

The maintenance and spread of cooperation in social networks in natural populations

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ABSTRACT

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Social interaction is crucial for social animals to thrive, but it comes with both benefits and costs. The social network approach helps to identify how social processes like cooperation are influenced by individual and population-level characteristics. Factors like individual recognition, familiarity, and social stability play a role in promoting tolerance and cooperation; and understanding these factors can provide insights into how social networks, cooperation, and other social behaviors evolve in different species. In this thesis, I examine how social processes interact with spatial and temporal factors to influence fitness and other outcomes in wild birds (*Paridae*).

I begin by establishing a theoretical foundation for my work by reviewing the concepts of cooperation and individual recognition and how they can be better understood through a social network approach (Chapters 2 & 3). Using experimental data, I explore the processes that may impact cooperative behavior by examining leading behavior during mixed-species foraging (Chapter 4) and demonstrate that motivation and dominance, as well as spatio-temporal effects, are determinants of this behavior. Drawing on these insights, I then use long-term breeding data to show that familiarity among neighbors as well as familiarity within breeding pairs influences fitness (Chapter 5). I also demonstrate that different kinds of social relationships have different effects on reproductive outcomes (Chapter 6).

All in all, I demonstrate that social connections have implications for fitness, and highlight the importance of accounting for spatial, temporal, and cognitive components when studying the ecology and evolution of sociality.

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AUTHOR CONTRIBUTIONS

Samin Gokcekus had independent intellectual input into all aspects of the thesis; contributed to winter and spring data collection, conceived of initial ideas, analyzed data, wrote first drafts, and incorporated co-author comments to produce final versions of all chapters.

Supervisors

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

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Greg F. Albery (co-author on chapters 5 & 6) provided support with statistics and helped carry out INLA analysis. Also gave feedback on chapter drafts.

Koosje P. Lamers (co-author on chapter 4) contributed to data collection and gave feedback on chapter draft.

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Chapter 1

Introduction

Introduction

Social cognition, behavior, and ecology

How individuals interact with others is a crucial determinant of fitness and almost all animals engage in social interaction (Snyder-Mackler et al., 2020). Encounters with others can be handled in many different ways, ranging from hostility, to tolerance, and even cooperation (Frank, 2007). Many species of primates can be highly cooperative in some settings, sharing food or information and engaging in reciprocal bouts of grooming or vigilance (Sussman, Chapman, Sussman, & Garber, 2019). On the other hand, individuals can also be highly aggressive, causing injury to others or even killing others or their offspring (Zinner & Wheeler, 2013). This wide range of encounters exists across taxa. Great tits (*Parus major*) have been observed to cooperate in terms of parental care (Johnstone et al., 2014), dyadic foraging (Firth, Voelkl, Farine, & Sheldon, 2015a), and nest defense (Grabowska-Zhang, Sheldon, & Hinde, 2012). In the winter, they join mixed-species flocks with blue tits (*Cyanistes caeruleus*) and other passerine species, engaging in various group behaviors (Hinde, 1952). However, great tits and blue tits may also fight to the death over competition for nest boxes (Typiak & Typiak, 2018). How and why do individuals choose to tolerate or cooperate with others; what are the ecological and evolutionary causes and consequences of these various forms of social interaction?

Living in groups is widespread throughout the animal kingdom, but close proximity to others has many costs including an increased: risk of disease transmission, within-group competition, and (for larger groups) risk of detection by predators (Krause & Ruxton, 2002). On the other hand, interacting with others can allow for the spread of information or novel behaviors that are beneficial to resource acquisition or predator detection (Beauchamp, 2014). Furthermore, if individuals choose the right cooperative partners, they can benefit by

engaging in mutually beneficial behaviors (Clutton-Brock, 2009). Understanding how individuals perceive and make decisions about their social environment in order to maximize the benefits that they receive through their social interactions has been a major undertaking in many fields including biology, psychology, anthropology, and philosophy (Birch, 2017; Bourke, 2014; Molina, Lubbers, Valenzuela-García, & Gómez-Mestres, 2017; Stevens, Cushman, & Hauser, 2005; Sutcliffe, Dunbar, Binder, & Arrow, 2012).

How do individuals navigate their social environment? The extent to which cognitive abilities are necessary for seemingly complex social behaviors and decisions has been discussed extensively (Brosnan, Salwiczek, & Bshary, 2010; Budaev, Jørgensen, Mangel, Eliassen, & Giske, 2019; Firth, Sheldon, & Brent, 2017; Shultz & Dunbar, 2007). It is possible that sociality and complex cognition evolve together, a view represented in various theories suggesting that the demands of living within a social group or engaging in repeated social interactions necessitate complex cognition, including the social brain hypothesis (Dunbar, 2009), the “relationship intelligence” hypothesis (Emery, Seed, Von Bayern, & Clayton, 2007), or the broader “social intelligence” hypothesis (Emery, Clayton, & Frith, 2007; Freeberg & Krams, 2015). There is also an inevitable influence of ecology on both social processes and the evolution of cognitive abilities (Godfrey-Smith, 2001; Holekamp, 2007). However, it is also possible that seemingly complex behaviors are being maintained by more simple mechanisms (Barrett, Henzi, & Kendall, 2007). Recently, social network analysis has been framed as a tool to uncover the relationship between social, cognitive, and ecological complexity (He, Maldonado-Chaparro, & Farine, 2019; Wascher, Kulahci, Langley, & Shaw, 2018).

The social network approach has become increasingly popular over the last decade and social network analysis can be used to understand various social behaviors and the processes

underlying them (Croft, Darden, & Wey, 2016; Farine & Whitehead, 2015; Firth, 2020; Kurvers, Krause, Croft, Wilson, & Wolf, 2014; Sih, Hanser, & McHugh, 2009; Wey, Blumstein, Shen, & Jordán, 2008). After a brief introduction to cooperation and the social network approach, I explore how social network analysis can be used to identify the individual and population-level characteristics that influence various social processes and then return to questions more specific to the interplay between various aspects of cognition, ecology, and cooperation.

Cooperation and social networks

The existence of cooperation, defined here as a behavior initiated by an actor that has a benefit to a recipient, has been regarded as an evolutionary puzzle for decades: if organisms are selected to maximize their own survival and reproduction, why do they engage in behaviors that may be beneficial to others and costly to themselves? Cooperation among related individuals has been explained by Hamilton's kin selection theory, where individuals will cooperate with genetically related others when the cost to themselves is outweighed by the benefit to the recipient relative to how closely related they are (Hamilton, 1964).

However, cooperation can also occur among non-kin (Dugatkin, 2002). It is possible that kin selection allowed for the emergence of cooperation, through decreases in aggression or the likelihood of hostility (Hatchwell, 2010; West, Griffin, & Gardner, 2007). Cooperative behaviors can be further categorized by looking at whether or not there is a net cost to the actor. Behaviors that lead to net benefits for all parties involved can be defined as mutualistic, while those that lead to a net cost to the actor are altruistic. Cooperation through reciprocity, where the actor incurs a temporary cost until the receiver of the beneficial behavior reciprocates - leading to eventual net benefit, can be understood as a subset of mutualism (Trivers, 1971). In generalized reciprocity, individuals cooperate when their most recent

partner was also cooperative, regardless of identity; this is the most simple form of reciprocity (Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005; Voelkl, 2015). In direct reciprocity, individuals cooperate with others that have cooperated with them before, requiring some tracking of previous cooperative interactions (Brandl & Bellwood, 2015; Voelkl et al., 2015). Finally, in the most complex form of reciprocity, indirect reciprocity, individuals cooperate with conspecifics that they have observed to cooperate with others, requiring individuals to be aware of third-party cooperative interactions (Bshary & Grutter, 2006). How do these various mechanisms allow for the maintenance of cooperation in different populations?

Because cooperation is an intrinsically social process, understanding it requires the consideration of characteristics at both the individual and group or population level which can be achieved with a social network approach. Social network analysis allows for an investigation of the relationship between the behavior of single individuals, the patterns and characteristics of their social interactions, and the structure and composition of the entire population (Croft et al., 2016). For example, cooperation is less likely to evolve in networks where there are high rates of random mixing (Akçay, 2018), and more likely to spread in highly structured and modular networks (van Doorn & Taborsky, 2011). Social network analysis can also give us insights into how the social environment differentially impacts individuals in different network positions, accounting for the relationship between the properties of single individuals and the processes that occur at the group level (Farine & Whitehead, 2015).

Using a network approach is also beneficial in the sense that it allows for a more detailed understanding of the reciprocal relationship between ecology and social structure (Deng, Liu, & Wang, 2017; He et al., 2019). There also may be a complementary relationship between

cooperative behavior and social network structure, lending more support to the assertion that social network analysis can be used to test empirical questions about cooperative behavior (especially in natural populations). More generally, the social network approach can help us to uncover: the reciprocal relationship between social processes and social structure, the relationship between ecology and social structure, the properties and processes that emerge due to social structure, and the ways information, disease, and other socially transmitted phenomena can spread among different types of social networks.

One of the biggest considerations when investigating how cooperation spreads in social networks is the existence of assortment. If individuals are assorted by cooperative-ness (in physical or social space) it is more likely that they will interact with co-operators, leading to higher fitness benefits for co-operators within the population (Fletcher & Doebeli, 2009). For example, (Brask et al., 2019) used a predator inspection set up to look at cooperative behavior in eight populations of guppies. After identifying a “cooperative phenotype”, they looked more closely at the social structures of two populations that have either high or low predation risk. They found that the population under high predation risk was socially assorted by co-operators, while the low predation risk population was not. This study highlights the utility of the social network approach for understanding, 1) how social structure is related to cooperation, 2) how ecological factors influence social structure, and 3) the consequences this has for cooperative behaviors. The social network approach can more generally be used to uncover the relationship between varying kinds and levels of social structure, perception, and other social behaviors.

Recognition and social foraging

Recognition, or the ability to identify stimuli within the environment and acknowledge characteristics and information associated with them, is crucial to survival in all animals.

Particularly relevant to the social domain is individual recognition, a precise form of recognition where an individual, x (the receiver), learns cues related to another individual, y (the signaler), which are associated with relevant information about y and are used by x to identify y and adjust their behavior towards them in future interaction (Tibbetts & Dale, 2007). Many have made a distinction between “true” individual recognition and other forms of individual recognition, where “true” individual recognition suggests that cues that are specific to the individual are learned and associated with information (usually fitness related) specific to that particular individual (Beecher, 1989; Tibbetts & Dale, 2007). However, what is arguably more important is determining how many sets of individuals can be identified (multiplicity), how many individuals are included in each set (specificity), and how long this information can be retained (longevity; Wiley, 2013). This can allow us to ask questions about the extent to which individuals perceive, recognize, and keep track of others and how this may influence social behavior.

An obvious consequence of varying levels of individual recognition on cooperation is differences in the ability to engage in direct or indirect reciprocity. In order to cooperate with others that were observed to be cooperative before, individuals must be able to identify and keep track of others' behaviors. For example, in the case of indirect reciprocity, this tracking is often called “image-scoring,” where individuals track the cooperative behaviors of others to create a mental “score” that increases or decreases based on the observation of instances of cooperation or defection (Nowak & Sigmund, 1998). More generally, keeping track of conspecifics and their characteristics can be advantageous if it allows individuals to make more informed decisions about who to follow, who to spend more (or less) time with, and even who to form strong bonds with. However, (as discussed p. 1) the extent to which recognition or tracking is necessary for many seemingly complex social behaviors is not yet

understood (Brandl & Bellwood, 2015; Couzin, Krause, Frankes, & Levin, 2005; Wiley, 2013).

One example of this can be seen in the context of passive-leading behavior (King, Johnson, & Van Vugt, 2009). In collective movements and actions, there are often individuals who are more likely to initiate or begin bouts of foraging, moving, etc. than others (King & Cowlishaw, 2009). Why do other individuals follow them? To what extent do these behaviors depend on recognition capabilities and social decision-making vs. simple spatial and temporal dynamics of group movement and behavior? Pollard, (2011, p. 94) modeled the consequences of individual recognition in relation to responding to alarm calling conspecifics under varying conditions; adjusting behavior based on the identity of the signaler was the most beneficial strategy. Identity signaling may be selected for because of the fitness benefits of individual recognition and the adjustments in behavior that result from it which can, in turn, influence various characteristics of social groups, the way that they are formed, and the dynamics of their collective movements and behaviors (Rios & Kraenkel, 2017). However, it is also possible for information to spread and collective behaviors to emerge within groups in the absence of recognition (Couzin et al., 2005). The relationship between individual recognition abilities and other social phenomena is still very poorly understood. It is hard to explain how familiarity, for example (whose consequences are discussed in the next section), could be kept track of without some sort of individual recognition system.

The effects of social stability and familiarity

In many species, familiarity and social stability allow for tolerance (at the least), which is an important precursor to cooperation (Croft et al., 2006; Griffiths, Brockmark, Höjesjö, & Johnsson, 2004; Wilkinson, Carter, Bohn, & Adams, 2016). Cooperation is most likely to be maintained when the probability that an individual will receive some benefit for cooperating

with others is relatively high, and this is most likely to occur in populations with a stable social structure and assortment by co-operators (Croft, Edenbrow, & Darden, 2015).

However, it's important to note that the ability to change or terminate social ties in a non-random manner is also important to the maintenance of cooperation; if individuals break ties with uncooperative partners and prefer cooperative ones instead, cooperation can stabilize within a network (E. Akçay, 2018; Rand, Arbesman, & Christakis, 2011). This highlights not only the relationship between social structure and the maintenance of cooperation, but also the utility of taking a social network approach.

An illustrative example of the effects of familiarity and social stability can be seen in the dear enemy effect. Here, residents of a territory will be less aggressive toward familiar neighbors, resulting in decreased energy expenditure on territory defense (i.e. a benefit) for both parties (Tumulty, 2018). Godard (1993) simulated intrusions (using audio playback of song) by strangers or by familiar neighbors in the territories of male hooded warblers' (*Wilsonia citrina*) and subsequently recorded the responses of focal individuals to their neighbors' songs. Individuals responded more aggressively to their neighbors after a simulated neighbor intrusion but not after a simulated stranger intrusion. In a similar study, Akçay et al. (2009) found that male song sparrows (*Melodia melospiza*) react more strongly to the calls of neighbors who were part of a simulated intrusion than towards "neutral" neighbors. These studies suggest that individuals will conditionally cooperate with their familiar neighbors (through tolerance and decreased aggression) as long as their neighbors do the same (i.e. do not intrude).

The dear enemy effect has also been demonstrated in a more explicit form of cooperation: joining in neighbor nest defense. In their study of nest defense among familiar great tit neighbors, Grabowska-Zhang et al. (2012) used simulated nest box intrusions during the

breeding season to look at whether or not neighbors would join in mobbing the “intruder.” They found that individuals who had shared a territory boundary in the previous year (and were therefore familiar) were more likely to join in nest defense than unfamiliar neighbors, demonstrating the direct benefits of familiarity. Furthermore, in the same population, having familiar neighbors during the breeding season comes with fitness benefits (Grabowska-Zhang, Wilkin, & Sheldon, 2012). Specifically, males and females with more familiar neighbors were more likely to have successfully fledged offspring. Even when active cooperation is not apparent, familiarity among individuals seems to be beneficial to the parties involved. Moreover, familiarity can transfer across time and settings, meaning that social interaction with others may be relevant to reproductive success even outside of this context (Firth & Sheldon, 2016; Shizuka et al., 2014)

Study system

This research will take place within the long-term study site (1947 - present) of Wytham Woods, Oxford, UK, where wild passerine birds, including great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*), and European nuthatches (*Sitta europaea*) live and breed. Tits at Wytham Woods forage in mixed-species flocks with fission-fusion dynamics that can additionally be joined by other species like tree-creepers (*Certhia familiaris*) and goldcrests (*Regulus regulus*) (Farine et al., 2015; Hinde, 1952). Dominance is related to body size both within and among species, with great tits, males, and adults being most dominant in these groups (Morse, 1978; Perrins, 1979). In this population, individuals continue to associate and interact with the same conspecifics over time, with evidence of non-random dyadic relationships and short-term community structure arising within the social network (theoretically) making way for cooperation (Firth & Sheldon, 2015, 2016). Individuals have been shown to reduce their own access to food in

order to maintain their social ties with their partner, going so far as to “innovate” new feeding techniques in order to reduce the costs of social relationships (Firth, Voelkl, Farine, & Sheldon, 2015b). Furthermore, relationships from the breeding season “carry over” to other seasons and contexts (Firth & Sheldon, 2016).

There are over 1,200 nest boxes installed across the 385ha of mixed deciduous woodland, which is surrounded by farm and grasslands (Savill et al., 2010). During the breeding season (March-May) around 60% of the boxes are occupied, mostly by great tits and blue tits. The boxes are visited regularly throughout the season by field workers to determine the first egg date, number of eggs, average egg weight, number of chicks, and fledgling success for each breeding attempt. Parents are also caught (between days 6-14 after first hatch) to determine their identity, sex (based on the presence of a brood patch), age class (based on plumage characteristics) and other morphometrics (wing, weight, tarsus), and un-ringed parents and all chicks are fitted with a unique BTO (British Trust for Ornithology) metal ring (after day 15) for future identification. Outside of the breeding season, individuals are caught (September-February) using mist nets in order to record morphometrics and ring immigrant birds or those that were born in natural cavities.

Since 2007, birds (excluding coal tits) are also fitted with plastic rings that house a passive integrated transponder (PIT tag). They remain inactive until coming within the range of a Radio Frequency Identification (RFID) antenna, prompting the tag to transmit a code that identifies each bird. These tags are lightweight (<0.1g), inexpensive (~£2), and highly accurate. Furthermore, PIT tags do not seem to be detrimental to the fitness of birds or influence their behavior in any way (Nicolaus, Bouwman, & Dingemanse, 2008; Schroeder, Cleasby, Nakagawa, Ockendon, & Burke, 2011). Bird feeders with RFID antenna (Dorset ID, Aalten, Netherlands) can automatically record the PIT tag code of each arriving individual,

generating a time, date, and location stamped record of each feeder visit. All in all, these tags along with the RFID feeders are extremely suitable for tracking wild birds over the course of their lifetime.

In addition to tracking the usual behavior of birds, RFID technology can also be used to create experimental feeding stations through selective feeding (Firth & Sheldon, 2015; Firth et al., 2015b). These feeders are fitted with a clear flap that covers the feeding hole that is locked into place. The mechanism to “unlock” the flap is activated (for two seconds) when certain PIT tag codes are registered by the RFID antenna (controlled by a programmable circuit board; Stickman Technologies, Southampton, UK). By specifying a certain set of PIT tag codes, rules that govern which individuals have access to the feeders can be automatically imposed. Although these feeders record the visits of all individuals, only those with the right PIT tag codes can actually access the food. In this way, we can manipulate where particular birds can feed. This approach also allows for the possibility of studying “scrounging”: a bird without access can arrive within two seconds of a bird with access, in order to feed at a feeder that they do not have access to (Firth et al., 2015b). How do birds perceive and learn who has access to which feeders? Data collected with these feeders will be used to explore various aspects of social behavior.

Thesis Outline

Using a social network approach is vital to gaining a better understanding of the maintenance and spread of cooperation. In **Chapter 2**, I examine the utility of the social network approach to studies of cooperation. I provide a thorough theoretical overview of cooperation, explore existing work on cooperation among kin and non-kin, and introduce social network analysis as a promising tool for furthering our understanding in this area. I review existing studies of cooperation in natural populations both with and without a social network approach. I then

propose future directions for the study of cooperation through a social network approach, emphasizing the importance of working with natural populations and the added benefit of having long-term data.

The extent to which individuals can recognize, remember, and keep track of conspecifics has important implications for the mechanisms that allow for cooperation in different populations. In **Chapter 3**, I review the concept of individual recognition and propose a new focus (on multiplicity, specificity, and longevity) in order to gain a better understanding of whether or not individuals can recognize others. I further suggest that the social network approach can be used to bring together studies of individual recognition and social structure in order to gain a more complete picture of the mechanisms that allow for cooperation and other social processes to occur.

I begin to build on this theoretical work by exploring the processes that may have an impact on cooperative behavior in **Chapter 4** which looks at leading behavior during mixed-species foraging. In all collective behaviors, there are some individuals that are more likely to initiate an activity or guide the group. What determines who will be the leader? In this chapter, I show that leading is influenced by motivation and dominance, where great tits (the largest and most dominant individuals) are most likely to be leaders. I additionally emphasize the utility of null models to tease apart various effects and drivers of leading behavior. Although leading behavior may be influenced by various aspects of the individual, I use null models to show that the observed effect of sex and activity level on leading rates is actually being driven by spatial and temporal dynamics (i.e. where individuals are and when they are there). Males feed more often at locations with higher levels of activity and at times when they are more likely to be leading.

Preferences in where to feed, and where to breed, are also related to social relationships and familiarity that may have consequences for future breeding success. Across many taxa, familiarity is a precursor for social tolerance (Aragón, López, & Martín, 2007). As discussed above (p. 5), having familiar neighbors (previous years' neighbors and/or winter familiarity) during the breeding season leads to increased cooperation among neighbors and increased reproductive success (Firth & Sheldon, 2016; Grabowska-Zhang, Sheldon, et al., 2012; Grabowska-Zhang, Wilkin, et al., 2012). In **Chapter 5**, I use long-term breeding data to assess the relationship between partner familiarity, neighbor familiarity, and breeding success. Utilizing Integrated Nested Laplace Approximation (INLA) with the stochastic partial differentiation equation (SPDE) allows for the control of spatial autocorrelation to simultaneously uncover spatial and social mechanisms that drive this fitness benefit. I find that neighbor familiarity has a positive influence on reproductive success for females, while partner familiarity has fitness benefits for both sexes. Although spatial autocorrelation in reproductive success exists, the benefits of pair and neighbor familiarity persist over and above these effects.

