Whitehead 2013; Kulahci & Quinn 2019). Whether tits selectively provide information to target audiences and thereby manipulate the composition of their social

environment is not known. Yet, my results demonstrate that tits consider their social environment when making signalling decisions, supporting a model of social adjustment (Chapter 2).

Separating effects of spatial pattern and social preferences

Understanding the mechanism of how foraging flocks are formed was one of the key aims of my thesis. When making social decisions about whether or who to join, individuals face trade-offs between benefits of grouping and intra-group competition. Associating with individuals from a different species might be a cost-mitigating social strategy that allows individuals to maintain grouping benefits while relaxing the costs of intra-group competition (Buskirk 1976). However, the benefits of heterospecific grouping are not equal for all species and individuals depending on morphological, behavioural, or ecological factors (e.g., Sasvari 1992; Hino 2000, 2005), and uneven benefits of sociality might result in uneven propensity for heterospecific associations, or avoidance. For example, social dominance has been shown to affect niche usage and interaction pattern between species (Morse 1974). I tested whether mixed-species foraging flocks of tits form as a result of active preference for heterospecific associations (mutualistic relationship), as a result of uneven preferences (parasitic relationship), or passive mechanism such co-occurrence driven by the distribution of resources (commensalistic relationship). Using an experimental design to test these explanations, I found support that mixed-species groups form through active preference for foraging with heterospecific, supporting the notion that they are based on mutualistic interspecies interactions (Chapter 4).

An important consideration when inferring social interactions from observational data is, that non-social factors can result in spatial co-occurrence of individuals, for example individuals gathering at a clumped resource. An individual's position in the social network depends, by definition, on interactions with other individuals, which means that individuals are limited in their social choices and depend on the behaviour and distribution of others in the population. For example, the social environment affects the availability of potential mates, and not accounting for social structure has implications for the interpretation of mate choice or sexual competition (McDonald et al. 2013).

The distribution of others in the network is itself likely to be affected by spatial features of the environment such as resource distribution, range overlap, or local population density (He et al. 2019). A powerful analytical approach for isolating social preferences from potentially confounding spatial factors are randomisation tests (Croft et al. 2008, 2011; Farine 2017). This involves running permutations of the observed data to create null models of the pattern of social association that would be expected in absence of the behaviour of interest (e.g., selective attraction). Null models have a long tradition in ecology because they facilitate hypothesis testing and are suitable for identifying underlying ecological mechanisms (Gotelli & Graves 1996; Croft et al. 2011).

Using such randomisations, I isolated and quantified the relative importance of individuals' spatial distribution from true heterospecific social decisions (Chapter 5). I demonstrate that spatio-temporal differences in species densities are important factors for explaining the community structure and the expression of repeatable heterospecific social behaviour. At the same time, I found that small-scale social decisions also significantly contribute to individuals' consistency in measures of heterospecific social behaviour, over and above the variation explained by space alone. Social choices can explain a relatively larger proportion of the measures of overall gregariousness (total number and strength of associations). In contrast, average flock size and relative number of conspecific to heterospecific flock could be explained to a larger degree by the distribution of individuals across the environment. Together with findings from Chapter 2 and 4, this suggests that individuals make proactive grouping decisions and adjust their social experience via short-term flock-by-flock decisions about who to interact with and who to avoid. Similarly, song sparrow (*Zonotrichia atricapilla*) express consistent social interaction pattern over time, which are partly explained by spatial range overlap, but also result from fine-scale social preferences (Shizuka et al. 2014). These findings highlight that analyses of social preference and social structure should account for potential effects of spatial structure and individuals' distribution.

I note that the social preferences inferred from our data represent an estimate of the behavioural phenotypes, which precision is affected by the collection and analysis of the association data. Interactions were inferred from individual feeder visits to artificial feeding stations that aim at simulating clumped patches of beech mast (fallen seed of the European beech, *Fagus sylvatica*), a common winter food source for tits (Hinde 1952; Perrins 1966). The feeders represent a non-depleting resource, and create minimal competition because two access holes allow two birds to take seeds simultaneously, and when birds visit the feeder, they tend to perch only briefly and process the collected seed in the nearby vegetation. We inferred interactions, relationships, and social preferences from the pattern of feeder visits using the gambit of the group approach, which assumes that all individuals in a flock associate with each other (Franks et al. 2010). While physical aggression between species is rare, supplanting behaviour is common at natural resources (Gibb 1954; Perrins 1979). Our data might therefore overestimate social attraction and underestimate competition, by missing dominance interactions such as displacement or queueing behaviour (cf. Milligan 2015). Detailed, dyadic dominance relationships could potentially be inferred from the records of feeder visits using machine learning algorithms (Evans et al. 2018).