Dyadic bonds exist between other individuals in addition to those with partners and neighbors. At the most basic level, individuals have spatial associations with others that they spend time around outside of reproduction or the breeding season. Individuals also have social associations outside of the breeding season with other individuals that are not only physically close to them but are also part of their in-group (Massen, Sterck, & De Vos, 2010). These four levels of dyadic bonds (spatial, social, neighbor, partner) may contribute to fitness in different ways. In **Chapter 6**, I use three years of social network data from the winter and breeding data from the spring to examine the consequences of these different types of dyadic relationships. I demonstrate that these different kinds of bonds do have different effects on

reproductive success. Surprisingly, I do not find a positive influence of over-winter neighbor bonds on fitness, and I discuss the possible role of individual recognition and cooperation in these relationships.

I will conclude with a brief general discussion in **Chapter 7**, summarizing my findings. All in all, I aim to clearly and concisely bring together our understanding of various social phenomena and their spatial underpinnings in an ecologically relevant context, the natural population of wild passerine birds at Wytham Woods, while also gaining new insights into the biological processes that allow for social behavior and cooperation.

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Chapter 2

Exploring the causes and consequences of cooperative behavior in wild animal populations using a social network approach

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Exploring the causes and consequences of cooperative behaviour in wild animal populations using a social network approach

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ABSTRACT

Understanding why individuals carry out behaviours that benefit others, especially genetically unrelated others, has been a major undertaking in many fields and particularly in biology. Here, we focus on the cooperation literature from natural populations and present the benefits of a social network approach in terms of how it can help to identify and understand factors that influence the maintenance and spread of cooperation, but are not easily captured when solely considering independent dyadic interactions. We describe how various routes to cooperation can be tested within the social network framework. Applying the social network approach to data from natural populations can help to uncover the evolutionary and ecological pressures that lead to differences in cooperation and other social processes.

Key words: cooperation, social network, assortment, social structure, reciprocity, mutualism

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I. INTRODUCTION

Theorists and scientists across disciplines have struggled to understand the evolutionary origins of cooperative behaviour for decades (Hardin, 1968; Axelrod & Hamilton, 1981); if organisms are working to maximise their

own survival and reproduction, why do they cooperate with others? Why are cooperative behaviours so widespread and how can we explain the cooperation that occurs across a variety of contexts? Although we now have a broad idea of why cooperation may exist (see Section I.1), the proximate mechanisms that allow for cooperation in natural populations are

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not well understood. A wide range of behaviours among many organisms have been described as cooperative, from the release of beneficial exoproducts or exoenzymes in bacteria to the regurgitation and sharing of blood in vampire bats (Czárán & Hockstra, 2009; Wilkinson *et al.*, 2016).

There are various ways to define and operationalise cooperation which reflects the multi- and inter-disciplinary nature of research in this area. Cooperation is studied in various sub-fields of biology, anthropology, psychology, sociology, economics, and political science, and there has been much variation in the way that it is defined, even within disciplines. It seems that definitions are often chosen to fit the specific context that is being studied or the nature of the 'cooperative' behaviour that can be quantified. Here, we adopt a widely accepted biological definition of cooperation: a behaviour that confers a direct fitness benefit on the recipient while providing a fitness benefit to the actor (either indirectly, directly, or both; Sachs *et al.*, 2004).

We can further categorise cooperative behaviours by considering if the behaviour incurs a net cost to the direct fitness of the actor (in which case it is altruistic) or not (mutualistic; Fig. 1). Mutualism refers to any interaction that involves direct benefits to both parties, either through a by-product of the interaction or reciprocity (generalised, direct, or indirect; discussed further in Section I.1). As West, El Mouden &

Gardner (2011) discuss, there seems to be a general feeling among researchers that altruistic behaviours are more puzzling than those that are mutually beneficial. However, possible decreases in the relative fitness of the cooperator are what make both scenarios interesting.

(1) Forms of cooperation

Mutualistic cooperative interactions, where there is no net cost to the actor, are instances where there are benefits to both individuals because their combined efforts lead to greater benefits than if each individual had acted on its own, or not at all (Clutton-Brock, 2009; Leimar & Hammerstein, 2010). Some restrict the term 'mutualism' to inter-specific mutualism (West, Griffin & Gardner, 2007); for the purposes of this review, all mutually beneficial behaviours are considered as mutualism and are labelled as inter-specific if this is the case. Mutualism can occur in many ways: through *by-product mutualism*, where an individual benefits from the behaviours of another that would be occurring anyway (West-Eberhard, 1975; Grinnell, Packer & Pusey, 1995); *by-product or pseudo-reciprocity*, where an individual benefits from the behaviours of another that would be occurring anyway by aiding them in some way (Bygott, Bertram & Hanby, 1979; Connor, 1986); or through *coercion*, where there are

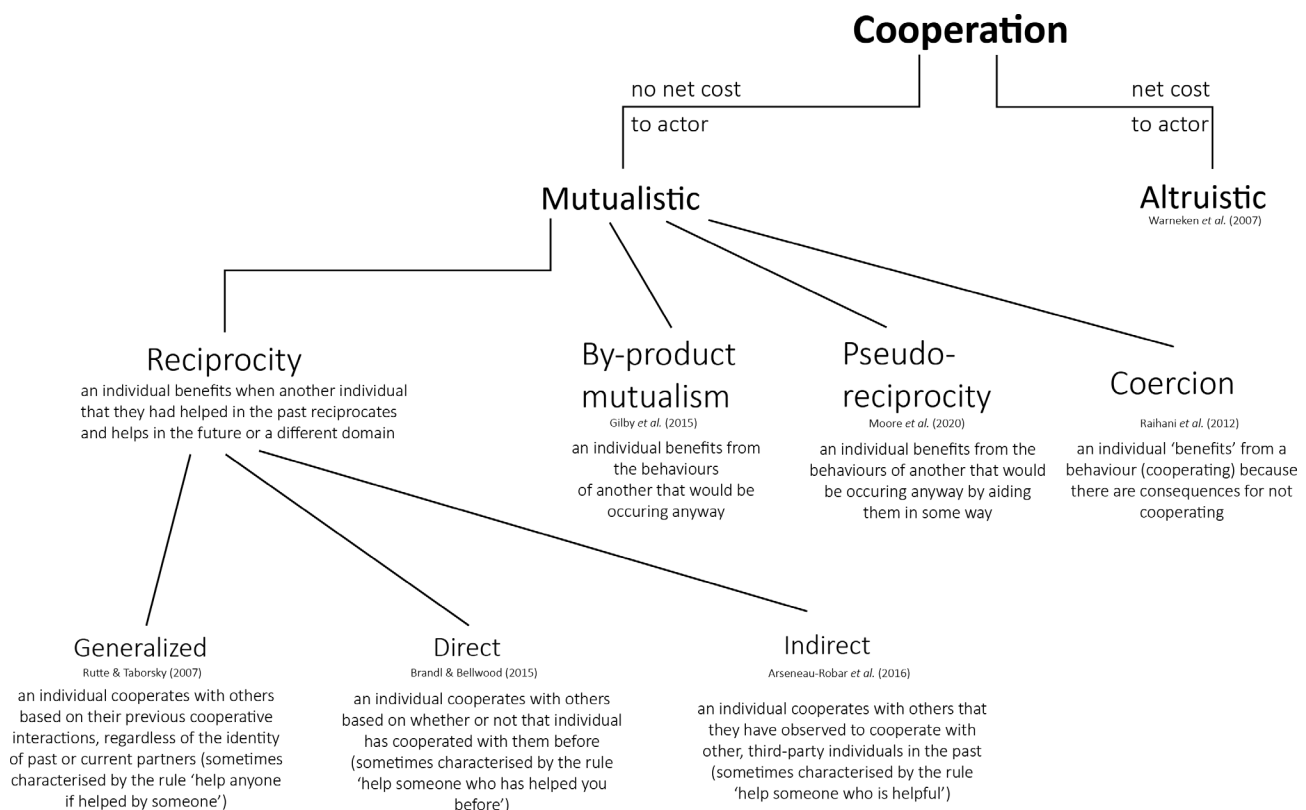


Fig 1. A simple visual representation of how different types of cooperation are related to one another, with an example and short definition of each (Rutte & Taborsky, 2007; Warneken *et al.*, 2007; Raihani, Grutter & Bshary, 2012; Brandl & Bellwood, 2015; Gilby *et al.*, 2015; Arseneau-Robart *et al.*, 2016; Moore *et al.*, 2020).

consequences for not cooperating (Kokko, Johnstone & Wright, 2002; Noë, 2006; Raihani *et al.*, 2012).

A subset of mutualistic cooperation occurs in the case of reciprocity, where individuals that the actor had once helped in the past will reciprocate and help them in the future or in a different domain (Trivers, 1971). This is especially relevant in stable populations where individuals can track and remember the contributions of individuals over time, but reciprocity can also occur in relatively simple, unstable, and changing populations (Kern & Radford, 2018; Smith *et al.*, 2018). Cooperation through reciprocity is more likely to evolve in situations where the cost of helping is low, the benefit to the receiver is high, and/or there are frequent opportunities for helping behaviour (Taborsky, Frommen & Riehl, 2016).

Sachs *et al.* (2004) identify two mechanisms that can enable reciprocity: partner choice and partner-fidelity feedback. In partner choice, an individual (x) has the opportunity to choose who to cooperate with (y or z), based on who will provide greater fitness benefits in return. In the case of partner-fidelity feedback, when one individual (x) cooperates with (y) for an extended period of time, they become “coupled in fitness” through feedback (Sachs *et al.*, 2004, p. 137). When y benefits from x, x also benefits indirectly by having a ‘better’ cooperative partner in y. Because of this, if x does not cooperate with y, their own fitness will also decline – meaning that they are then “coupled in fitness”.

In *generalised reciprocity*, perhaps the most basic form of reciprocity, individuals are more likely to cooperate if they have had cooperative interactions in the past, regardless of the identity of past or current partners (van Doorn & Taborsky, 2011); this form of reciprocity does not require memory of the partner but only of the nature of the interaction, that is cooperation or defection (Voelkl, 2015). Cooperation can emerge and be maintained through generalised reciprocity alone if individuals are repeatedly interacting in small social groups (Pfeiffer *et al.*, 2005). Captive rats (*Rattus norvegicus*), capuchin monkeys (*Cebus apella*), and dogs (*Canis familiaris*) have been shown to engage in generalised reciprocity when tested on a cooperative task requiring the pulling of a stick or rope which presents food to their partner (Rutte & Taborsky, 2007; Leimgruber *et al.*, 2014; Gfrerer & Taborsky, 2017). In a more recent study (Darden *et al.*, 2020), a predator inspection arrangement was used to explore cooperation in Trinidadian guppies (*Poecilia reticulata*), showing that individuals would either stay with or switch their social partner on the basis of whether the partner had cooperated or defected in their most recent interaction (see Section I.3).

Direct reciprocity is one of the most widely hypothesised routes to cooperation in animals but is also a highly contested explanation (Clutton-Brock, 2009). Here, individuals are more likely to cooperate with others that have cooperated with them before. In a study of avian cooperation, Voelkl *et al.* (2015) investigated human-guided migratory V-formation flight in captive northern bald ibises (*Geronticus eremita*). Birds switched positions with the leader frequently to match the leaders’ leading time to their own. More

generally, the amount of time an individual spent as the leader was strongly positively correlated with how much that individual could benefit from being a follower. Direct reciprocity seems to require not only memory and individual recognition – the recognition and tracking of other individuals’ identities and actions to guide future interactions and behaviour – but also numerical discrimination (distinguishing between many instances of something *versus* a few instances) and the ability to account for benefits that will come in the future (Stevens & Hauser, 2004; McAuliffe & Thornton, 2015). Challenging the idea that reciprocity is cognitively complex or demanding, Brandl & Bellwood (2015) describe the ‘coordinated vigilance’ of coral reef rabbitfishes (Siganidae); one individual remains vigilant while the other forages (allowing for more efficient and thorough foraging), and pairs alternate between these two roles relatively equally. They argue that advanced social skills or complex cognition are not necessarily essential to the emergence and maintenance of direct reciprocity in animals.

Finally, the most complex form of reciprocity is *indirect reciprocity*: where individuals are more likely to cooperate with conspecifics that they have observed to cooperate with others before – this presumably requires the ability to remember and keep track of conspecifics and the interactions that they engage in. This has been discussed in terms of ‘image-scoring’, where individuals keep track of the cooperative behaviours of others and increase or decrease their scores based on cooperation or defection (Nowak & Sigmund, 1998) – a process that requires individual recognition (Tibbetts & Dale, 2007). Whether or not animals can engage in this image-scoring is a matter of great debate across many disciplines due to the proposed role of complex cognition in recognising and remembering the behaviours of conspecifics interacting among themselves (Wiley, 2013). Nevertheless, existing studies suggest that non-human animals do engage in indirect reciprocity. This has been demonstrated in: (i) birds, in the context of sentinel behaviours and experimental manipulations using the ‘dear enemy’ effect, when there is a mutual decrease in aggression among neighbours at the territory boundary that comes with increased familiarity (Akçay *et al.*, 2010; Bell *et al.*, 2010); (ii) fish, where cleaner fish engage in behaviours consistent with image-scoring and prefer more cooperative cleaners (Bshary & Grutter, 2006); and (iii) primates, in the formation of coalitions and defence of food resources (Berghänel *et al.*, 2011; Arseneau-Robar *et al.*, 2016).

Studies of human cooperation have also considered the possibility that individuals cooperate in order to increase their reputation or signal something about themselves to others (Lotem, Fishman & Stone, 2003; van Vugt & Hardy, 2010). This has been discussed in terms of ‘costly signalling’, where cooperation emerges as way to signal one’s competence or quality as a reproductive or coalition partner, or competitor (Gintis, Smith & Bowles, 2001). Several studies entertain this possibility by looking for the presence or absence of audience effects (changes in behaviour in the presence of others) on various cooperative behaviours. While

some find increases in cooperative behaviours when audiences are present (Hector, Seyfarth & Raleigh, 1989; Doutrelant & Covas, 2007), others fail to find an effect (McDonald *et al.*, 2008; Schweinfurth & Taborsky, 2016), or find the opposite (i.e. more cooperative behaviour without audience; Brügger, Kappeler-Schmalzriedt & Burkart, 2018); scepticism exists as to whether or not non-human animals adjust their behaviour in this way.

It is important to consider the possibility that these seemingly more complex routes to cooperation can also be maintained in different, less cognitively demanding ways (Carter, 2014). For example, Tognetti *et al.* (2017) suggest that cooperation may be maintained through sexual selection; if the 'cooperative phenotype' is associated with other sexually selected traits then cooperation can evolve and be maintained through its association with them. Steppe mice (*Mus spicilegus*) invest in cooperative mound building, which can be understood as a form of parental care (Tognetti *et al.*, 2017). After classifying males as more or less cooperative based on their mound building investment in the autumn, Tognetti *et al.* (2017) exposed females to one high-cooperation male and one low-cooperation male in pairs during the breeding season. Choosing a mate that makes higher investments in mound building can lead to having a larger mound which can increase the probability of offspring survival. Each pair of males had either been previously observed by the females during mound building or not. Tognetti *et al.* (2017) found that more cooperative males are preferred regardless of whether or not they were previously observed by the females, indicating that a preference for more cooperative individuals is not necessarily indicative of indirect reciprocity. It is possible that cooperative propensity is correlated with another attractive, sexually selected trait. Further research is necessary before coming to any conclusions about the skills or cognitive characteristics that are essential to these forms of cooperation and whether or not various non-human animals are capable of engaging in them.

(2) A social network approach to cooperation

Cooperative behaviours are intrinsically social, with two or more individuals interacting. Accordingly, understanding the mechanisms of cooperation requires an investigation of characteristics of social interactions at the dyadic, group, and population level. Social network analysis provides a variety of tools to look at the relationship between an individual's behaviours and the structure and characteristics of their social interactions (Croft, Darden & Wey, 2016). In some populations, cooperative behaviour and social network structure may have a complementary relationship, where the assortment and organisation of individuals allows for cooperation to spread more or less easily (Fehl, van der Post & Semmann, 2011). By systematically describing social structure at the population and individual level, social networks can help us understand how the social environment impacts individuals differently based on their position within the network. Due to the direct link between social network structure

and the maintenance and spread of cooperation, which will be explored in this review, social network analysis can be a powerful tool for empirically testing questions about cooperative behaviour that have been previously left unanswered. For example, Covas & Doutrelant (2018) stress the roles of social and sexual selection in maintaining cooperation, and point to advances in social network analysis as a promising avenue to understanding how selection pressures influence cooperation in natural populations.

When taking a social network approach, various measures of social relationships and structure can be extracted which give us insights into the nature and strength of pathways and bonds among and between different individuals and groups (Farine & Whitehead, 2015). At the most basic level, social networks consist of nodes which represent single entities or components (usually an individual but can also be a group) and the edges (sometimes referred to as links or ties) or relationships (interactions or associations) among them. Edges can have different weights or directions to provide information about the nature of relations between nodes. Using this basic information, various measures of the social network can be extracted. These measures can be grouped into three levels (Wey *et al.*, 2008): individual, intermediate, and group. The individual (or local) network measures reveal information about particular, single nodes in the network while intermediate measures provide information about how edges are distributed within the network. Group (or whole) network measures account for all of the nodes and edges within the network and can give us a sense of overall social structure. Network metrics that are particularly relevant to cooperation are shown in Fig. 2.

Social network measures and positions can also be related to other social characteristics (Wilson *et al.*, 2013). For example, different levels of social connectivity may be associated with the likelihood that an individual can acquire and spread novel information or behaviours (Firth, 2020). Network positions have also been linked to stable differences in personality (Aplin *et al.*, 2013; Díaz López, 2020). More generally, individuals in more central positions may have a higher chance of entering cooperative interactions than less social individuals who may be at the periphery of the network. This can be further linked to personality differences (e.g. if bold individuals are more likely to be in central network positions). As discussed earlier, the characteristics of the entire social network can also give us an idea of how likely it is for cooperation to be maintained or spread in certain types of networks or populations (Luthi, Pestelacci & Tomassini, 2008).

The advantages of using a social network approach to understand cooperation and other emergent social properties better in animal populations have been considered by many scholars (Wey *et al.*, 2008; Sih, Hanser & McHugh, 2009; Kurvers *et al.*, 2014; Croft, Edenbrow & Darden, 2015; Farine & Whitehead, 2015; Croft *et al.*, 2016), and various empirical examples are beginning to emerge (see Section III). In particular, the social network approach is useful because it can be used to: (i) examine the relationships between properties of single individuals and

Measure	Definition	Visualisation	Potential implications for cooperation
Direct measures: measures related to the ties that a particular individual has	Number of edges (node degree)	The number of edges a particular node has	Populations with a low average node degree may be more likely to cooperate (van Doorn & Taborsky, 2011)
	Strength of edges	The strength or weight of the edges a particular node has; based on the number of interactions or associations among two nodes	Individuals with stronger connections (or, in other words, higher familiarity) may be likely to cooperate with one another (Croft <i>et al.</i> , 2006)
Indirect measures: measures related to the ties of all of the individuals that a particular individual is associated with	Betweenness centrality	Centrality based on the extent to which a node 'bridges' the network which is calculated as the number of times a node appears on the shortest pathways between every other pair of nodes; gives an idea of how important an individual is for connecting different parts of the network	Cooperative individuals with high betweenness centrality may foster cooperation by allowing for the 'bridging' of different social clusters or groups that would not interact or cooperate in their absence (Edelman & McDonald, 2014)
	Eigenvector centrality	Centrality based on the centralities of a node's edges; high centrality can reflect a high node degree or having edges with many nodes that have a high degree	If individuals with high eigenvector centrality are cooperative, cooperation may be more likely to spread (Bird & Power, 2015)
Centrality measures: express how structurally important an individual is on the basis of their network position in different contexts	Clustering coefficient	Calculated by dividing the number of edges an individual has with their neighbours by the maximum amount of edges that could exist among neighbours; gives an idea of how well connected an individual's immediate network is	More clustered networks may be more likely to allow for the spread of cooperation, especially through reciprocity; this is amplified if individuals are clustered by cooperativeness (Fehl <i>et al.</i> , 2011)

Fig 2. A sample of network metrics relevant to studies of cooperation. The nodes are coloured to denote examples of high (x, yellow) or low (y, purple) values of each metric.

processes that occur at the group level, rather than considering these aspects separately (Farine & Whitehead, 2015); (ii) quantify the strength, persistence, and dynamics of social ties and individual changes in network positions; (iii) understand how network positions, measures of group connectivity, and social structure may be linked to individual or group levels of cooperative behaviour (Eguíluz *et al.*, 2005; Clutton-Brock, 2009); (iv) gain a more holistic understanding of how individuals interact and how these interactions impact the spread of cooperative behaviour in different social structures, through the identification and quantification of indirect

connections (Brent, 2015); and (v) predict, measure, or even manipulate who cooperates with whom (Croft *et al.*, 2006).

Limiting studies of cooperation to behaviour among dyads can have several limitations that can be accounted for by using the social network approach. A wide range of studies have shown that interaction with or the presence of third-party individuals can influence dyadic cooperative interactions (Connor, 2010; Earley, 2010; Aplin *et al.*, 2013; Ilany & Akçay, 2016; Newton-Fisher & Kaburu, 2017; Brügger, Willems & Burkart, 2021). By using a network approach, we can expand our understanding from dyadic interactions

to taking account of the whole social structure, therefore giving us a more complete picture of cooperation that occurs in different populations.

Examining social structure through the social network approach becomes even more pertinent when considering direct *versus* indirect genetic effects on phenotypic variation in cooperation (Dakin & Ryder, 2018). Direct effects on phenotype are based on variation among individuals in their 'intrinsic biology' while indirect effects are related to the influence of the social environment (Dingemanse & Araya-Ajoy, 2015; Dakin & Ryder, 2018, p. 1). As Kasper & Voelkl (2009) argue, while traditional research investigating social behaviour can sometimes be clouded by the complex interactions of various factors, social network analysis allows us to study the interactions themselves, alongside the behaviours that they are impacting. Furthermore, the ability to utilise social network analyses with data from natural populations allows for the study of cooperation in a more ecologically relevant manner. What is necessary now is a control for and/or explicit investigation of how complex long-term social interactions and structure influence cooperative behaviour and *vice versa*. As such, experimental approaches to manipulating, quantifying, and evaluating natural animal populations' social networks are needed to gain a better understanding of cooperation (see Section III.3).

(3) Assortment by cooperation

Identifying the social network structure of a population is also crucial for understanding how cooperation spreads and is maintained in that population because of the importance of assortment (Fletcher & Doebeli, 2009; Croft *et al.*, 2015). One route to assortment by cooperation results from spatial population structure (non-random spatial distribution) where individuals with similar phenotypic or behavioural traits are clustered in space, and this spatial structure drives social structure (Nowak, Tarnita & Antal, 2010). When individuals are neighbours in physical space, it is more likely that they will interact with one another. Furthermore, similar phenotypes may have similar space-use preferences, making spatial assortment even more likely (Schirmer *et al.*, 2019). It is also possible for populations to have a similarly non-random social distribution. Individuals of the same phenotype may be more likely to interact with one another and have stronger bonds regardless of their physical distance (Farine, 2014; Firth & Sheldon, 2016), for example if their phenotype governs the type of social interaction they are likely to engage in. This clustering of cooperators can allow for cooperation without assortment in spatial structure (Antal *et al.*, 2009). More generally, individuals have been found to assort by phenotype with regard to age, sex, dominance rank, and even personality (Carter *et al.*, 2015; Johnson *et al.*, 2017; Perryman *et al.*, 2019).

When there is assortment based on cooperation, cooperative individuals are more likely to interact with other cooperators, allowing them to obtain higher fitness benefits than those that do not cooperate in the same network (Nowak

et al., 2010; Brask *et al.*, 2019). In other words, cooperation can be selected for when there are non-random associations between individuals of similar phenotypes (Pepper & Smuts, 2002; Rankin & Taborsky, 2009). The characteristics of social networks therefore have an inevitable influence on how cooperation can spread or be maintained in that population (Bergmüller, Schurch & Hamilton, 2010).

Initial studies have suggested that there may be a correlation between measures of cooperation (e.g. propensity to cooperate, number of cooperative partners, etc.) and other phenotypic traits (Croft *et al.*, 2009). If this is the case, assortment based on other phenotypic traits may also lead to assortment based on cooperation (Croft *et al.*, 2015). However, some studies have shown that cooperative propensity is not repeatable over time and can vary based on an individual's internal (Wright, Maklakov & Khazin, 2001; Young, Carlson & Clutton-Brock, 2005; Scheid & Noë, 2010; Madden & Clutton-Brock, 2011) and external (Komdeur, 2006; Nichols *et al.*, 2012) environment. On the other hand, others report stable qualitative and quantitative individual differences in cooperative behaviour (reviewed by Bergmüller *et al.*, 2010; English, Nakagawa & Clutton-Brock, 2010; Le Vin *et al.*, 2011; Sanderson *et al.*, 2015; Wismer *et al.*, 2014). Further work is needed to gain a better understanding of the 'cooperative phenotype' and what explains the stability of this trait within individuals. As Bergmüller *et al.*, 2010 discuss, one of the main challenges of studying the cooperative phenotype is trying to tease apart variation due to social interactions and social structure as well as other non-social factors; social network analysis can be used to control for social relationships (by including whole networks in models, or by extracting metrics like strength or degree) when assessing overall cooperative propensity.

In the absence of a spatial or social distribution, conditional cooperation can also lead to assortment by cooperation in social networks. When there are repeated interactions between individuals, an individual's current behaviour and who they choose to interact with may be based on the previous behaviour of their social partners. Contingent responding is also possible through more basic movement rules or heuristics like the 'walk away' rule, which simply entails moving away from an individual in physical space once they defect once (Aktipis, 2004; Darden *et al.*, 2020). Network 'rewiring', or the ability of individuals to terminate or change social ties, is an important aspect of the maintenance of cooperation (Rand, Arbesman & Christakis, 2011). Cooperation is more likely to evolve in social systems where the random creation of social ties is low (Akçay, 2018), and it is important to keep in mind that rewiring can occur passively – due to turnover and general demographic and fission–fusion processes (Shizuka & Johnson, 2020). These factors can all be accounted for when using social network analysis to look at network structure and composition over time.

The utility of a social network approach for understanding how cooperation can be maintained in natural populations is clearly illustrated by a study of cooperation in the Hadza,

a human hunter–gatherer population (Apicella *et al.*, 2012). By asking individuals about who they would live with in the next camp and who they would donate honey to, Apicella *et al.* (2012) created two networks (“campmate” and “gift”) to look at how Hadza social network structure compares to a random one. All individuals were more likely to choose others who had chosen them (without being aware of this) in both networks even when controlling for genetic relatedness, suggesting that reciprocity may maintain cooperation among both kin and non-kin. Furthermore, social ties were more likely among individuals with similar physical characteristics (age, height, mass, body fat, and handgrip strength) and among individuals with similar cooperative tendencies. More specifically, there are clusters of cooperators – with more between- than within-camp variation in cooperative behaviour (Apicella *et al.*, 2012, p. 499). As individuals who donate more did not have higher measures of in- or out-degree, it is unlikely that all individuals in this population are consistently preferring cooperators. It seems that cooperators prefer to interact with cooperators. The authors emphasise the idea that cooperation is impacted by social network structures; they suggest that cooperation and the behaviours that underpin social structure may have evolved together.

Reviewing the causes and consequences of assortment by cooperation in social networks, Croft *et al.* (2015) stated that understanding the mechanisms that allow for “assortment among cooperators” is the “key” to understanding cooperation among non-kin. Accordingly, herein we examine the utility of applying social network approaches to empirical data from natural populations for uncovering the mechanisms that allow for the maintenance and spread of cooperation.

II. EXISTING WORK

(1) Existing work on cooperation in natural populations

It is possible that different combinations of multiple factors are influencing the presence or persistence of cooperation in different animal populations (Krützen *et al.*, 2003). Existing studies of cooperation among non-kin in non-human animals are detailed in Table 1, which demonstrates the wide range of behaviours that have been studied as cooperation. There is no standardised way to test cooperation in natural populations, nor is it always clear that tests actually measure cooperation. For example, a string-pulling task has often been used with captive populations to look at individual differences in cooperative propensity/ability. This usually consists of some form of an apparatus where food is on a shelf behind a mesh. The shelf is connected to a string on each side. If only one side of the string is pulled, the shelf is either pulled into a position where the food is still out of reach, or the string comes out of its nook and the shelf can no longer be pulled. However, if both individuals pull the string, the

food is moved within reach. However, whether this is a test of cooperation or coordination is unclear and it seems that individuals can solve the task without necessarily understanding or engaging in the cooperative component, as individuals can continue to solve the task even when visual access to the other participating individual is blocked (Tassin De Montaigu *et al.*, 2019). Understanding cooperation is challenging, as cooperative behaviours in different populations may be maintained by different mechanisms and similar populations may maintain the same type of cooperation in different ways.

It is important to keep in mind that the studies in Table 1 explicitly set out to examine cooperation; many studies with a different focus, but which fit under the various definitions of cooperation in Section (1) may be missing. For example, studies that consider various aspects of social tolerance, food-sharing, signalling/alarm-calling and other behaviours that are generally accepted as prosocial (defined as unsolicited acts of help or assistance to others) can give us insights into the way cooperation spreads or is maintained in natural populations (Brown, Brown & Shaffer, 1991; Jaeggi, Burkart & Van Schaik, 2010; Jaeggi & Gurven, 2013; Bonadonna *et al.*, 2020). There may be other systems which are well suited for the study of cooperation that have not previously been directly framed in this context.

Finally, there is some inherent overlap in cooperation and social interaction/association; many of the behaviours described as cooperation in the studies listed in Table 1 can also be used in the construction of social networks. This is especially apparent for the primate literature where grooming associations can be used to construct social networks and describe social structure, but grooming can also be understood as a form of cooperation in itself (Cheney *et al.*, 2010; Kawazoe & Sosa, 2019; Wooddell, Kaburu & Dettmer, 2019). Moving forward, it is important to ensure that, if we are studying cooperation with a social network approach, the measure of spatio-temporal co-occurrence that is used to ascertain social structure does not overlap with the behaviour that has been defined as cooperative in that population.

(2) Existing modelling of cooperation

Early work modelling cooperation revealed several insights about the way cooperation may spread in structured populations. As reviewed by Croft *et al.* (2015), cooperation is more likely to spread in networks where assortment by cooperation is higher; this is especially the case when networks are dynamic and heterogeneous with low connectivity. Previous modelling studies have shown that social structure can give rise to properties like resilience to loss (Lusseau, 2003) or a decrease in social contagion (Jordan *et al.*, 2013), which can have important consequences for cooperation. When Luthi *et al.* (2008) simulated three games in three types of social networks they found that cooperators were more likely to be in positions that maximised their links to other cooperators – a property which encourages the spread of cooperation.

Table 1. Studies examining non-kin cooperation in natural non-human populations

	Study	Species	Sample size	Cooperative act
Bird	Godard (1993)	Hooded warbler (<i>Wilsonia citrina</i>)	12	Mutual restraint in aggression
	McDonald & Potts (1994)	Long-tailed manakin (<i>Chiroxiphia linearis</i>)	33 pairs of males	Courtship
	Krams & Krama (2002)	Chaffinch (<i>Fringilla coelebs</i>)	76	Interspecific mobbing of predators
	Krams, Krama & Igaune (2006b); Krams <i>et al.</i> (2008)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	34 pairs of nest boxes, 44 'nest box triplets'	Mobbing of predators
	Krams, Krama & Igaune (2006a)	Great tit (<i>Parus major</i>)	24	Alarm calling to warn others of predator
	Akçay <i>et al.</i> (2009)	Song sparrow (<i>Melospiza melodia</i>)	12	Mutual restraint in aggression
	Akçay <i>et al.</i> (2010)	Song sparrow (<i>Melospiza melodia</i>)	10	Mutual restraint in aggression
	Bell <i>et al.</i> (2010)	Southern pied babbler (<i>Turdoides bicolor</i>)	21	Vigilance behaviour
	Krams <i>et al.</i> (2010)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	28 pairs of nest boxes	Mobbing of predators
	Riehl (2011)	Greater ani (<i>Crotophaga major</i>)	35 two-pair groups and 22 three-pair groups	Cooperative nesting (several pairs lay eggs in a single nest; communal care of the clutch)
Fish	Grabowska-Zhang, Sheldon & Hinde (2012)	Great tit (<i>Parus major</i>)	24 pairs of nest boxes	Mobbing of predators
	Krama <i>et al.</i> (2012)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	50 pairs of nest boxes	Mobbing of predators
	Johnstone <i>et al.</i> (2014)	Great tit (<i>Parus major</i>)	21 pairs of parents	Parental care
	Voelkl <i>et al.</i> (2015)	Northern bald ibis (<i>Geronticus eremita</i>)	14	Turn-taking in V-formation flight
	Ryder <i>et al.</i> (2020)	Wire-tailed manakin (<i>Pipra flicauda</i>)	210 males	Courtship
	Bshary & Schäffer (2002)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	43	Host choice
	Bshary & Grutter (2006)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	28	Cleaner choice
	Adam (2010)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	24	Host choice
	Railhani <i>et al.</i> (2012)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	45 pairs	Cleaning behaviour
	Brandl & Bellwood (2015)	Coral reef rabbitfish (Siganidae)	59 pairs, 24 solitary individuals	Vigilance behaviour
Mammal	Darden <i>et al.</i> (2020)	Trinidadian guppy (<i>Poecilia reticulata</i>)	136 females	Predator inspection
	Grinnell <i>et al.</i> (1995)	Lion (<i>Panthera leo</i>)	36	Mobbing of predators
	Murrant, Bowman & Wilson (2014)	Southern flying squirrel (<i>Glaucomys volans</i>)	72	Social foraging
	Wilkinson <i>et al.</i> (2016)	Greater spear-nosed bat (<i>Phyllostomus hastatus</i>)	144	Infant care
	Kern & Radford (2018)	Wild dwarf mongooses (<i>Helogale parvula</i>)	12 groups (4–9 individuals each; mean = 7)	Vigilance behaviour, grooming
	Moore <i>et al.</i> (2020)	Bottlenose dolphin (<i>Tursiops truncatus</i>)	59	Courtship
Mammal (Primate)	Packer (1977)	Olive baboon (<i>Papio anubis</i>)	18	Coalition formation
	Seyfarth & Cheney (1984)	Vervet monkey (<i>Ceropithecus aethiops</i>)	9	Agonistics support in conflict
	Whitehead (1987)	Mantled howling monkey (<i>Alouatta palliata</i>)	20	Inter-group avoidance
	Muroyama (1991)	Japanese macaque (<i>Macaca fuscata</i>)	7	Grooming
	Manson <i>et al.</i> (2004)	White-face capuchin (<i>Cebus capucinus</i>) and bonnet macaque (<i>Macaca radiata</i>)	36	Grooming
		Chimpanzee (<i>Pan troglodytes</i>)	41	

(Continues)

Table 1. (Cont.)

Study	Species	Sample size	Cooperative act
Langergraber, Mitani & Vigilant (2007)			Associations, grooming, proximity maintenance, coalition formation, meat sharing, and joint participation in territorial boundary patrols
Cheney <i>et al.</i> (2010)	Baboon (<i>Papio hamadryas ursinus</i>)	57 dyads	Grooming, responses to calls for help
Fruteau <i>et al.</i> (2011)	Sooty mangabey (<i>Cercocebus atys</i>) and vervet monkey (<i>Chlorocebus aethiops</i>)	46	Grooming
Newton-Fisher & Lee (2011)	Chimpanzee (<i>Pan troglodytes</i>)	12 (66 possible dyads)	Grooming
Dubuc <i>et al.</i> (2012)	Rhesus macaque (<i>Macaca mulatta</i>)	43 pairs	Co-feeding
Arseneau-Robar <i>et al.</i> (2016)	Wild vervet monkey (<i>Chlorocebus aethiops pygerythrus</i>)	34	Vigilance behaviour
Moscovice <i>et al.</i> (2017)	Bonobo (<i>Pan paniscus</i>)	78 dyads	Party association, proximity, grooming, GG-rubbing, and aggression
Haney & Fewell (2018)	California harvester ant (<i>Pogonomyrmex californicus</i>)	18 colonies	Reproductive investment
Invertebrate			

A large number of modelling studies have explored the consequences and coevolution of aspects of social structure for/with the emergence, spread, and maintenance of cooperation. These studies consider a wide range of factors, including: whether networks are static or dynamic (Jordan *et al.*, 2013; Rand *et al.*, 2014; Li *et al.*, 2020), whether the structure is hierarchical or not (Eguíluz *et al.*, 2005), the number of neighbours or ties individuals have (Fletcher & Doebeli, 2009; Allen *et al.*, 2017), the modularity, clustering, and assortment of the network (Riolo, Cohen & Axelrod, 2001; Antal *et al.*, 2009; Marcoux & Lusseau, 2013), the way in which ties are created in the network (Akçay, 2018), and many others. Further studies investigate how these aspects may interact with other characteristics of cooperation in the population, including: the cost of cooperating (Ohtsuki *et al.*, 2006), mechanisms for group coordination (Angus & Newton, 2020), mechanisms that maintain cooperation (e.g. generalised reciprocity: Voelkl, 2015), etc.

Many theoretical papers have considered the mechanisms underlying the maintenance and spread of cooperation, which have been accompanied by empirical studies of individuals ‘cooperating’ in the wild with little discussion of the link between them. As Noë (2006) discusses, theoretical studies of cooperation often have one of three goals: to analyse existing, naturally occurring cooperation, to identify the proximate mechanism of cooperation, or to test game-theoretical models. Social network analysis can allow us to work towards multiple goals at once by facilitating the integration of theoretical and empirical work – an important precursor to understanding cooperation (West *et al.*, 2007).

One particularly relevant example of this is a simulation study on primate social networks. Using data from 70 different primate groups, Voelkl & Kasper (2009) created weighted graphs for each of the groups to simulate the spread of two strategies (cooperation and defection) using a death–birth update rule. 1000 simulations were run for each group and the authors looked at how long it took for either strategy to reach fixation. By calculating a ‘fixation difference’ they show that in a majority of the groups (87%), cooperation is more likely to reach fixation than it would be in a better mixed group of the same size, and conclude that social structure promotes cooperation in primate groups. By using social network analysis alongside other methods (as done by Voelkl & Kasper, 2009), it is possible to make and test predictions in a manner akin to evolutionary graph theory while additionally accounting for important details about actual social structure(s). Social network analysis is a promising approach for investigating the impact of social structure on actual cooperative behaviour in real, natural populations.

(3) Existing empirical, social network studies of animal cooperation

We identified 10 existing studies that utilise social network analysis with data from natural populations to uncover the mechanisms of cooperation. The first series of studies that

used social network analysis to investigate cooperation were conducted on guppies (Croft, Krause & James, 2004; Croft *et al.*, 2006, 2009; Brask *et al.*, 2019). In their initial study, Croft *et al.* (2004) confirmed that guppies have stable social structures with repeated pairwise associations among females, making way for cooperation through reciprocity. Guppies engage in predator-inspection behaviours where an individual will leave the group to obtain information about a predator, taking a risk to gauge the probability of future aggression (Dugatkin & Alfieri, 1991). This has been studied and characterised as a form of cooperation, as individuals often take part in inspection with a cooperative partner (Dugatkin & Wilson, 2000). In a follow-up study, Croft *et al.* (2006) again found evidence for a stable social structure with stable interactions among females. Individuals with stronger social connections were more likely to engage in predator inspection together. Furthermore, pairs of individuals that engaged in predator inspection more frequently, changed their relative position (leader, follower) more quickly, perhaps to combat the increased risk associated with the leading position to carry out inspection in a more cooperative manner (Croft *et al.*, 2006).

In a subsequent study, Croft *et al.* (2009) additionally quantified each individual's behavioural phenotype by assessing predator inspection and shoaling tendencies. They found positive assortment among individuals with similar behavioural phenotypes which they suggest is an “amplifier of selection” for cooperation in predator-inspection behaviour. Finally, in their most recent study, Brask *et al.* (2019) used a similar predator-inspection procedure to assess individual repeatability of cooperative behaviour in eight populations of guppies. After finding evidence for the existence of a “cooperative phenotype”, they used social network analysis to look at the social structure of two populations with varying levels of predation risk. They found that although both populations were not kin-structured, only the population under high predation risk (where cooperative behaviours may have higher fitness consequences) was socially assorted by cooperative phenotype. This final study highlights not only the utility of social network analysis for understanding how social structure is related to cooperation, but also how its use alongside data from natural populations can give us insights into how ecological factors may play a role in shaping social structure and/or the propensity of individuals to cooperate.

Studies that utilise social network analysis with data from natural populations to study cooperation have also been conducted with mammalian and avian species. In their study of aggression and grooming in three groups of capuchins, Crofoot *et al.* (2011) looked at responses to the playback of calls indicating that neighbouring groups were ‘intruding’ on their territory as well as creating association matrices of aggression, grooming, and proximity. In terms of social structure, they found that the aggression network was comprised of small clusters while the grooming network was one large group held together by an individual with high betweenness centrality. They also note that the number and strength of associations in the proximity network was related to the

structure of the grooming network but not the aggression network. In terms of the reciprocation of behaviours, individuals who received aggression more often were also more likely to initiate grooming of others. Finally, after analysing the networks in relation to the intrusion simulation responses, the authors argue that females who pay the lowest costs for living in the group (i.e. receive low aggression) are also most likely to participate in group defence. Although it is difficult to draw conclusions from this study about the mechanisms that allow cooperation among non-kin because genetic relatedness between individuals was not considered, this study highlights the range of measures and characteristics of social structure that can be extracted and the comparisons that can be made using social network analysis. Consideration of the ‘multi-layered’ nature of social interaction types within particular social settings and groups (Silk *et al.*, 2018; Finn *et al.*, 2019; Hasenjager, Silk & Fisher, 2021) can be useful for detailing which particular contexts of social associations may be related to cooperation.