Evolutionary implications

Consistent inter-individual differences are likely to be subject to selection (Dingemanse et al. 2004; Dingemanse & Wolf 2010). Consistency in behavioural traits has been investigated in a wide range of species, usually with regard to individual measures of boldness, aggression, or activity, and a growing body of work has been examining the relationship between consistent inter-individual differences and fitness (Dall et al. 2005; Sih et al. 2004; Réale et al. 2007). However, only a few studies have addresses behavioural consistency in social behaviour (e.g., Jacoby et al. 2014; Aplin et al. 2015; O'Brien et al. 2018), and whether individuals maintain consistent social strategies within their broader multi-species environment has, to my knowledge, not been investigated before. I analysed individual interaction pattern in a large natural population of wild songbirds and assessed whether individuals express consistent social strategies in their multi-species social environment (Chapter 5). Individual blue tits and great tits varied markedly and consistently in

their propensity to associate with heterospecific flock members and their overall connectedness in their multi-species social networks.

The finding that individuals express consistent heterospecific social phenotypes raises questions about the adaptive significance of interspecies sociality; for example, whether individuals with different heterospecific social strategies experience different fitness consequences. Consistency in the propensity to associate with heterospecifics might affect individuals' fitness outcome through carry-over effects into the breeding season (cf. Firth & Sheldon 2016). For example, an individual that has a high propensity to interact with heterospecifics in winter, might also breed close to heterospecifics in spring, which could affect resource competition and reduce opportunities for extra-pair mating. In great tits, reproductive performance was recently found to be affected by the focal individual's social environment, with a higher proportion of blue tits in the breeding neighbourhood increasing the number of fledglings and the proportion of the clutch that fledged (Roth 2019).

Social selection theory provides an analytical framework to investigate potential selection on individual phenotypes (Wolf et al. 1999). This framework considers not only natural selection on individuals' phenotypes, but also selection resulting from the social environment, i.e. its phenotypic composition and non-random social interactions between the focal individual and its associates. A prerequisite for using social selection analysis for identifying selective pressures on social interactions is a correlation between the traits of interest in the focal individual and its social partners, i.e. non-random phenotypic assortment, or preferential associations among social interaction partners (Wolf et al. 1999; McGlothlin et al. 2010; McDonald et al. 2017). In summary, social selection analyses can be very useful to understand whether, or how, evolutionary mechanism affect heterospecific social strategies and ultimately contribute to social structure in multi-species environments.

CONCLUDING REMARKS

Animal social groups are strikingly diverse in their organisation and structure, and understanding why individuals form groups is a central focus in evolutionary ecology. However, some of the prominent hypothesis for the evolution of group living have been developed based on single-species groups, and do not apply to mixed-species groups. In particular, associations of individuals from different species are not driven by kin selection, and heterospecific group members do not increase mating opportunities. Heterospecific sociality is therefore particularly interesting for understanding how direct grouping benefits, such as reduced predation risk and improved access to social information, can affect interaction pattern and forming of social groups. In this thesis, I addressed key questions relating to the formation and maintenance of mixed-species flocking, and identified different scales at which individual social decisions and optimal social adjustment scale up to the social structure at a higher level. With the work presented in this thesis, I highlight the importance of breaking down apparently complex patterns, such as grouping with potential competitors, to the mechanisms underlying individual decisions. In doing so, I demonstrate the strength of applying bottom-up approaches to questions in community ecology, which is dominated by species-level analyses. However, recent theoretical advances in the field have highlighted the importance of intraspecific variation for understanding emerging properties of individual interactions, such as species coexistence (Bolnick et al 2011; Violle et al. 2012; Hart et al. 2016). A better understanding of how ecological factors shape non-trophic interactions between species will also be able to inform conservation biology, for example by making predictions about the stability of mixed-species groups in response to disturbances through habitat fragmentation or species loss (Goodale et al. 2015; Marthy & Farine 2018; Zou et al. 2018).

Technological advances facilitate automated tracking of animals in the wild, allowing us to gather detailed interaction data of individuals from multiple species. Applying analytical approaches that consider inter-individual differences, such as social network theory, to multi-species societies has the potential to expand current evolutionary theories of sociality and provide new insights into the evolution and ecology of social behaviour.

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