Daura-Jorge *et al.* (2012) conducted a study with bottlenose dolphins (*Tursiops truncatus*) in the lagoon systems of southern Brazil who are said to cooperate with fishermen by driving schools of fish towards them and signalling when to throw their nets. This can be understood as a form of inter-specific pseudo-reciprocity (Simões-Lopes, Fabián & Menegheti, 1998). After classifying individuals as cooperative or non-cooperative and quantifying the association strength between them, the authors find that association values are higher among individuals of the same foraging tactic (cooperative or not). Clusters of individuals exist and the clustering coefficient for cooperative dolphins was significantly higher, suggesting that they are better connected with stronger relationships, which Daura-Jorge *et al.* (2012) suggest may promote the spread of this behaviour through social learning. Again, genetic relatedness was not accounted for in this study. Nevertheless, the authors do demonstrate that assortment by cooperation does exist in this population. The fact that individuals who cooperate with humans are also better connected to one another may point to a cooperative phenotype in this species.

Using a different approach, Madden, Nielsen & Clutton-Brock (2012) looked at the relationship between kinship and networks of social interaction (dominance interactions, grooming, foraging competition) in meerkats (*Suricata suricatta*). Although there was a correlation between kinship and dominance interaction networks, kin were not more likely to groom each other or to avoid competition for food. They claim that although meerkat social networks are highly kin-structured, cooperation is unlikely to be maintained by indirect fitness benefits alone. Their study emphasises the utility of social networks for understanding the effects of kinship *versus* other mechanisms on cooperative behaviours and the importance of considering other mechanisms facilitating cooperation among non-kin, even in populations that may be highly structured by kin.

In a study of male cooperation in long-tailed manakin (*Chiroxiphia linearis*) leks (areas where unrelated males carry

out communal breeding displays) with a slightly different focus, Edelman & McDonald (2014) demonstrate that individuals are more likely to cooperate if their partner is: close in space, an indirect connection ('friend of a friend'), or an individual that they had cooperated with before. Similarly, in an explicit attempt to quantify the indirect genetic effect of the social environment, Dakin & Ryder (2018) looked at cooperative (male–male) coalitions in a natural population of wire-tailed manakins (*Pipra filicauda*). This research found that individuals with high numbers of 'cooperative relationships' who engaged in frequent cooperation elicited similar behaviours in their partners, highlighting not only the importance of indirect effects through variation in social influence but also the further impact that assortment by cooperators can have on the spread of cooperation (through social contagion).

Most recently, Ripperger *et al.* (2019) captured female vampire bats (*Desmodus rotundus*) to form an artificial group in captivity. Individuals were fasted to induce food sharing and bouts of social grooming were recorded in order to quantify social bonds and levels of cooperative behaviour over the course of 22 months. When these bats were subsequently released into the wild, indicating a drastic change in their social and physical environments, they preferentially associated with one another and levels of cooperation in captivity predicted who they would roost with in the wild. However, some strong bonds were lost in the wild and the change in environment did lead to some changes in roosting associations. The authors argue that this highlights the fact that both partner choice and partner-fidelity feedback (see Section I.1) are vital to the maintenance of cooperation. Social network studies also provide the opportunity for gaining detailed insights into the relative strength of dyadic bonds, and thus partner choice and partner fidelity, exceeding the insight available from considering information at the individual level alone. For instance, by considering the social associations across the entire social network, a study on great tit (*Parus major*) pair-bonding was able to quantify the pre-breeding strength of future breeding partner bonds in relative terms, and determine individuals' propensity to associate with their partners more often than expected simply from individual differences in general sociability (Firth *et al.*, 2018). As such, through incorporating these analytical methods and considering the wider social network structure, studies on cooperation will be able to separate out variation in individuals' general propensities to associate with others from preferences for forming specific partnerships/relationships.

For cooperation to be maintained, the probability that an individual will receive some benefit (immediately or in the future) for cooperating in the present needs to be relatively high – the existing work suggests that this is more likely to occur in social networks with a stable social structure and assortment by cooperators (Croft *et al.*, 2015). Reciprocity is most likely to be facilitating the maintenance of cooperation when interactions are heterogenous and there are high levels of social clustering (van Doorn & Taborsky, 2011); indicated by low average node degree, a high clustering coefficient, and

high modularity in the network. The probability of there being edges between individuals with similar levels of cooperative behaviour can also be used to measure the degree of assortment by cooperation. It seems that we can use social network analysis not only to observe and describe different forms of cooperation but also to comment on the relevant contributions of different mechanisms.

III. FUTURE DIRECTIONS

(1) A social network approach and experimental manipulation

A particularly effective way of studying cooperation in natural populations is through experimental manipulation, because it can be used to establish causal (rather than correlational) relationships between the social environment and the phenomena being observed (in this case, cooperation). By imposing experimental manipulations on natural populations and comparing rates of cooperation and network metrics before and after the manipulation takes place, we can directly observe the impact of social networks on cooperation and *vice versa*. Due to advances in various technologies that allow for automated monitoring of large numbers of individually identifiable animals [Radio-Frequency Identification (RFID), Global Positioning Systems (GPS), deep learning algorithms, image analyses], manipulations can be imposed and the consequences tracked in natural populations in several different ways.

One approach is to manipulate who can interact with whom to see how this alters the social structure and what consequences this may have for cooperative behaviours. For example, Firth *et al.* (2015) programmed selective feeders, which detect visits from individually RFID-tagged great tits, so that they only delivered food to different halves of the population (those whose RFID tag codes ended with either odd or even digits). Individuals from pair bonds with incongruent RFID tags (one odd, one even) continued to forage together even though they could not feed in the same locations, presumably in order to maintain their social relationships. Furthermore, members of these pairs developed a potentially cooperative 'scrounging' technique: the individual who could not access the feeder directly was more likely to approach it immediately after their partner to retrieve food before the feeder was locked (which occurred within 2 s of the initial detection). The manipulation had implications for overall social structure, with individuals becoming more likely to interact with others of the same PIT tag type (greater assortment). Here, individuals were divided randomly and some breeding pairs happened to be separated. However, manipulations can be on the basis of factors like age, sex, breeding status, or species or on measured traits that have been previously related to rates of cooperation, such as familiarity or dominance (Fraser & Bugnyar, 2012; Grabowska-Zhang *et al.*, 2012). We can also manipulate how often individuals interact or the relative pay-off that individuals

get for cooperating and assess how this impacts social structure and population levels of cooperation (measured through observation or experimentally). Some suggestions for the use of a social network approach alongside experimental manipulations and observational data collected from natural populations are detailed in Table 2.

The suggestions in this section have been more focused on mechanisms of cooperation that occur through reciprocity (although many can be applied to cases of mutualism that do not include reciprocity). To our knowledge, there are no studies which explicitly consider the relationship between social structure and mutualism (without reciprocity) in natural populations. However, Daura-Jorge *et al.*'s (2012) study on dolphin–fisherman cooperation may give us some insights. It is possible that repeated interactions among individuals with strong social bonds are necessary for the spread and possibly the emergence of mutualism through the facilitation of social learning; an individual must first observe that another individual is performing a behaviour that they can also benefit from before they can engage in any form of mutualism. It may also be possible that in cases of inter-specific mutualism, initial

mutualism may allow for the development of more complex social structures which make way for further benefits and future cooperation. For example, Kasson *et al.* (2016) argue that the initial mutualistic relationship between a clade of ambrosia beetles (*Ambrosiophilus*) and a wood-decaying fungus (*Flavodon ambrosius*) allowed for the evolution of a more complex social structure than is found in other ambrosia beetles, with an extensive overlap of generations and large communal colonies.

In their study of mixed-species flocks, Farine & Milburn (2013) suggest that individuals who join these flocks may start to forage in areas that are not necessarily their most preferred niches in order to benefit from the reduction in predation risks that comes with group foraging, which itself increases the likelihood of interspecific interaction. They argue that flocks are mutualistic, as membership in the flock comes with mutual benefit for all individuals. Further investigation through the observation and manipulation of the social structures of various interspecific groups could help us to gain a better understanding of how mutualism spreads or is maintained and how it shapes various other social processes (Ross & Fletcher, 1985).

Table 2. Examples of ways that a social network approach can be combined with experimental manipulations or observational data to understand questions related to the emergence, development and maintenance of cooperation

Examples of using experimental manipulations on natural populations in combination with a social network approach	
Manipulating which individuals can interact	• Can familiarity (increased rates of interaction) alone initiate or lead to increases in cooperation? • How long do individuals need to interact before they are familiar or cooperating? How does this vary with various characteristics of the focal individual?
Manipulating how often individuals can interact	• How often do individuals need to interact in order to become cooperative partners? • Do individuals who can no longer interact often, stop cooperating? How does this vary with various characteristics of the focal individual?
Manipulating the relative pay-off individuals receive for cooperating	• If one individual (x) from a pair is consistently rewarded for a cooperative behaviour but the other individual (y) is not, for how long will y continue cooperating with x? Is this mediated by the relationship between x and y and/or by their relative social positions? • Are unequal rewards in cooperative endeavours enough to break social ties? If cooperation is maintained through reciprocity, how equal does this reciprocation need to be for cooperative relationships to persist?
Examples of using observational data from natural populations in combination with a social network approach	
Creating multiple networks on the basis of different cooperative behaviours over time	• Does reciprocity occur across domains? • What is the timescale for the reciprocation of cooperative acts in different species? • Are individuals consistent in their cooperativeness? If an individual is highly cooperative in one domain, do they exhibit similarly high levels of cooperation in other domains? Is there a trade-off between being highly cooperative in some contexts/relationships and not others?
Identifying the consequences of network positions	• Are individuals in different network positions influenced in different ways by experiences of cooperation <i>versus</i> defection (and consequently react in different ways)? Does this interact with the characteristics of the individual? • Can the reciprocation for a cooperative act in one domain be the facilitation of movement to or maintenance of a more advantageous network position? In other words, do individuals who cooperate receive benefits in the social domain? • Are individuals who seem to be at a 'loss' for cooperating actually occupying more beneficial network positions as a result of their cooperative behaviour?
Testing wild-caught individuals on a cooperative task	• How are individuals distributed within the network in terms of their level of cooperativeness? • Is there assortment by cooperativeness? • How does the occupation of particular network positions by highly cooperative/uncooperative individuals influence population-level cooperation?

Table 3. The six advantages of long-term, individual-based studies (Clutton-Brock & Sheldon, 2010), with regard to cooperation and social structure

	General benefit	Relation to cooperation/social structure: possible questions
Analysis of age structure	“Documenting age-related changes in life history parameters” to “identify and assess age effects” on “behaviour, reproductive performance, and survival” which allows for the exploration of “ecological and evolutionary processes” while controlling for these effects (p. 563)	How does age structure impact cooperation at the population level? Does age have an impact on the likelihood of individuals adopting novel cooperative behaviours? Do certain age structures make certain social structures more likely?
Linkage between life-history stages	Can “connect events at one stage of the life history to those at another” which allows for “insights into the cause of variation in growth, breeding success, and survival” (p. 563)	How does cooperative propensity change over the lifetime? Is there a crucial period in development which determines cooperative propensity? Does occupying certain network positions early in life influence future position and overall fitness?
Quantification of social structure	To “document the kinship structure of populations and to assess the effects of social relationships on survival and breeding success” (p. 563)	Which social structures are conducive to cooperation? How does cooperation impact social structure? Is assortment by cooperators necessary for the maintenance of cooperation? Can an individual’s ties to cooperators be used to estimate their own levels of cooperation? Do manipulations to monitored social structure carry over to shape cooperation?
Derivation of lifetime fitness measures	To “measure the extent to which breeding success differs between individuals and their offspring and to assess the causes of these differences” (p. 563)	Does cooperation have net fitness benefits? Do individuals that occupy certain network positions have higher fitness?
Replication of estimates of selection	“Provide[s] opportunities for repeated measurement of the strength and direction of selection” for “exploring the effects of demographic factors such as population density or environmental variation on selection” (p. 563–564)	Does cooperative propensity covary with other traits? Do certain demographic factors or environmental conditions make the spread of cooperation more/less likely?
Linkage between generations	Can study “quantitative genetics of phenotypic traits in wild populations” (p. 563)	To what extent is cooperative propensity heritable and/or a plastic response? To what extent does social structure carry over between generations, and what are the implications for cooperation?

Currently, few studies explicitly examine mutualism within species, highlighting the need for further examination of mutually beneficial behaviours occurring among individuals in natural populations. As discussed by Farine, Garroway & Sheldon (2012) social network analysis allows for an investigation of the relationships among social interactions, social structure, and the immediate benefits that individuals obtain through various forms of mutualism to explain the relationship between mutualism and social structure (and *vice versa*). These methods can be adjusted to the circumstances and the combination of species and systems that are being studied.

(2) The utility of long-term data from natural populations

Throughout this review we emphasised the utility of social network analysis for understanding cooperation; this is also

driven by the fact that social network analysis can be used with data from natural populations which can provide us with more ecologically relevant results. In the wild, individuals are frequently able to choose their social partners (Dakin & Ryder, 2018), but these interactions and choices take place within the context of the environment they experience. This is especially important when considering how the prevalence of cooperation may impact social structure itself. Furthermore, cooperation is shaped not only by evolution but also by ecology. It is more likely that we can tease out these ecological effects when working with natural populations because it is possible, to some extent, to quantify their real social environment and the physical environment that they are in (He, Maldonado-Chaparro & Farine, 2019). By testing populations of the same species in different locations, for example, we can tease apart the variation in cooperative behaviour that is being driven by social *versus* non-social factors (Bergmüller *et al.*, 2010).

As discussed by Clutton-Brock (2002), although there may be some similarities between various cooperative populations (of the same, or different species), there are also meaningful qualitative and quantitative differences in how cooperation is maintained. Working with natural populations gives us the opportunity to identify these differences and how they may be related to social structure. Using natural populations also potentially allows for the experimental manipulation of certain factors (social or non-social) that may be related to cooperative behaviour. Finally, social network analysis can also be used in concert with detailed monitoring of individuals, for example physical measures, hormone and stress levels or with genetic analysis, simultaneously to investigate the biological basis of differences in cooperative propensity and social network structure (Samuni *et al.*, 2018). All of the advantages of using social network analysis become amplified when using natural populations over long periods of time (Clutton-Brock & Sheldon, 2010; see Table 3).

(3) A reciprocal relationship: the study of cooperation and the study of networks

Studying cooperation can also give us insights into social network structures and positions themselves. Varying levels or forms of cooperation may be associated with different social structures (Apicella *et al.*, 2012). As Voelkl & Kasper (2009) reveal with their simulations on real graphs, although some social network structures are more likely to promote the fixation of cooperative behaviour (when compared to a random, well-mixed group), others do not. Even among those groups with conducive social networks there was still a considerable amount of variation in social structure and the level of cooperation. Fehel *et al.* (2011) suggest that the co-evolution of social structure and cooperation-enhancing behaviours (i.e. breaking ties with defectors) allowed for assortment and consequently, the evolution of cooperation. Looking at the co-variation of real and/or simulated cooperation with social structure in natural populations may provide insights into how cooperation and social structure are correlated and why various animal societies are structured differently to one another.

At a more individual level, studying cooperation in relation to social network structure can help us to explain how and why the occupation of certain positions in different types of social structures by certain types of individuals might make way for or hinder the spread of cooperation (Hauser *et al.*, 2019). Studies of human social networks have already investigated how the occupation of certain positions impacts behaviour and the dynamics of social interaction in gangs (Papachristos, 2006) and businesses (Venkataramani *et al.*, 2016). For example, if individuals in highly influential network positions, such as those with many connections to many well-connected others (i.e. high eigenvector centrality), are frequent, or infrequent cooperators, what consequences does this have for the spread of cooperation in that population? Finally, different social network positions can also be associated with varying rates of survival, contracting diseases, and reproductive success (Lehmann, Majolo & McFarland, 2016;

Page *et al.*, 2017; Balasubramaniam *et al.*, 2019); do cooperation and social structure evolve together to allow more cooperative individuals to benefit from more advantageous network positions (Kern & Radford, 2018)? It seems that cooperation and social network structure have a reciprocal relationship in so far as understanding one of the two phenomena more thoroughly can enhance our understanding of the other and *vice versa*.

IV. CONCLUSIONS

- (1) It is now widely accepted that cooperation exists due to the direct and indirect fitness benefits that individuals can receive for cooperating with others. However, there are still major gaps in our understanding of how cooperation is manifested in different natural populations.
- (2) Using a social network approach can help to further understanding of the emergence, spread, and maintenance of cooperation. It appears that it is more likely that cooperation will spread when individuals are assorted by cooperative propensity in social and/or physical space (Croft *et al.*, 2015). Therefore, investigating the characteristics of social networks, which account for the interactions and relationships among individuals, is crucial to uncovering the mechanisms of cooperation.
- (3) Advances in various technologies that allow for large-scale tracking of natural populations allow for the observation and description of cooperative behaviours through a network approach. The impact of social and/or physical manipulations to the environment can also be explored, leading to a more detailed understanding of the ecological factors that impact cooperation.
- (4) Studying cooperation with a social network approach can also give us insights into how differing mechanisms or levels of cooperation may impact social structure, social dynamics, and other social processes.
- (5) The benefits of taking a social network approach to studying cooperation are amplified when working with wild, long-term populations. By quantifying real social environments, it is possible to untangle the evolutionary and ecological pressures that lead to differences in cooperation among different species or populations.

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Chapter 3

Recognising the key role of individual recognition in social networks

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Review

Recognising the key role of individual recognition in social networks

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Many aspects of sociality rely on individuals recognising one another. Understanding how, when, and if individuals recognise others can yield insights into the foundations of social relationships and behaviours. Through synthesising individual recognition research in different sensory and social domains, and doing so across various related social contexts, we propose that a social network perspective can help to uncover how individual recognition may vary across different settings, species, and populations. Specifically, combining individual recognition with social networks has unrecognised potential for determining the level and relative importance of individual recognition complexity. This will provide insights not only on the ecology and evolution of individual recognition itself, but also on social structure, social transmission, and social interactions such as cooperation.

Understanding individual recognition

Identifying stimuli within the environment and responding to the characteristics and information associated with these stimuli over time is a key component of survival in almost all animals. Particularly relevant to the social domain is **individual recognition** (see [Glossary](#)): the ability to remember and recognise individuals [1]. Individual recognition abilities have been studied widely, in amphibians, birds, cephalopods, crustaceans, fish, insects, mammals, and reptiles [2–9]. Further, individual recognition can occur in many sensory domains within species; zebra finches (*Taeniopygia guttata*) can recognise conspecifics not only through vision [10] but also through their song [11] and chimpanzees (*Pan troglodytes*) can identify individuals from other troops using the scent of their urine [12]. Some studies even show evidence for cross-modal individual recognition [7,13,14]. For example, African lions (*Panthera leo*) seem to match the roars (audio) of particular individuals to their physical appearance (visual) and respond strongly to incongruent presentations of these cues ([7]; reviewed in [Table 1](#)).

Because it has been studied in various different contexts and species, definitions of individual recognition vary widely [15]. All forms of recognition are currently unobservable cognitive processes, making it difficult to understand the mechanisms and the nature or complexity of the cues and representations that allow for individual recognition [16,17]. Furthermore, processes enabling recognition may be distinct from those that govern responses after initial recognition.

However, rather than considering separate kinds or discrete types of recognition, it seems more plausible that these different routes to recognition lie on a continuum [18]. **Binary individual recognition** requires only a discrimination between one group and another and is usually on the basis of familiarity (e.g., ‘familiar’ or ‘unknown’), kin (e.g., ‘parent’ or ‘non-parent’), or simply classifying individuals as ‘in-group’ or ‘out-group’ [19,20]. Taking things one step further, **class-level individual recognition** requires associations between different physical characteristics of the signaller, the traits that they represent, and how these traits may influence the signaller’s behaviour

Highlights

The ability of individuals to recognise and keep track of others influences many social processes (e.g., formation of social structure, social learning, and cooperation) yet the role of individual recognition is rarely considered.

Social network analysis entails quantifying the social associations among individuals to provide insights into patterns of individual behaviour, interactions, and social structure.

Integrating our understanding of individual recognition into the social network approach allows for a better understanding of the basis for social relationships within networks in different populations.

Combining the currently largely distinct, but intimately related, areas of social networks and individual recognition will lead to new perspectives in both and improved understanding of the evolutionary and ecological causes and consequences of sociality.

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Table 1. Types of cues that can be used for individual recognition with examples of their operation

Cue type	Examples
Auditory: on the basis of vocal cues; used most often (playback experiments); may be dependent on perceptual requirements and anatomical constraints may make it less likely that individual identity can be transmitted through calls in some species	Olive frogs (<i>Babina adenopleura</i>) use the distinctive vocal signals of conspecifics to identify their neighbours and exhibit lower levels of aggression towards them in a vocally mediated example of the dear-enemy effect [19]. Shapiro [23] discusses the existence of 'signature vocalisations' that allow for individual recognition. Vocal individual recognition is reviewed by [15].
Visual: on the basis of visual cues of distinctive physical appearance or distinctive behaviours/movements; the face may be the best identified where vision is the primary sense	Kendrick <i>et al.</i> [24] used both electrophysiological recordings of brain activity and behavioural measures to show that sheep (<i>Ovis aries</i>) can remember 50 other sheep faces for time periods of over 2 years and suggest that sheep have specialised neural mechanisms for processing faces. Visual cues can also be based on movement. For example, Japanese macaques (<i>Macaca fuscata</i>) exhibit consistent individual differences in their movement patterns that can serve as cues for individual recognition [25].
Olfactory: on the basis of scent cues	Bumblebees (<i>Bombus terrestris</i>) can discriminate between the scents of conspecifics to identify locations where their nest-mates have been before [26] and house mice identify conspecifics through the scent of their urine [27]. It is possible that, similar to vocal cues, individuals have 'signature mixtures' that allow for individual recognition. Individual recognition on the basis of olfactory and chemical cues are reviewed by [28,29].
Tactile: on the basis of touch; only briefly studied in humans	The only studies of individual recognition through tactile cues are with human parents, who are able to recognise their newborn offspring by touch alone [30,31].
Multisensory: on the basis of multiple cues in conjunction; cue chosen may be on the basis of the primary sense of the species	Lions (<i>Panthera leo</i>) match audio-visual cues (roars and physical appearance) to identify individuals, as demonstrated by their strong reactions to incongruent presentations of these cues [7]. Individual recognition on the basis of multiple cues may also be used to identify individuals of other species; it has been found that domestic horses (<i>Equus caballus</i>) could match familiar humans to their voices [13].

[21]. This kind of recognition can vary in complexity, depending on the details of classification (e.g., within-species classification more difficult than between-species). **'True' individual recognition** may be even more complex, as individual-specific characteristics are matched to individual-specific information (which itself can vary in amount and type) [22]. Placing the recognition that we observe on this continuum can be difficult because it is unclear if animals are using individual cues or more general class-level cues. Indeed, whether or not 'true' individual recognition is necessary for individual recognition, even in humans, can be debated.

One way to overcome issues with definitions is by focusing on the **multiplicity, specificity, and temporality of individual recognition** without getting caught up in debate over true versus untrue individual recognition and the nature of the representations that are used to achieve it [18]. This can give us a better sense of the amount and complexity of the information that can be transmitted through these processes. What are the causes of varying levels of individual recognition? How are varying levels of complexity related to the social or physical characteristics of a given population or species, and how do differences in these factors influence the predictions we make about the consequences of individual recognition? For example, higher specificity and multiplicity of individual recognition may be more likely to lead to conditions favouring the emergence and maintenance of cooperative behaviours [18].

Glossary

Binary individual recognition:

sometimes referred to as 'individual discrimination', cases where individuals from a population can be categorised into two heterogeneous groups, usually on the basis of previous experience; most often studied in terms of familiarity, kinship, or group membership more generally. This does not entail the use of individual-specific cues.

Class-level individual recognition:

an individual's class (or phenotype) is matched to a representation of that class which contains information associated with individuals from it (i.e., the phenotypes of individuals are associated with class-specific information that has been previously learned); can be on the basis of physical characteristics that are indicative of dominance, aggression, reproductive success, etc. This is similar to binary individual recognition in that it does not entail the use of individual-specific cues, but different because it includes more than two classes/categories/groups. This may rely more heavily on the left hemisphere because of the more general role in category-based distinctions [16].

Cooperation: behaviours initiated by an actor that have a benefit to a recipient (other than, or in addition to, themselves).

Individual recognition: recognition where an individual, x (the receiver), learns cues related to another individual, y (the signaller), which are associated with relevant information about y and are used by x to identify y and adjust their behaviour towards them in future interactions (blanket term to refer to cases of true, class-level, and binary recognition).

Multiplicity of individual recognition:

the total number of sets (groups) that can be differentiated with individual recognition.

Social network: the web of social connections between individuals within a group/population. Nodes (i.e., individuals) are connected by edges (i.e., associations, bonds, relationships) in a way that represents the overall social structure and the position of each individual within this structure.

Social network approach: an approach aimed at understanding a range of different social phenomena and their evolutionary causes and consequences by quantifying diverse

Individual recognition is most likely to evolve in situations when: (i) individuals have varying phenotypes, (ii) remembering conspecifics and responding according to their previous behaviours will be advantageous, (iii) and there are low costs (i.e., necessary cognitive mechanisms are already present) [32,33]. Having distinctive phenotypes (identity signals) is often expected to be selected for in social species because it allows for various forms of communication and familiarity (reduced aggression) and can increase genetic diversity that is beneficial at the individual level and, also potentially, the kin-group level [34]. Pollard [35] modelled the benefits of individual recognition and four other ‘response strategies’ to alarm calling signallers when deciding between ‘foraging’, ‘being wary’, or ‘hiding’, under various conditions. The individual recognition strategy was the most advantageous under most conditions, lending support to the idea that identity signalling may be selected for due to potential fitness benefits of individual recognition and the adjustments in behaviour that result from it. For example, facial distinctiveness may have evolved in order to allow for more precise individual recognition in some social species [36,37]. Further, features may evolve as signals of quality rather than identity and it is possible that there is a trade-off between these signals on the basis of each species’ ecology and reproductive system [38,39].

Recent advances and general approaches in individual recognition

The ability to perceive and recall information about individuals based on previous interactions is an important component of many social behaviours [32]. Tibbetts and Dale [1] previously identified the three areas that individual recognition was most widely studied in as: (i) territoriality, (ii) aggressive competition, and (iii) parental care, and called for further work in the area of (iv) mate choice/recognition (reviewed in Table 2).

Territoriality

Individual recognition may play a large role in territoriality, where recognition of others allows individuals to reduce or correctly divert aggression towards conspecifics, which can reduce the costs of establishing dominance hierarchies and resolving conflict within or between groups. This is often studied in terms of the ‘dear-enemy effect’, where individuals that reside in a territory will be less aggressive towards familiar neighbours and may even ‘cooperate’ with them; this decreases the costs of territory defence for both parties [19,40].

Aggressive competition

Similarly, by remembering the identity, temperament, and competitive ability of others, individuals can make more accurate assessments of their chances of winning contests and adjust their interactions accordingly. In one example, the ‘facial’ markings of Australian crayfish (*Cherax destructor*) engaging in contests were experimentally manipulated to assess their ability to visually recognise other individuals [41]. After exposing focal individuals to multiple manipulated individuals in a test arena, the authors report that crayfish recognise others using facial cues that they encode in memory during aggressive contests and can remember this information for at least 24 hours and use it to adjust their behaviour in future interactions for up to 2 weeks.

Offspring identification

Identifying offspring correctly is crucial to accurately providing preferential care, safety, and resources to offspring, especially in cases where the offspring of multiple individuals are housed in the same area, when social group sizes are big, when intra- or interspecific brood parasitism is at play, when extra-pair paternity rates are high, and/or in species where reproduction occurs relatively simultaneously within the year/season. Offspring also benefit from recognising their parents because it allows them to respond appropriately to them versus unfamiliar adults. This is especially crucial in situations where offspring must follow parents, find them in larger groups,

kinds of interactions among individuals within a population to create a social network.

Social transmission: the social spread of social information and behaviours between socially connected individuals.

Specificity of individual recognition: the total number of individuals included in a set; together, specificity and multiplicity give us an indication of the total number of individuals that can be recognised.

Temporality of individual recognition: how long information about individual identity can be retained and used for individual recognition over time.

True individual recognition: cues that are specific to the individual are learned and associated with information (usually fitness related) specific to that particular individual. Neurologically, this may rely more heavily on the right brain hemisphere because of the more general role in assessing novelty and encoding unique features of individual stimuli (reviewed in [16]).

Table 2. Main methods used to study individual recognition with examples of their application

Method	Description	Examples
Partner choice tests	The focal individual is given the ability to show their preference for a partner by joining them or their identifying cues in physical space. If the individual chooses the more familiar or 'target' individual, they are said to be recognising that individual. This can be done with the y-maze and other set-ups that allow for a choice between individuals (or their calls, smells, etc.), or by quantifying the amount of time individuals spend in the presence of others/looking at others.	Australian sea lion (<i>Neophoca cinerea</i>) [43], red jungle fowl (<i>Gallus gallus</i>) [45]
Contests	Individuals are placed in an arena and subject to multiple contests. The focal individuals' level of aggression or tolerance is noted in each instance. If they adjust their behaviour on the basis of familiarity or their previous experiences with the 'rivals' it is assumed that recognition is occurring.	Crayfish (<i>Procambarus clarkii</i>) [6], golden-crowned sparrows (<i>Zonotrichia atricapilla</i>) [46]
Habituation/dishabituation	A stimulus is repeatedly presented to the focal individual until they stop or decrease their responding to it (habituation). Then, a new stimulus is presented to them. If they perceive the new stimulus as different to the previous one, they will start responding to it (dishabituation); whereas if they do not perceive the difference, they will continue to ignore it.	Superb fairy wrens (<i>Malurus cyaneus</i>) [22], greater false vampire bat (<i>Megaderma lyra</i>) [47]
Violation of expectancies	The responses of a focal individual to the presentation of cues in a manner that is physically impossible are used to ascertain if individuals pick up on this irregularity. For example, the calls of the same individual can be played from two distinct locations. If the focal is more attentive (looking time, vigilance, etc.) in this scenario than in a 'normal' one, it suggests that recognition is occurring.	African lions (<i>Panthera leo</i>) [7], domestic cat (<i>Felis catus</i>) [14]

and when other adults are particularly dangerous [42]. Parent–offspring identification can also contribute to inbreeding avoidance strategies.

Mate recognition

Finally, the ability to identify one's mate has important consequences for initial mate choice, monogamy, biparental care, and carry-over effects from reproductive periods [43]. It is also advantageous because it allows individuals to assess the value of possible mates through individually distinctive traits before deciding; 'eavesdropping' on the behaviours and interactions of potential mates can inform mating decisions and the pursuit of extra-pair copulations.

There are many routes to studying the presence, multiplicity, specificity, and longevity of individual recognition. Most often, interactions among individuals are observed in a controlled setting to see if individuals behave differently in the presence of different conspecifics immediately and over time [44]. Another method entails the presentation of cues that are presumed to be used for individual recognition and looking at the responses of receivers. This can include playbacks of calls or other vocalisations, visual presentations of faces or parts of the body with distinct markings, or the scent or chemical makeup of other individuals. Cues can also be presented after altering them

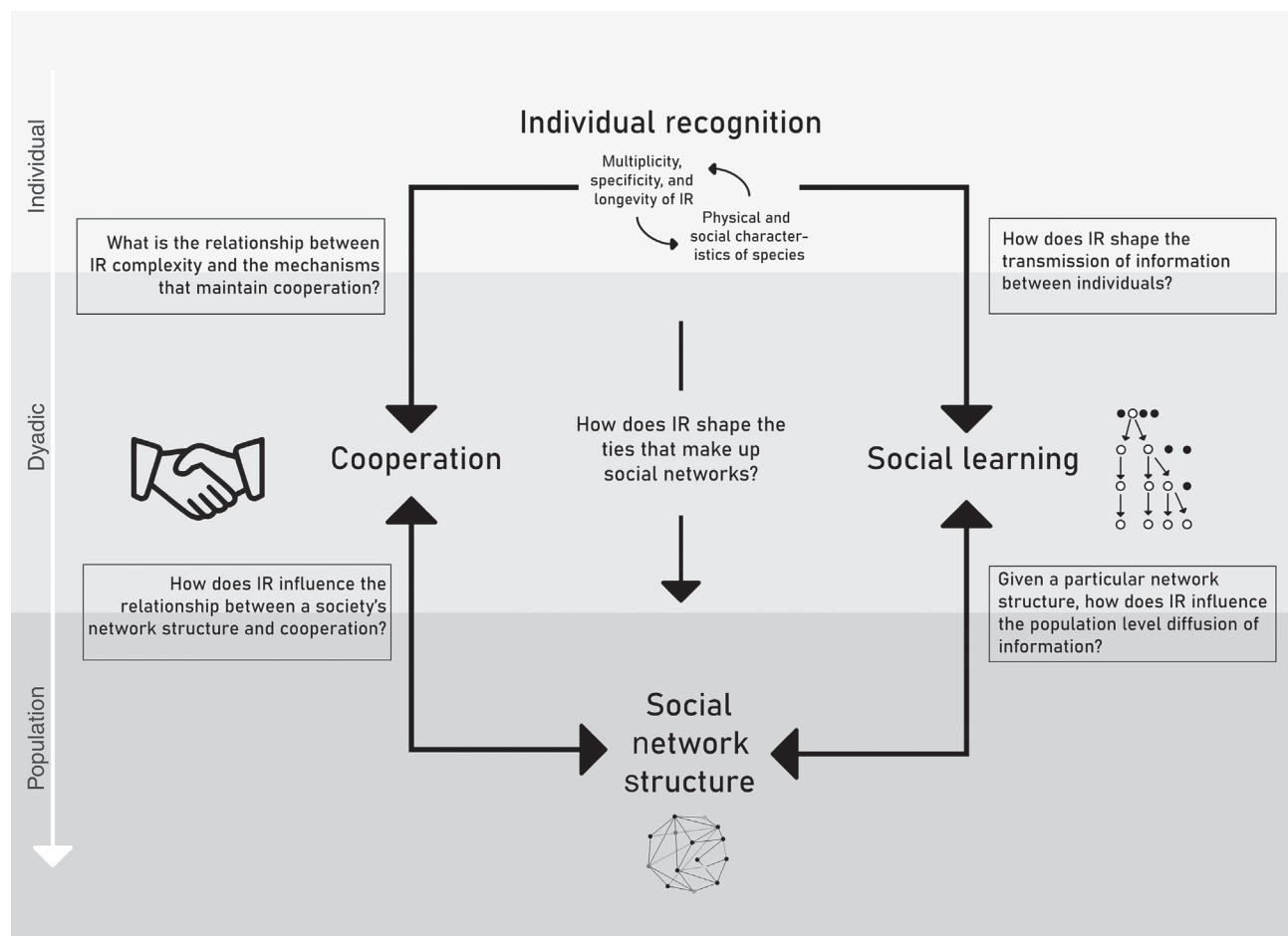
slightly to get a better understanding of, first, whether individuals are engaging in individual recognition and, second, which components of those cues are being used to signal individual identity. Although playback experiments are the most common (reviewed by [15]), physical appearance, genes/hormones, and scents or chemical compositions can also be manipulated to look at how changing certain characteristics of the cues that would presumably be used for individual recognition can impact behaviour ([31] described earlier). All of these approaches can be taken alongside methods and set-ups detailed in Table 2, with varying numbers of individuals (specificity) and groups of individuals (multiplicity), and over different time periods (longevity).

Studying individual recognition with a social network approach

Over the past decade, **social network** analysis has become an increasingly influential method for understanding a range of different social phenomena and their evolutionary causes and consequences [48,49]. By quantifying diverse types of interactions among individuals within a population, the **social network approach** allows for a generalised quantification of social structure that can, in turn, provide insights into empirical patterns of individual behaviour and interactions. In this way, it provides a platform for examining how social network characteristics may lead to emergent properties that can make way for, and influence, other social processes such as **social transmission** of information, behaviours, or contagious disease. In addition to the areas discussed, individual recognition plays a key role in social-bonds that are not motivated by kinship, territoriality, or future reproduction [50]. For example, domestic donkeys (*Equus asinus*) show preferences for their 'friends' (individuals that are most often their nearest neighbour) over other individuals, suggesting that donkeys recognise those that they have the strongest social bonds with and use this information to decide who to spend time with [51]. It seems plausible that individual recognition can have an important influence on all types of interactions and relationships, necessarily influencing social network structure. However, direct incorporation of the effects and influence of individual recognition into the social network approach remains relatively limited, despite much potential for doing so.

The integration of social network analysis with investigations of individual recognition creates multiple opportunities to improve our understanding of how individual recognition interacts with other social processes (Figure 1). For example, social network analysis can be used to advance insights into mate choice [52–54]. In many avian species, individuals recouple with the same partner over many breeding seasons; whether or not individual recognition is playing a role is important. What is the null expectation if individuals are choosing based on preference (for physical attributes, e.g., size, coloration, signalling characteristics, etc.) rather than identity? Are partners chosen repeatedly over time through the use of recognition or solely based on preference? Incorporating the study of individual recognition can bring another layer of understanding.

Finally, studying individual recognition with a social network approach is advantageous because of the potential broader role of individual recognition in shaping individual differences. McNamara *et al.* [55] model the effects of 'social awareness' on the trait of trustworthiness, demonstrating that in populations where individuals trust conspecifics based on their previous behaviour, variability in individual trustworthiness increases in the population. It is possible that the ability to recognise and track conspecifics can lead to variation in observable traits that influence social network structure, the rate and mode of social transmission, and **cooperation**. Marrying studies of social network structure and dynamics with findings about individual recognition can now lead to novel insights and new support for conclusions in many lines of inquiry that have not been considered in conjunction with individual recognition before (Figure 1).



Trends in Ecology & Evolution

Figure 1. Pathways that link individual recognition (IR) and other social phenomena, and questions that can potentially be answered (ranging from the individual to population level) using a social network approach to studying individual recognition.

Social structure and individual recognition

Previous studies have demonstrated that the presence or absence of individual recognition can have consequences for social organisation, the formation of dominance hierarchies, and the way various phenomena may shape social structures [6,46]. Although many mechanisms shape and maintain the structure of social networks in any species, recent simulation studies have shown that the complexity of individual recognition can influence social dynamics in group formation and the resulting numbers or size of various groups [56]. This may be due to cognitive limitations on individual recognition that could potentially lead to further limitations on how social networks form and are maintained [57]. Understanding the relative impact of varying levels of complexity of individual recognition can give us insights into how and why different populations are structured in the ways that they are, which, in turn, can inform our understanding of individual and group-level social processes (Figure 1). For instance, network analysis allows for the quantification of various characteristics of social structure, such as quantifying the level of nonrandom clustering (i.e., how much a social network is structured by friend-of-a-friend relationships in comparison with what would be expected from the general network structure in terms of number of individuals and number of observed associations between these individuals), or quantifying the

extent of between-individual variation in social positions (how different individuals are from one another in their observed sociability metrics compared with what is expected under that general network structure). Quantifying social structure in such ways, for different but closely related species, for example, could allow for the investigation of possible differences in social structure that may be associated with differing levels of complexity in individual recognition.

In a study of human subjects, Parkinson *et al.* [58] used functional magnetic resonance imaging in conjunction with social network analysis to show that network positions (information about how well connected individuals are to others in the network) are perceived accurately, encoded, and activated in the presence of familiar others. In human studies like this one, it seems obvious that individual recognition is necessary to keep track of numerous individuals and how they are related to the self and to one another. However, it is possible that complex social network phenotypes are actually represented by simple behaviours [59], which other individuals can then recognise. In other words, some complex population-level patterns found in social networks can be explained by simple social differences (in general sociability and tendencies to reassociate with within-group or out-group members) at the dyadic level. Future studies can use simulations in combination with real social networks to consider how individuals identify network positions of others and how differences in individual recognition abilities may lead to different types of social structure.

Social transmission and individual recognition

The ability to identify individuals can also have an influence on the way information flows through different populations. While social network connections provide the substrate for information to potentially diffuse through a system, social learning strategies (based on choosing which individuals to learn from, or when to learn) may govern how behaviours actually spread [60]. Indeed, by recognising the identity of others, individuals can assess the reliability of information that they receive and subsequently adjust their behaviour accordingly, by deciding whether or not to follow or act on the information provided by particular individuals [61,62]. Dwarf mongooses (*Helogale parvula*) adjust their vigilance behaviour on the basis of the dominance rank of their sentinel [63], fairy wrens (*Malurus cyaneus*) are more responsive to the alarm calls of mates and kin than those of unfamiliar individuals [22], and vervet monkeys are more likely to copy solutions from higher ranked individuals [64]. The use of information about individual identity when deciding which information sources are most reliable can feed back and shape social structure [65]. For example, ‘homophily’ (like-with-like, i.e., assortment) in social influence increases behavioural similarity and reinforces strong bonds between similar individuals while further separating those that have distinct behaviour (clustering).

However, it is also important to keep in mind that there may be similar effects on information flow in the absence of the recognition of who is producing the information. For example, modelling has demonstrated that information can flow, and collective decisions can be made, in the absence of individual recognition and without accounting for how informed or reliable the individual that provided the information is [66]. Seemingly ‘complex’ actions or decisions can be taken on the basis of very simple principles or mechanisms. Developing methods to tease apart the various mechanisms that allow for social information flow in different populations is a vital part of our understanding of the relationship between individual recognition and how social information spreads [67,68].

One instance where understanding the influence of individual recognition may be particularly important is in cases of conformist social learning (learning behavioural options that are favoured in the local population, even though alternative options are available) that may have implications

for animal culture [69,70]. How we expect conformist transmission to occur may depend on whether individuals recognise others; do individuals conform to the behaviour that is being performed by the majority of individuals (a larger proportion of individuals perform a behaviour), or do they simply conform to the behaviour that they observe in the majority of instances (the behaviour is performed a larger number of times, but not necessarily by a higher proportion of individuals) [71–73]. Understanding which of these approaches to establishing the majority is taken is vital to interpreting how socially learnt behaviours influence and interact with social transmission and cultural evolution. More generally, do more ‘complex’ mechanisms allow animals (including humans) to identify, keep track of, and learn from others, or is the appearance of complexity being maintained by several, simpler processes? One potential way to explore these questions may be to manipulate the cues that allow for individual recognition and examine resultant changes (or the lack of) in the way information, and emerging behaviours, spreads.

Cooperation and individual recognition

Finally, the presence or absence and even the complexity of individual recognition abilities may have major implications for the emergence and spread of cooperation, especially when the processes proposed to enable this cooperation assume that unique individuals and their behaviours can be tracked and recalled by others over time (e.g., image-scoring or reciprocity [74]). Tibbetts and Dale [1] note that individual recognition is particularly important when ‘there are repeated interactions among multiple individuals with differing intentions’, which is exactly the case in most settings where cooperation arises; cooperation (especially among non-kin) is most likely to occur when there are stable social structures and heterogenous interactions [75–77].

It is also possible that individual recognition allows for more fine-tuned cooperation (through direct and indirect reciprocity) while other populations rely on more simple, conditional rules (e.g., generalised reciprocity). For example, guppies (*Poecilia reticulata*) have been shown to behave consistently with the use of the ‘walk-away’ heuristic, where they keep their partner after experiencing cooperation but switch partners after experiencing defection, regardless of the identity of the individual [78]. Are species lacking individual recognition abilities more likely to engage in generalised reciprocity? Does this translate to differences in social structure? A better understanding of individual recognition is crucial to uncovering the mechanisms that allow for cooperation in different populations.

Individual recognition and the ability to track the cooperative or uncooperative behaviours of others can help to maintain group cohesion and prevent ‘cheating’ (‘a trait that is beneficial to a cheat and costly to a cooperator in terms of inclusive fitness (ii) when these benefits and costs arise from the actor directing a cooperative behaviour towards the cheat, rather than the intended recipient’ [65,79]). Social eavesdropping has significant implications for how cooperation spreads, as the presence of a bystander can increase the benefit that is received (by the actor) by engaging in a cooperative behaviour as their signal will be perceived by not only the recipient of the behaviour but also the bystander, potentially increasing the possibility of future cooperation by either party [80]. This selective pressure that comes with the presence of bystanders, and social eavesdropping, is only possible if individual recognition is involved.

Although the dear-enemy effect is taken advantage of in studies of both cooperation and individual recognition, the link between them is rarely ever explicitly acknowledged. Assortment can allow cooperation to be maintained: if individuals are assorted by cooperativeness in social or physical space, it is more likely that cooperators will interact with other cooperators, increasing the benefits of being a cooperator in that population [75,81]. With the dear-enemy effect, it is possible that cooperators are clustered in physical space simply because of this phenomenon; individuals may not be cooperative in other contexts, but establish and maintain this mutualism with their familiar

neighbours on the basis of individual recognition. But do individuals really recognise their dear enemies, or do they associate particular cues with particular locations? How does this translate into relationships within social space? New advances are now needed to determine whether dear enemies are better connected to each other than to unfamiliar others (in the case of individual recognition) or whether they are no more likely to have strong ties with familiar neighbours than with unfamiliar conspecifics (in the absence of individual recognition; Figure 2).

Concluding remarks and future directions

Existing studies of if and how individuals recognise others have focused on the effects of individual recognition on contests, territoriality, parent–offspring recognition, and mate selection, revealing fundamental differences in the way different species recognise and react to their social partners. New experiments can offer especially powerful insights, such as through manipulating the ability of individuals to identify others or removing particular individuals from the population and examining how different manipulations impact social network structure, the rate and mode of social transmission, and cooperation. Further, continuously modifying the appearance of some individuals (making them unrecognizable) and assessing their arising network position, and their ability to form new ties, would provide a deeper understanding of how the maintenance of relationships (edges) in social networks is dependent on individual recognition.

Social network studies can also now be integrated with cognitive experiments. Traditional methods of studying individual recognition (reviewed in Table 2) can be paired with social network analysis to directly answer questions about how complexity of individual recognition is related to social network characteristics. This can be done both within and among populations/species.

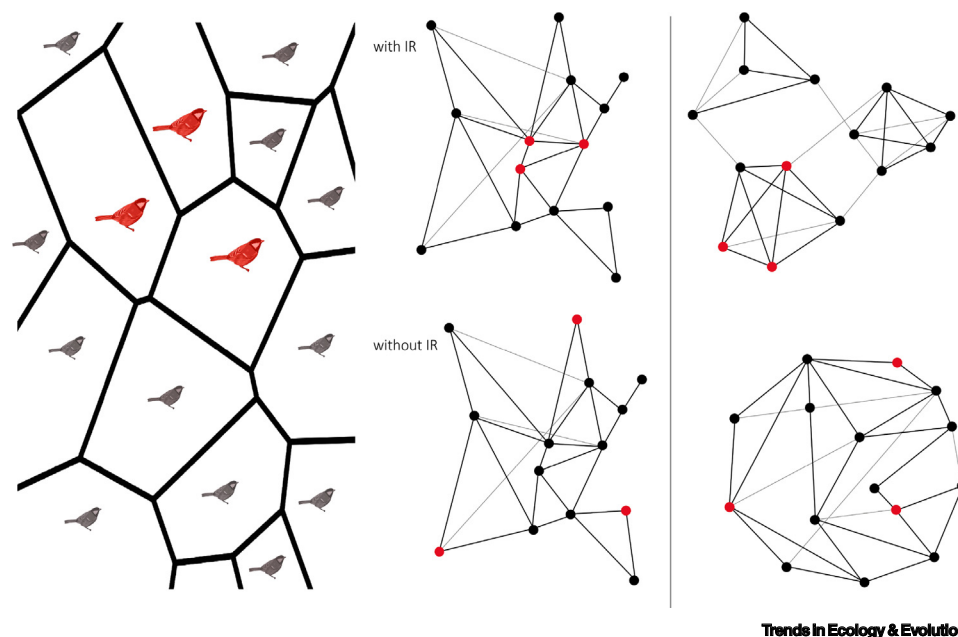


Figure 2. A hypothetical illustration of the dear-enemy effect in territorial breeding birds (here exemplified as a great tit, *Parus major*), with breeding territories on the left and expected social associations and cooperative social structure for the subsequent nonterritorial season on the right. Although the dear-enemy effect may be maintained in the absence of individual recognition (IR) during the breeding season, whether or not individuals are using individual recognition or simple associative learning may have an impact on how those individuals are associated and interact in the nonterritorial season. Using data from real populations, these relationships can be tested.

Outstanding questions

How does individual recognition shape the ties and social bonds that make up social networks, and what patterns of social connectivity do we expect under different forms of recognition?

What is the relationship between individual recognition complexity and the formation and maintenance of social preferences?

How does the complexity of individual recognition impact the social and physical characteristics of different species?

What is the relationship between individual recognition abilities and overall social architecture, as well as individuals' positions within the structure?

How might individual recognition shape social learning strategies and how might this then affect the transmission of social information and the spread of socially informed behaviours?

What is the relationship between individual recognition complexity and the mechanisms that maintain cooperation in different societies? Do populations lacking individual recognition mechanisms rely solely on conditional cooperation rules?

Does individual recognition shape how individuals within social systems respond to disruptions of social structure or social processes?

Are there stable individual differences in individual recognition abilities? If so, what factors shape these differences (genetic, environmental?) and how do these interact with individuals' social network positions and roles within the society?

Specifically, such questions might include considering whether species with more complex individual recognition abilities also have more variation in the edge weight between individuals within their networks, whereby recognition allows bonding over long time periods. If individuals can identify exceptionally high numbers of individuals (in comparison with others in their population), are they also more likely to have a larger number of social connections? Investigating social choices can also provide insights into what information individuals hold about others. Are focals more connected (higher bond strength) to the individuals that they choose in the partner-choice test (described in [Table 2](#))?

Another potential approach would be observing changes in social structure and individual recognition in response to anthropogenic impacts. Human pollutants in aquatic habitats can potentially disrupt the chemosensory abilities that fish use for recognition [82]. Similarly, noise pollutants may impact individual recognition abilities in terrestrial species that rely on auditory cues for communication. Studying populations of the same species with varying degrees of exposure to potentially disruptive anthropogenic impacts can allow for a deeper understanding of how individual recognition is influenced by changes in the surrounding environment and how this may have carry-over effects for individuals' social behaviour and the arising social network structure and social processes that depend on this structure.

Aside from experiments and empirical observational research, it is becoming apparent that modelling (similar to [35]) may also aid in elucidating how the absence/presence or multiplicity/specificity/temporality of individual recognition influences the three proposed areas (social structure, social transmission/learning, and cooperation) under different circumstances. This more detailed investigation could help tease apart effects of other external (season, climate, resource availability, etc.) and internal (emotional reactivity, reproductive status, etc.) characteristics on the outcomes of individual recognition investigations [83]. A focus on the relationship between individual recognition and social networks would allow for the study of individual and group-level differences in individual recognition and their influences on how social structures are established, how information and behaviours spread through the population, and how cooperation is maintained, as well as how these aspects of sociality may feedback and shape recognition (see [Outstanding questions](#)).

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Declaration of interests

No interests are declared.

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Chapter 4

Drivers of passive leadership in wild songbirds: species-level differences and spatio-temporally dependent intraspecific effects

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Drivers of passive leadership in wild songbirds: species-level differences and spatio-temporally dependent intraspecific effects

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Abstract

Collective behaviors are typical for many social species and can have fitness benefits for participating individuals. To maximize the benefits obtained from group living, individuals must coordinate their behaviors to some extent. What are the mechanisms that make certain individuals more likely to initiate collective behaviors, for example, by taking a risk to initially access a resource (i.e., to act as “leaders”)? Here, we examine leading behavior in a natural population of great tits and blue tits. We use automated feeding stations to monitor the feeder visits of tagged individuals within mixed-species flocks, with a small cost (waiting < 2 s) associated with the initial unlocking of the feeder. We find that great tits, males, and individuals with high activity levels were more likely to be leading in each of their feeder visits. Using a null model approach, we demonstrate that the effects of sex and activity on passive leading behavior can be explained by patterns of spatial and temporal occurrence. In other words, these effects can be explained by the times and locations of when individuals visit rather than the actual order of arrival. Hence, an analysis of the causes of leading behavior is needed to separate the effects of different processes. We highlight the importance of understanding the mechanisms behind leading behavior and discuss directions for future experimental work to gain a better understanding of the causes of leadership in natural populations.

Significance statement

Many species are social and engage in collective behaviors. To benefit from group actions, individuals need to fulfill different roles. Here, we examine leading behavior during feeding events; who feeds first when birds arrive at a resource? In mixed-species flocks of passerines, great tits (the larger and more dominant species), males, and individuals with higher levels of activity lead more often than blue tits, females, and individuals with lower levels of activity. While the species effect remains even when we control for the locations and dates of individual feeder visits, the effects of sex and activity are dependent on when and where birds choose to feed.

Keywords Leading · Sociality · Leadership · RFID

Introduction

Many species are social, spending a majority of their time in the presence of others, especially when moving or acting in groups is beneficial (Couzin et al. 2002; Krause and Ruxton

2002; Couzin and Krause 2003). Collective action can occur in day-to-day contexts, for example, when individuals come together to forage in pairs or groups, presumably to increase their feeding efficiency and avoid predators (Conradt and Roper 2003; Rands et al. 2003; McClure et al. 2011). How are collective actions initiated and carried out in different species and contexts?

Various lines of research suggest that in social or group-living species, there are some individuals that are more likely to initiate behaviors (leaders), while there are others that are more likely to follow once behavior is initiated (followers; King and Cowlshaw 2009; King et al. 2009; King 2010). Patterns of leading and following can occur not only during coordinated collective movements but also during

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social encounters (King et al. 2009) and remain consistent over time (Kurvers et al. 2009). However, the terms leader and follower can be ambiguous if clear definitions are not used (Dumont et al. 2005; Pyritz et al. 2011). Leader may be used in the more intentional sense, where individuals actively, and sometimes explicitly, make their intentions known and attempt to recruit group members to follow their behaviors (King et al. 2008; King and Sueur 2011). However, leadership in animal groups is rarely shown to be “active” or with the intention of eliciting followers. In a more passive sense, leading can be characterized in terms of the order that a behavior is occurring in, as an emergent property of the particular make-up of the given group or population (Couzin and Krause 2003; King 2010; Lucon-Xiccato et al. 2019). Conceptualizing passive leaders as individuals that take on an initial cost to access a resource and are followed by others more often than they follow others themselves, as we do here, allows for a flexible and generalized investigation of leadership across a range of systems.

There are many possible ways to explain leading behavior, based on morphological, physiological, and behavioral characteristics (King et al. 2009). One explanation is that leadership is driven by motivation, where individuals that are most in need of a particular resource are most likely to initiate behaviors to retrieve them (Furrer et al. 2012; Öst and Jaatinen 2013; Hansen et al. 2016). This is sometimes referred to as the “leading according to need” hypothesis (Conradt et al. 2009; Sumpter 2009). Dominant individuals may also be more likely to lead group movement if they operate more autonomously or have more command over the group (Rands et al. 2006). This may be related to the link between energetic intake (motivation) and dominance, where more dominant individuals are also more in need of resources (Muller and Wrangham 2004; Sueur et al. 2013). Alternatively, it is possible that subordinates have reduced access to resources and are therefore hungrier, or more risk-averse, and may attempt to arrive at a resource first to increase their probability of retrieving food. More generally, dominant individuals may be more successful in fostering following behavior (King et al. 2008).

For individuals to take advantage of and maximize the benefits that come from collective actions, individuals within a group must be coordinated to some extent (King and Cowlishaw 2009). Coordination can be hard to achieve as group members may have conflicting interests that must be resolved, making way for the emergence of leaders. Studies of leadership aim not only to uncover the mechanisms behind collective actions but also to investigate how dyadic interactions at the individual level translate to group-level patterns (Strandburg-Peshkin et al. 2018). Understanding the dynamics of leading and following behavior is crucial to our understanding of how social groups emerge and are maintained in different species and settings (Tóth and

Griggio, 2011). Leaders and followers may experience different fitness consequences of group membership; for example, leaders may receive a larger share of resources but be at a higher risk of being predated, while followers may not receive as much but benefit from the resource discoveries of leaders (Beauchamp 2000).

Uncovering the details of leading and following behavior can also help to refine our understanding of other social phenomena, for example, cooperation. It may be the case that individuals that are “leaders” during migration or foraging contexts are also those that are most likely to initiate cooperative behaviors (King et al. 2009). On the other hand, it is possible that cooperation occurs within social groups such that leaders are “helped” by others in exchange for their leadership (Kern and Radford 2018). Dynamics of leading and following may also be a form of cooperation in themselves. In their study of captive Northern bald ibis (*Geronticus eremita*) leading and following in V-formation flight, Voelkl et al. (2015) found that individuals would change positions in order to match their own leading time to the current leader’s (direct reciprocity). Furthermore, how much an individual could benefit from being a follower was strongly correlated with how long they were the leader.

Foraging behavior and efficiency have direct consequences for fitness (Clark and Mangel 1986; Stephens et al. 2007), can vary widely both within and among groups (Milligan et al. 2017), and may influence social structure and dynamics (Methion and Díaz López 2020). Previous studies have explored leading behavior during foraging in birds in terms of moving from one patch of resources to another. In an early study, Beauchamp (2000) looked at the order of arrival of size- and food deprivation-matched pairs of zebra finches (*Taenopygia guttata*) to reach a foraging patch and found that the same individual was consistently arriving first. After additionally looking at their solitary activity and exploration levels in a novel environment, this research suggests that leadership is dependent most on activity and exploration levels, rather than dominance or motivation. However, it could be argued that individuals with higher levels of activity have higher energetic needs (Réale et al. 2010).

In their study on leading and following in rock sparrows (*Petronia petronia*), Tóth and Griggio (2011) found that individuals with a larger breast patch, a sexually selected trait, were more likely to be leaders regardless of sex or body condition. Because the breast patch is related to the ingestion of carotenoid-rich food (and condition dependent), they suggest that following these individuals may lead to more efficient foraging. Alternatively, it is possible that those individuals with larger breast patches are more in need of resources (particularly carotenoid-rich ones) and are more likely to initiate foraging trips. Larger breast patches in this species are also indicative

of dominance in terms of the ability to acquire territories and access to food resources (Griggio et al. 2007).

Understanding the relative contributions of spatio-temporal and individually driven mechanisms is a central aim of behavioral ecology because of the consequences for phenotypic selection (Kasumovic et al. 2008; Farine et al. 2015; Kay et al. 2017). Further work is necessary to gain more insight into the relative roles of different ecological drivers in causing leading behavior. What are the mechanisms behind various predictors of leadership? Are leader–follower dynamics maintained by the same mechanisms in different contexts, populations, and species? It may be that some classes of individuals are more likely to be leaders than others, but it is not always clear *why* this is the case; some effects may be dependent on spatial (where individuals are present) or temporal (when individuals are present) mechanisms. Furthermore, it is possible that certain individuals prefer to feed in particular locations because they are more (or less) likely to be leaders there.

Here, we study the individual feeder visits of birds once they arrive at a resource (as opposed to collective movement between areas). We explore patterns of passive leadership in mixed-species foraging flocks of passerine birds in order to uncover the factors (age, sex, species, activity level) that influence this behavior. In the winter, great tits and blue tits forage in mixed-species flocks that exhibit fission–fusion dynamics (Farine et al. 2012). As described by Hinde (1952), mixed-species flocks of tits often move in “integrated movements,” arriving at a resource in a flock together and subsequently commencing feeding. Here, we use an experimental manipulation of feeder access to investigate the factors that predict whether individuals are leading or not at the scale of individual feeder visits. We define leaders as individuals that initially arrive and unlock a feeder, taking on the time “cost” (that comes with a higher chance of interference or risk) of waiting for feeders to open and also take any costs of being the first individual to approach and use the feeder, while those who feed from feeders that have already been unlocked are not; and leaders are individuals that are followed by others more than they follow others themselves. Based on the assumption that motivation and dominance are associated with higher rates of leading behavior, we predicted that great tits, males, adults, and individuals with higher levels of activity would be more likely to be engaged in leading behaviors. We additionally compare our results with specific null models, which directly incorporate consideration of patterns of non-independence within the data, and we use these to tease apart the influence of spatial and temporal drivers on these effects.

Material and methods

Study system

This work took place within a larger study on the social ecology of wild birds, conducted in Wytham Woods, Oxford, UK, on the long-term study population of great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*), and European nuthatches (*Sitta europaea*). Birds are marked with unique BTO (British Trust for Ornithology) metal leg rings and aged (juvenile if they were born in the most recent breeding season) and sexed during the breeding season at nest boxes or during the winter with mist netting. Captured birds are also fitted with a plastic leg ring housing a PIT (passive integrated transponder) tag that can be detected automatically when in the range of an RFID (radio frequency identification) antenna. It is estimated that more than 90% of the resident population is tagged (Aplin et al. 2013). In this system, sunflower seed feeding stations with RFID antennae (Dorset ID, Aalten, The Netherlands) are used to generate time (in seconds), date, and location stamped records of each individual’s feeder visits. Mixed-species tit flocks feed on patches of resources that are scattered across the environment, and competition for food is most intense in mid-winter (Gibb 1954). Due to the relatively low number of individual coal tits, marsh tits, and nuthatches, we restricted our analyses to great tits and blue tits, the numerically dominant species within this system. However, data on individuals of other species were only removed after the labeling of inter-visit intervals and leading-following events (“[Determining leading and following behavior](#)” section), in order to retain information about the true order of visits and whether they were a “following” event.

Feeder sites

The current study was conducted between November 2016 and January 2017 in the southernmost part of Wytham Woods (Bean Wood; 51° 45′ 28.8″ N, 1° 19′ 47.4″ W) which is partially separated from the remainder of the woods (and the main study area) by farmlands (Fig. 1). It was not possible to record data blind because our study involved focal animals in the field.

After an initial period (34 days) of acclimation, during which three standard, open-access feeders in this area were provided, they were replaced by six controlled access feeders (see Supplementary Image 1) with a single feeding hole (experimental design described further in Firth and Sheldon (2015) and Firth et al. (2015, 2016)). The

Fig. 1 Map displaying Wytham Woods; the inset displays Bean Wood and the locations of the feeders used (original feeder sites marked by an x). The sizes of the circles represent the relative numbers of individuals that visited, while the colors represent the proportion of male (darker shade) and female (lighter shade) blue tit (blue) and great tit (brown) feeder visits



access hole of each feeder was blocked by a transparent flap locked into place; the feeder was unlocked when a PIT tag was registered by the RFID antenna. Once opened, the flap stayed open and unlocked for 2 s. These feeders were used as opposed to normal (open access) RFID-detecting feeders because only tagged birds can initially open the flap. When using open-access feeders (without flap), untagged birds may be regularly feeding at the sites; calculating leading and following based on this open-access data-stream carries the potential of mis-labeling individuals that arrived with untagged birds.

Here, we use two selective feeders placed approximately 100 m apart at each site (each 50 m away from the initial standard feeder location). All six feeders were identical and afforded the same opportunities in terms of (1) type and quality of food available and (2) space to access the food from. The selective feeders were open from pre-dawn until after dusk every day. During an initial 34-day acclimation period (30 November to 2 January), the controlled access feeding mechanism was introduced to give PIT-tagged individuals time to learn how to use the selective feeders, i.e., only birds with a tag could visit these feeders. Additionally, this period would discourage untagged individuals from visiting these feeders. Then, once they learned to use the selective feeders, the behavior of the birds was recorded for 16 complete days (3 January to 18 January); any bird with a PIT-tag could unlock the feeders (i.e., same exact procedure as in the acclimation period). Throughout both periods, each feeder visit by a PIT-tagged bird was recorded with

the individual's ID as well as the date, time, and location of their visit.

Determining leading and following behavior

When an individual arrived at a feeder, they had to unlock the flap if another bird had not already done so. Once unlocked, the flap stayed open for 2 s. Initially unlocking the flap came with an associated cost, as the unlocking individual had to wait < 2 s for the flap to open (the time it takes for the feeder to register the tag and initiate the opening mechanism), making it more likely that there could be interference while they were feeding. On the other hand, those who arrived within the next 2 s could retrieve food and leave instantly with a smaller risk of others becoming involved or preventing them from feeding. This period of 2 s is also relevant when we look at the distribution of visit intervals over the course of the test period, with a majority of visits being within 1 or 2 s of one another (Fig. 2).

Using the spatio-temporal data stream produced by the recorded feeder visits, we labeled each feeder visit as a "lead" or not, according to the following logic and criteria. First, we calculated a leading time (the number of seconds that passed until another PIT-tagged individual visited that feeder) and following time (the number of seconds that passed since the previous PIT-tagged individual visited) for each visit. Based on the distribution of inter-visit intervals and the fact that the flap stayed open for 2 s upon being unlocked, we defined a feeder visit as a lead if no PIT-tagged

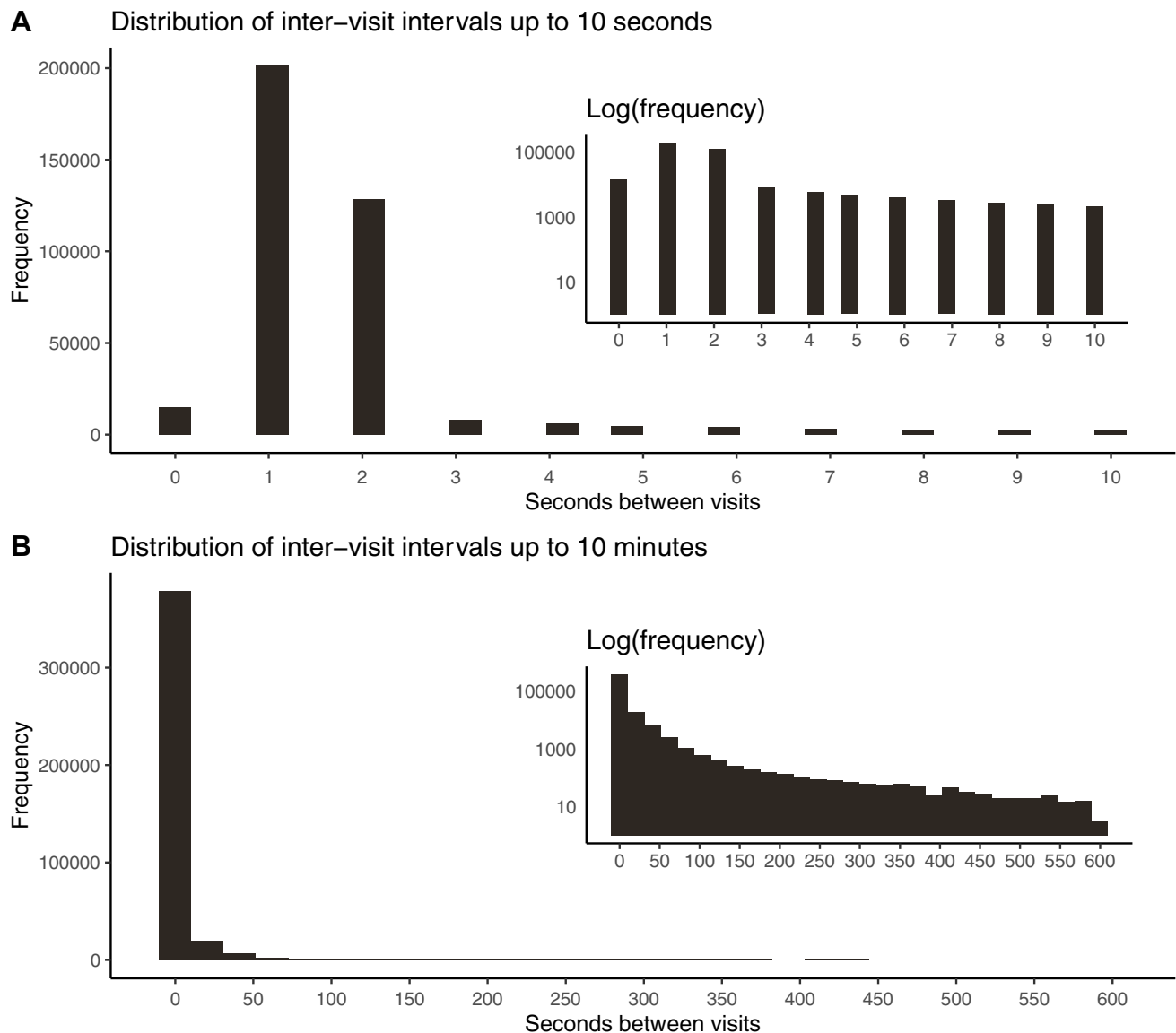


Fig. 2 Panels A and B display the distribution of inter-visit intervals up to 10 s and 10 min, respectively, over the entire test period; inset plots show the same distribution with the y-axis (frequency) on a log scale

birds had arrived within the previous 2 s (> 2 s following time), and a PIT-tagged bird had arrived within the following 2 s (≤ 2 s leading time; illustrated in Fig. 3).

In this way, we capture those feeder visits where a bird is a “leader” and is not following another bird. This variable was used for all of the following analyses. A feeder visit was defined as a “follow” if the focal individual arrived within 2 s of another PIT-tagged bird (≤ 2 s following time), regardless of whether or not the prior bird was labeled as a leader or follower. To assess leading in an alternative way, we calculated a leading to following ratio (described further in Supplementary Material Sect. 1). We additionally calculated four stricter leadership measures for supplementary analysis where no individual preceded the focal individual’s

arrival, within 5, 10, 20, or 30 s (e.g., ≤ 5 , ≤ 10 , ≤ 20 , ≤ 30 following time; Supplementary Material Sect. 2). Rather than focusing on the more relevant cut off of 2 s (the target of manipulation), these supplementary measures capture a slightly different behavior but still demonstrate fine-scaled within-species differences.

Overall, leaders are individuals that take on the initial cost of the slight time delay (< 2 s) of unlocking the feeders along with any risk associated with being the first individual to approach a feeder/area while others are not there using it. Followers are individuals that arrive immediately after leaders and, therefore, do not have to unlock the feeders themselves and also do not experience any risk associated with being first. This method of labeling leaders and followers

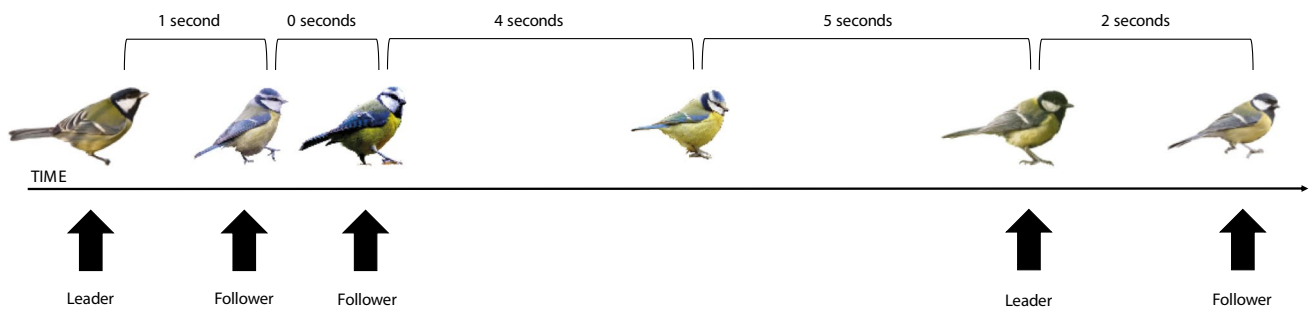


Fig. 3 A visual representation of how leads and follows were determined. Starting from the left (earliest in time), the first bird is classed as a leader, as a bird arrives < 2 s after, but no bird arrives before them. The second bird is a follower, but not a leader because a bird arrived < 2 s before them. The third bird is a follower because they arrive < 2 s after another bird, but no bird arrives < 2 s after

them. The fourth bird is not a leader or follower, because no birds arrive within < 2 s of them (before or after). The fifth bird is a leader, because they do not follow anyone themselves (i.e., does not arrive < 2 s after another bird), but the sixth bird arrives < 2 s after they do (making the final bird a follower)

assumes that the presence of some untagged birds does not significantly change our estimation of leading/following events. We believe this is true as (a) the acclimation period deters untagged birds from using the feeders (as they cannot use any of the feeders directly) and (b) as the “following” window uses such a short time cut-off, the birds which are classed as “followers” are likely to not have been preceded by an untagged individual, and—even in the rare occasions when they were—they are still carrying out the following activity (albeit just coming after a different individual).

Statistical analyses

To analyze whether leading in this context was associated with factors related to motivation and dominance that we had hypothesized as predictors of leading behavior, binomial generalized linear mixed models (GLMM) were run in R using the package “lme4.” These models were run with the dependent variable of “lead or not,” based on each individual feeder visit. We explored various fixed effects and their interactions (age and species and sex and species; detailed in Supplementary Material Tables S8, S9). In all the models, date, location (i.e., feeder), and individual ID were

included as random effects. In the final model (Table 1), species (great tit or blue tit), age (juvenile or adult), sex, and activity (total number of feeder visits in test period) were included as fixed effects. The model was checked using several model diagnostics and visual inspection of residuals (with the “DHARMa” package); none were indicative of any deviations from the assumptions of normality and homogeneity of residuals.

In these primary models, all records for great tits and blue tits are included. However, some individuals were leading and following at similar rates. To perform supplementary sensitivity analysis, we asked whether the same patterns would hold if we removed those individuals in the central part of the distribution and only focused on individuals that are consistently leading or consistently following. In other words, we remove those individuals that are leading and following at similar rates and therefore do not have a strong propensity/preference to be a leader or follower. We first calculated the total number of leads and total number of follows that each individual engaged in to come up with a leading proportion (mean = 0.54, min = 0, max = 0.86, median = 0.60, SD = 0.23). We then calculated the first and fourth quartile of the leading proportion and labeled

Table 1 Binomial GLMM model summary of the observed results with the dependent variable set as lead or not lead, analyzing if each feeder visit is a lead or not

Dependent variable	Fixed factor/effects	Estimate $\pm$ SE	z	p
Lead or not $N = 314,809$	Intercept	0.087 ± 0.129	0.673	0.501
	Species (blue tit vs. great tit)	-0.350 ± 0.054	-6.416	< 0.001
	Age (juvenile vs. adult)	0.065 ± 0.051	1.262	0.207
	Sex (male vs. female)	0.132 ± 0.050	2.616	0.009
	Activity	0.168 ± 0.029	5.846	< 0.001
	Random effects	Variance	Standard deviation	
	Ring (ID; $N = 169$)	0.087	0.295	
	Date ($N = 16$)	0.008	0.088	
	Feeder (location; $N = 6$)	0.092	0.303	

individuals as having high, middle, or low rates of leads. Records for individuals with “middle” rates of leading (i.e., from the second and third quartiles) were removed from the dataset. We then re-ran the models (Supplementary Material Table S10).

One way to examine the drivers behind various effects is through the use of null models, where the model used for the observed results is re-run numerous times after the response variable is shuffled over chosen spatial and temporal scales (i.e., different restriction types). The observed results are compared to the null model results to separate out predictors that are significantly different from what would be expected by random, i.e., the variable measuring the behavior in question is randomized, but spatial and temporal patterns are retained. Furthermore, because the actions of each individual in a leader–follower pair are somewhat dependent on one another, null models are especially useful for teasing out the patterns that we would expect by chance due to this relationship. To further investigate these results and uncover patterns of non-independence here, null models were run using the “lead or not” model with five different sets of restrictions (Gotelli 2001; Veech 2012). These restrictions keep some characteristics of the data intact while randomizing others, so that we can assess if the observed effects differ from the effects that we would observe by chance (i.e., if birds arrived in a random order). We swapped (randomly re-allocated) the “leading time” and “following time” (the time differences between visits) among individuals (which manipulates the order of arrival) with the following restrictions and ran 10,000 permutations for each restriction type. This swap also ensures that leader–follower pairs are not dependent on one another.

- Site, day, and activity restriction: time differences (leading and following time) are swapped at each feeder on each day. This conserves the spatial and temporal structure of the data, as well as the activity level of each individual.
- Site and activity restriction: time differences are swapped at each feeder. This conserves the activity level of each individual and the spatial but not temporal structure of the data.
- Day and activity restriction: time differences are swapped on each day. This conserves the activity level of each individual and the temporal but not spatial structure of the data.
- Activity restriction only: time differences are swapped with no restriction. Only the activity level of each individual is retained.
- No restrictions: time differences are swapped with no restriction, activity is re-calculated post-swap. The structure of the data is not conserved, effectively allowing for a comparison to what we would expect at random.

Z-values for each of the effects in each model were compiled and compared to the observed z -value in our real model. The p -value was calculated by calculating where the observed value lies within the distribution of values obtained from the null models; results were labeled as “significantly different from expected by the null” if the observed z -value was outside of the 95% range generated by the null models.

Results

During the 16-day test period, there were a total of 411,158 visits by 128 blue tits (161,496 visits), 71 great tits (164,148 visits), 13 marsh tits (68,559 visits), two nuthatches (16,922 visits), and two coal tits (33 visits; see Supplementary Material Table S11 for further details). All following analyses considered great tits and blue tits with known sex only ($N = 169$; sex was not known for some birds because they had been ringed as nestlings when sex cannot be reliably determined from visual cues). However, as noted for data on other species, data on individuals of unknown sex were only removed after the labeling of inter-visit intervals and leading-following events (“[Determining leading and following behavior](#)” section) was conducted, in order to retain information about the true order of visits and whether they were “following” events.

Observed effects

Over the test period, species was the strongest predictor of whether a feeder visit was a lead or not with great tits leading more often than blue tits (Table 1, Fig. 4). This is followed closely by activity level, where higher activity is indicative of leading. There was also a much smaller effect of sex (males more likely to be leading). The same patterns are present when considering the leading to following ratio (Table S2). Similar patterns can also be seen at the level of individual feeder visits when records from individuals with similar rates of leading and following (“middle” individuals) are removed from the dataset; however, the effect of sex is no longer significant while the effect of age is larger and significant, suggesting that the sex effect is enhanced by “middle” individuals while the age effect is weakened by “middle” individuals (Supplementary Table S10). When using a stricter definition of leading, only the effect of species remains significant (Table S3–S6).

We additionally ran the same model (from Table 1) for each species separately and with the interaction of sex and age included (Supplementary Material Table S12–S15). For great tits, there is an effect of sex and activity (Table S12), while for blue tits, activity is the only significant predictor (Table S15). For both species, the effect of the interaction

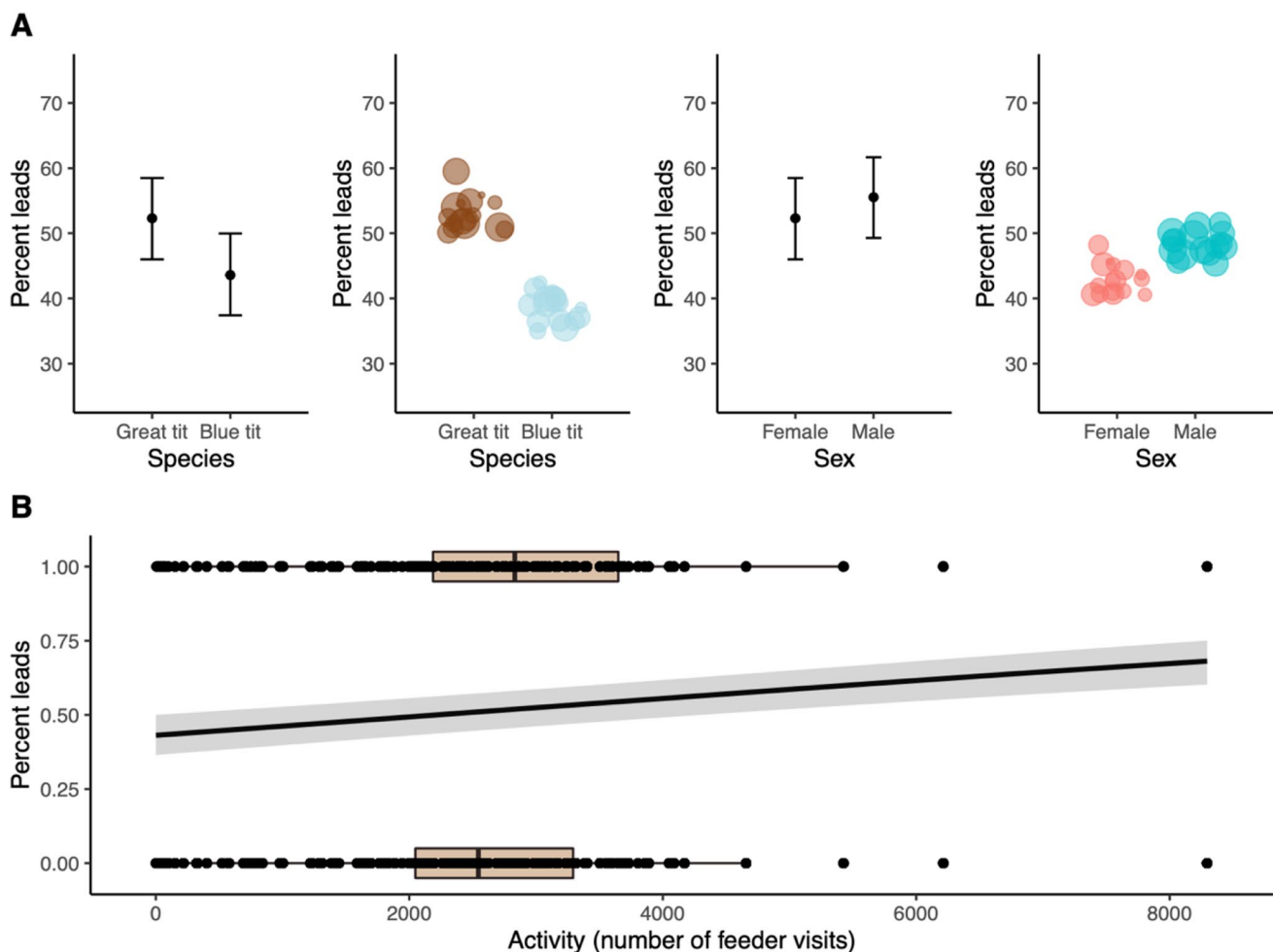


Fig. 4 Plots showing model estimates and raw data for the observed significant ($p < 0.01$) effects of species (panel A, left), sex (panel A, right), and activity (panel B) for the model at the level of feeder visits (Table 1). In plot A, black point and error bars represent model estimates and 95% confidence intervals, while colored points repre-

sent the percentage of leads for each day ($N = 16$) in the test period. In plot B, the boxplots and points represent the observed data, while the fitted line and shading show model estimates and 95% confidence intervals

between age and sex is small and not significant (Table S13, S15).

Null models

In the most restrictive null model (Fig. 5A), the observed effects of species ($p_{\text{null}} = 0.0001$) and age ($p_{\text{null}} = 0.0406$) are significantly different than what would be expected if birds were arriving in a random order but still on the same day, at the same feeder, and the same number of times as observed. However, the effects of sex ($p_{\text{null}} = 0.9648$) and activity ($p_{\text{null}} = 0.1522$) are not, suggesting that these effects in the model are driven by spatial and temporal dynamics. This is also the case when the day restriction is lifted (Fig. 5B); the observed effects of species ($p_{\text{null}} = 0.0001$) and age ($p_{\text{null}} = 0.0448$) are significantly different than what would be expected if birds were arriving in a random order but at

the same feeder and the same number of times as observed. When the site restriction is lifted instead (date and activity only; Fig. 5C), the observed effect of age ($p_{\text{null}} = 0.0554$) is on the margin, while species ($p_{\text{null}} = 0.0008$) remains significantly different than expected, and sex ($p_{\text{null}} = 0.6982$) and activity ($p_{\text{null}} = 0.0904$) do not.

In the activity restriction null model (Fig. 5D), only the effect of species ($p_{\text{null}} = 0.0006$) is significantly different than what we would expect if birds arrived in a random order, but the same number of times as observed. Again, age is on the margin ($p_{\text{null}} = 0.0512$) and sex ($p_{\text{null}} = 0.7138$) and activity ($p_{\text{null}} = 0.0994$) are not different than expected. When there are no restrictions (Fig. 5E), allowing the birds to arrive in a completely random order, all of the observed effects are significantly different than what we would observe by chance, suggesting that the observed effects of age and sex are dependent on activity levels, while the effect of species is not dependent

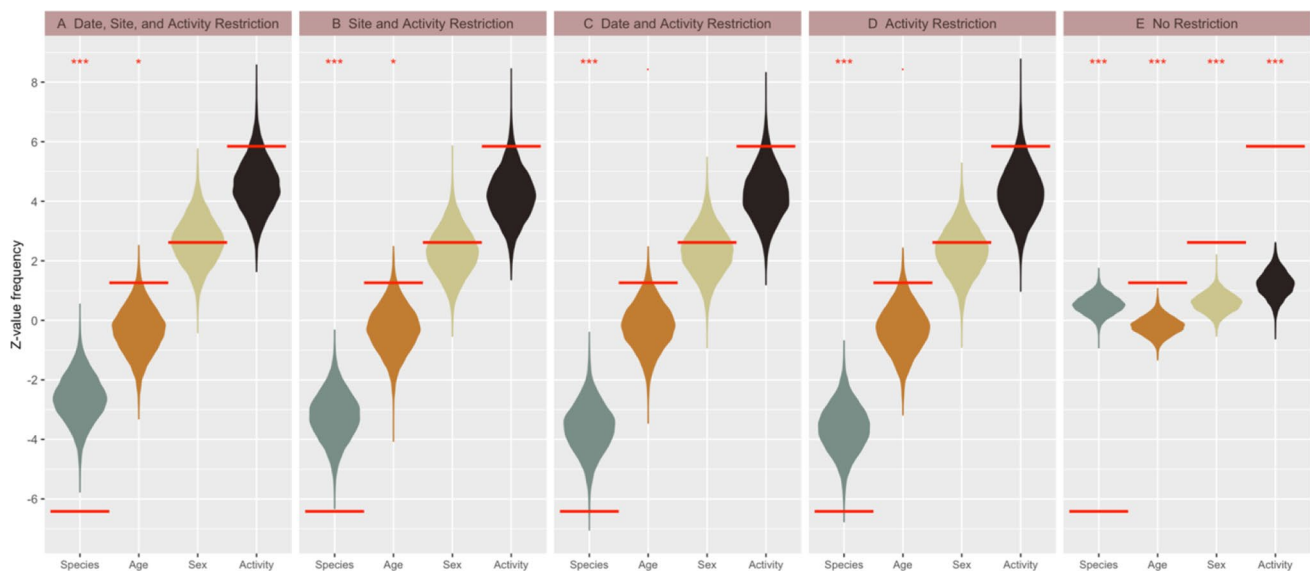


Fig. 5 Violin plots displaying the results of the null models with all five restriction types. Each panel denotes a restriction type, while the fixed effects (of species, age, sex, and activity) are along the x-axis. Solid red lines indicate the observed z -value for each effect, and the

stars at the top of the y-axis denote significance levels, i.e., whether the observed z -value is significantly different from those derived from the null models (***) = < 0.001 , * = < 0.05 , . = < 0.1)

on any of these restrictive factors. Running the same set of permutations with the great tit only model (Table S12) reveals that the effects of sex and activity are significantly different than what we would observe by chance (no restriction) but not with any of the other restriction types, suggesting that the observed effect of sex within great tits is dependent on where and when birds feed and their activity levels (details in Fig. S1).

Additional following-level species effects

Having demonstrated a robust effect of species on leading behavior, we further examined the identity of those individuals following great tit vs. blue tit leaders. Of the 164,148 visits by great tits, 86,965 (52.98%) were leading events. Great tit leaders were followed by blue tits 869 times (1%), by marsh tits 190 times (0.22%), and by nuthatches 37 times (0.04%), with the remainder (85,869, 98.74%) being followed by great tits. Of the 161,496 visits by blue tits, 62,340 (38.60%) were leading events. Blue tit leaders were followed by great tits 511 times (0.82%), by marsh tits 190 times (0.30%), by nuthatches 18 times (0.03%), and by one coal tit, with the remainder (61,605, 98.82% of the time) being followed by blue tits.

Discussion

Patterns of passive leading behavior can be dependent on various characteristics of the individual, and the effects of these characteristics can themselves be driven by spatial and

temporal dynamics (where and when individuals are feeding). Here, we defined passive leaders as individuals who (1) initially unlocked a feeder, taking on the cost of waiting for feeders to open, and (2) did this more often than they followed others. In wild mixed-species flocks of passerine birds, leading behavior within locations is influenced by species, sex, and activity. As expected, indicators of dominance and motivation appear to shape which individuals arrive at feeders without following others. Overall, great tits lead more often than blue tits. In terms of within-species effects, blue tits with higher activity levels were more likely to be leaders, but there was no significant effect of age or sex. For great tits, males and individuals with higher levels of activity were more likely to be leaders, but both effects are spatio-temporally driven. It is unclear if this is driven solely by these mechanisms or if individuals prefer to feed in particular locations at specific times because they are more (or less) likely to be leaders there. The most robust finding here is that great tits lead more often than blue tits; great tits are more likely to initially unlock a feeder once a group has arrived at a feeding location.

By using null models, we were also able to investigate the mechanics of this leading behavior. The effect of sex and activity is driven by spatial and temporal dynamics (where and when individuals feed), while the effect of species is robust to a wide range of alternative null models (not driven by the time or location of feeding). Additionally, estimates of leading behavior are highly dependent on the total number of feeder visits an individual made (individuals with higher feeder visits have higher estimates of leading

behavior), suggesting that the number of times an individual is observed may influence results regardless of differences in leading behavior.

The results obtained here emphasize the importance of using null models for understanding the drivers of different processes. Previous studies that identify leading behavior often ascribe effects to individual-level processes when they may have other drivers. Although some effects (like sex and activity here) may be spatio-temporally driven, it is still important to consider them. Is it the case that the effect of sex seems to be driven by temporal and spatial aspects simply because that is what constrains these results, or is it because males and females have different preferences in terms of being a leader and follower in this system? In other words, individuals may be non-random in their choices of where and when to feed. For example, juvenile great tits have been found to have more social connections than adults, and this is driven by spatial dynamics—juveniles visit locations with larger groups or with higher levels of activity (Farine et al. 2015). However, it is still possible that juveniles prefer to be more social and are engaging in feeding at these times and locations for precisely that reason. To test causality in these situations, further experimental evidence is necessary; by manipulating where and when individuals can feed or be, we can look at whether individuals continue to be leaders (or followers) in the absence of the possibility to influence their own spatial and temporal decisions. For example, in the case of this system, if an individual that does not engage in leading often is restricted to a feeder where there are high activity levels, will they begin leading?

In this mixed-species population, dominance is related to body size both within and among species (Morse 1978, p. 300; Gosler and Carruthers 1999). Great tits are the largest and most dominant species in these flocks and regularly succeed over blue tits in competition for nest boxes (Dhondt and Eyckerman 1980; Minot and Perrins 1986; Kempenaers and Dhondt 1991). The fact that great tits are leading more often in this population is in line with existing theories of leading on the basis of dominance and energetic requirements (Rands et al. 2006; Conradt et al. 2009; Öst and Jaatinen 2013). Furthermore, more dominant individuals in this population are more vigilant during foraging, and there is a causal relationship between dominance and competence in choosing the safest foraging locations (Krams 1998), making great tits ideal leaders. What is striking, however, is the fact that great tits and blue tits almost exclusively follow conspecifics. In other words, individuals are unlikely to initially approach a feeder that has been opened by another individual unless that individual is a conspecific. The reason for this is unclear and remains to be tested.

All studies focusing on a particular aspect of leadership are limited to drawing conclusions within that particular context. Indeed, leadership is not absolute, meaning that leading in

each instance may depend on the identity of leader–follower pairs even in a passive context. Within this particular study, for example, even though the experimental feeding system allows examination of leadership under natural settings, it is difficult to determine if the activity that occurs here would directly reflect the leader–follower relations that would occur within other foraging conditions (e.g., on natural food sources without centralized feeders) or other differing environmental conditions (Carrascal et al. 1998). Furthermore, it is also important to note that when studying leadership in the context of activity within a particular area (such as done in this study), this may not directly relate to leadership in the context of collective movement between areas (such as is done in many other studies). As such, future work directly testing how leadership carries over across different contexts (e.g., different foraging situations or within- vs. between-area movement) would be of much interest. Finally, the precise costs and benefits of being a leader or follower could not be ascertained in this study. For example, precise monitoring of predation risk is difficult with this set-up (but see Voelkl et al. (2016) for findings on predation dynamics in a separate experiment). Further experimental (in captivity) and observational (in the wild) studies are necessary to uncover and quantify the relative costs of leadership (Ioannou et al. 2019).

There are also other possible factors that may have an influence on leading. Temperament or personality may have an impact; in their study on pairs of sticklebacks (*Gasterosteus aculeatus*), Harcourt et al. (2009) found that bold individuals were more likely to lead and less likely to follow than shy individuals. Kurvers et al. (2009) go so far as to argue that individual differences in personality may be maintained in order to foster social coordination. Social relationships can also play a role, with individuals following the behaviors of their close social partners (Jacobs et al. 2011). Some studies have even shown that reproductive status may have an impact on leading behavior, most likely due to the energetic requirement that comes with breeding (Pyritz et al. 2011). In some situations that are more movement-based than the passive leadership studied here, having more information or knowledge about how or where the collective action will take place can increase the probability that an individual leads. This is especially the case in joint navigation, where previous experience or knowledge of a route is crucial to success (Flack et al. 2012). Further work is needed to gain a more complete picture of the drivers of leading behavior and how they may operate in different settings.

Conclusion

Collective behaviors are widespread in the animal kingdom, and discovering which individual initiates them, and which individuals follow initiation, is crucial to our understanding

of sociality and several social processes (King et al. 2009). Here, we show that there are species differences in passive leading behavior, in a natural population of wild birds, that are in line with theories on leading that are related to motivation in terms of nutritional requirements as well as dominance. Great tits, the larger and more dominant species, are leading more often than blue tits. However, when individuals do lead, they are almost exclusively followed by conspecifics. Furthermore, our use of null models shows that the observed effects of sex (males leading more than females) and activity (higher activity levels associated with more leading) are driven by spatial and temporal dynamics; this highlights the utility of using null models to explore patterns of non-independence and uncover the mechanisms behind various effects. Future work can integrate other proposed predictors of leadership (measures of personality, more precise measures of metabolic rate, social structure, etc.) to gain a more holistic understanding of passive leadership. There would also be much benefit in manipulating spatial and temporal dynamics to provide further insights into how experimental changes impact leading behavior and to allow for concrete conclusions regarding the causes of leading behavior to be drawn.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-03103-3>.

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Data availability The dataset analyzed during the current study is available in the “leadingsongbirds” repository, <https://github.com/samin gokcekus/leadingsongbirds>.

Declarations

Ethics approval All work was reviewed and approved by the local ethical review committee (Department of Zoology, University of Oxford, UK) and adhered to UK licensing requirements as well as the ASAB/ABS Guidelines for the Use of Animals in Research. This work was conducted as part of a larger, ongoing research project at Wytham Woods. All birds were caught and ringed by appropriate BTO license holders.

Conflict of interest The authors declare no competing interests.

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Supplementary material

1. Leading to following ratio

To calculate the leading to following ratio, we calculated the number of leads and follows that a bird engaged in at each feeder on each day. We retained a record of individual leads and follows for each day and feeder where there were more than two leads and two follows. There was a total of 2,607 records (unique bird-day-feeder combinations) from 146 individuals (median = 19, IQR = 9.51). Of these records, 1557 (59.72%) were from blue tits and 1050 (40.28%) were from great tits (detailed by day and feeder in Table S1). The ratio vs. lead or not models explain a similar behavior but on slightly different time scales; lead or not examines each individual feeder visit while the ratio summarizes leads and follows for each location on each day. Therefore, it is not surprising that the patterns from the full lead or not models are mirrored in the results for the ratio of leads to follows: great tits, males, and those with higher average activity have a higher number of leads than follows (Table S2).

Table S1 - Breakdown of number of ratio records (unique bird-day-feeder combinations with more than two leads and two follows) from blue tits and great tits on each day at each logger

Logger - species	Days															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Aa – blue tit	16	17	14	16	15	18	12	15	14	16	24	18	23	22	16	26
Aa – great tit	3	6	4	4	4	5	4	4	3	3	6	4	5	5	3	5
Ab – blue tit	5	1	4	2	2	3	3	4	3	2	1	5	4	1	1	1
Ab – great tit	4	2	5	3	3	3	3	3	3	2	3	3	3	3	2	3
Ba – blue tit	30	34	35	34	35	39	30	40	39	38	36	37	48	36	43	50
Ba – great tit	16	23	25	18	27	27	16	23	21	21	17	16	21	18	22	25
Bb – blue tit	34	24	34	31	26	32	27	25	31	31	31	22	25	22	18	5

Bb – great tit	25	29	30	21	24	20	19	15	19	16	17	14	13	10	10	0
Ca – blue tit	10	12	2	6	15	14	8	8	2	8	11	8	10	9	5	11
Ca – great tit	6	14	2	2	18	18	12	4	4	8	7	6	19	4	2	9
Cb – blue tit	5	0	5	2	2	2	1	2	4	4	11	7	4	6	4	13
Cb – great tit	13	5	9	1	5	7	8	3	6	18	24	22	19	12	11	18

Table S2 – observed results with the dependent variable as a ratio of leads to follow at each feeder on each day

Dependent variable	Fixed factor/effects		Estimate ± SE	z-value	p-value
Leads, follows N=2607	Intercept		0.799 ± 0.147	5.425	<0.001
	Species (blue tit vs. great tit)		-0.359 ± 0.056	-6.338	<0.001
	Age (juvenile vs. adult)		0.035 ± 0.053	0.654	0.513
	Sex (male vs. female)		0.162 ± 0.053	3.077	0.002
	Activity		0.111 ± 0.025	4.384	<0.001
	Random effects	Variance	Standard deviation		
	Ring (ID; N=146)	0.087	0.295		
	Date (N=16)	0.009	0.096		
	Feeder (location; N=6)	0.109	0.330		

2. Stricter leading measures

Here, a feeder visit was defined as a lead if no PIT-tagged birds had arrived within the previous 5, 10, 20, or 30 seconds, and a PIT-tagged bird had arrived within the following two seconds. These measures do not focus only on those who take on the initial time cost of opening the feeder (and associated risk of being first), but also a propensity to come to the feeders when others have not been to the feeder in a while (especially in the case of 30 seconds). In comparison to models using less strict definitions of leading, here we see that the effect of species remains while the effects of sex and activity are not significant; this is mirrored in the null model results (Figure 5).

Table S3 - observed results with the dependent variable as a strict leading measure with 5 second cut off

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=314,809	Intercept		4.422 $\pm$ 0.260	17.037	<0.001
	Species (blue tit vs. great tit)		-0.325 $\pm$ 0.098	-3.330	<0.001
	Age (juvenile vs. adult)		-0.082 $\pm$ 0.089	-0.919	0.358
	Sex (male vs. female)		-0.128 $\pm$ 0.087	-1.475	0.140
	Activity		-0.041 $\pm$ 0.055	-0.752	0.452
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.201	0.448		
	Date	0.066	0.257		
	Feeder (location)	0.404	0.635		

Table S4 - observed results with the dependent variable as a strict leading measure with 10 second cut off

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=314,809	Intercept		4.646 $\pm$ 0.340	13.697	<.001
	Species (blue tit vs. great tit)		-0.345 $\pm$ 0.114	-3.023	0.003
	Age (juvenile vs. adult)		-0.072 $\pm$ 0.105	-0.688	0.491
	Sex (male vs. female)		-0.175 $\pm$ 0.102	-1.715	0.086
	Activity		-0.088 $\pm$ 0.064	-1.387	0.165
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.271	0.521		
	Date	0.073	0.271		
	Feeder (location)	0.606	0.779		

Table S5 - observed results with the dependent variable as a strict leading measure with 20 second cut off

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=314,809	Intercept		4.889 $\pm$ 0.365	13.386	<0.001
	Species (blue tit vs. great tit)		-0.426 $\pm$ 0.132	-3.219	0.001
	Age (juvenile vs. adult)		-0.072 $\pm$ 0.119	-0.606	0.544
	Sex (male vs. female)		-0.164 $\pm$ 0.118	-1.384	0.166
	Activity		-0.132 $\pm$ 0.074	-1.779	0.075
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.362	0.601		
	Date	0.079	0.281		

	Feeder (location)	0.734	0.857
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Table S6 - observed results with the dependent variable as a strict leading measure with 30 second cut off

Dependent variable	Fixed factor/effects		Estimate ± SE	z-value	p-value
Lead or not N=314,809	Intercept		4.975 ± 0.383	12.986	<0.001
	Species (blue tit vs. great tit)		-0.305 ± 0.130	-2.339	0.019
	Age (juvenile vs. adult)		-0.050 ± 0.118	-0.427	0.669
	Sex (male vs. female)		-0.111 ± 0.117	-0.949	0.342
	Activity		-0.082 ± 0.074	-1.105	0.269
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.334	0.578		
	Date	0.089	0.299		
	Feeder (location)	0.844	0.919		

3. Further material

Table S7 – lead or not model with day included as a fixed effect

Dependent variable	Fixed factor/effects		Estimate ± SE	z-value	p-value
Lead or not N=314,809	Intercept		0.086 ± 0.115	0.749	0.454
	Species (blue tit vs. great tit)		-0.349 ± 0.053	-6.594	<0.001
	Age (juvenile vs. adult)		0.065 ± 0.051	1.284	0.199
	Sex (male vs. female)		0.132 ± 0.050	2.638	0.008
	Activity		0.168 ± 0.029	5.891	<0.001
	Day		-0.014 ± 0.022	-0.643	0.520
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.087	0.295		
	Date	0.007	0.087		
	Feeder (location)	0.092	0.304		

Table S8 - lead or not model with the interaction between species and age included

Dependent variable	Fixed factor/effects		Estimate ± SE	z-value	p-value
Lead or not	Intercept		0.091 ± 0.120	0.755	0.450

N=314,809	Species (blue tit vs. great tit)		-0.358 ± 0.066	-5.439	<0.001
	Age (juvenile vs. adult)		0.051 ± 0.077	0.662	0.508
	Sex (male vs. female)		0.133 ± 0.050	2.638	0.008
	Activity		0.168 ± 0.029	5.809	<0.001
	Species:age (bluti:juvenile)		-0.023 ± 0.098	0.232	0.817
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.087	0.295		
	Date	0.007	0.088		
	Feeder (location)	0.092	0.303		

Table S9 - lead or not model with the interaction between species and sex included

Dependent variable	Fixed factor/effects		Estimate ± SE	z-value	p-value
Lead or not N=314,809	Intercept		0.032 ± 0.125	0.259	0.795
	Species (blue tit vs. great tit)		-0.251 ± 0.074	-3.402	<0.001
	Age (juvenile vs. adult)		0.061 ± 0.051	1.211	0.226
	Sex (male vs. female)		0.228 ± 0.071	3.192	0.001
	Activity		0.169 ± 0.029	5.916	<0.001
	Species:sex (bluti:male)		-0.166 ± 0.091	-1.828	0.068
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.086	0.293		
	Date	0.008	0.088		
	Feeder (location)	0.092	0.304		

Table S10 - lead or not model where records from individuals that lead and follow at similar rates are removed

Dependent variable	Fixed factor/effects		Estimate ± SE	z-value	p-value
Lead or not N=132,308	Intercept		0.227 ± 0.147	1.541	0.123
	Species (blue tit vs. great tit)		-0.580 ± 0.098	-5.920	<.001
	Age (juvenile vs. adult)		0.220 ± 0.096	2.279	0.023
	Sex (male vs. female)		0.113 ± 0.098	1.152	0.2495
	Activity		0.278 ± 0.058	4.773	<.001
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.125	0.353		
	Date	0.008	0.088		
	Feeder (location)	0.072	0.269		

Table S11 – Detailed summary of feeder visits, leads, and follows for each age, sex, and species at each feeder site

Feeder				Aa		Ab		Ba		Bb		Ca		Cb	
Species	Sex	Age	TOTAL visits	Leads	Follow	Leads	Follows	Leads	Follows	Leads	Follows	Leads	Follows	Leads	Follows
Great tit	Male	Juvenile	30603	1798	717	42	8	5575	1434	3970	1499	2400	1184	3995	1370
		Adult	64895	1328	597	3226	836	12056	5979	12887	4500	635	325	5697	1826
	Female	Juvenile	18785	1226	769	16	4	1703	1123	1798	965	1360	600	3255	1034
		Adult	48458	241	100	1726	569	7099	4408	7056	4113	2936	1523	4208	1670
Blue tit	Male	Juvenile	40746	3208	1911	717	244	4390	4340	4486	3288	3042	1305	1132	453
		Adult	52949	1684	1038	87	38	7111	7380	8036	5707	2530	982	1465	523
	Female	Juvenile	25973	2625	1903	373	177	1972	2620	4069	3430	117	71	131	36
		Adult	32400	1712	1298	49	29	5210	5000	3480	2971	541	279	1108	386
Marsh tit	Male	Juvenile	8764	10	7	18	11	118	134	1675	1410	1700	822	154	75
		Adult	8950	350	223	1754	464	244	210	648	458	1514	722	0	0
	Female	Juvenile	12919	1360	605	423	105	1444	1240	1652	1077	763	397	7	4
		Adult	14086	587	305	2668	774	208	172	1982	1270	1726	716	0	0
Coal tit	Male	Juvenile	0	0	0	0	0	0	0	0	0	0	0	0	0
		Adult	31	0	0	0	0	0	0	0	0	0	1	3	13
	Female	Juvenile	0	0	0	0	0	0	0	0	0	0	0	0	0
		Adult	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuthatch	Male	Juvenile	0	0	0	0	0	0	0	0	0	0	0	0	0
		Adult	6653	0	0	0	0	1022	254	3506	762	0	0	0	0
	Female	Juvenile	0	0	0	0	0	0	0	0	0	0	0	0	0
		Adult	10269	0	0	0	0	944	259	6043	1350	0	0	0	0

Table S12 - lead or not model with great tits only

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=162,741	Intercept		0.043 $\pm$ 0.115	0.372	0.709
	Age (juvenile vs. adult)		0.068 $\pm$ 0.069	0.985	0.324
	Sex (male vs. female)		0.227 $\pm$ 0.065	3.469	0.001
	Activity		0.177 $\pm$ 0.036	4.975	<0.001
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.060	0.246		
	Date	0.009	0.097		
	Feeder (location)	0.062	0.250		

Table S13 - lead or not model with great tits only and interaction of age and sex included

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=162,741	Intercept		0.042 $\pm$ 0.118	0.358	0.721
	Age (juvenile vs. adult)		0.070 $\pm$ 0.104	0.672	0.502
	Sex (male vs. female)		0.228 $\pm$ 0.078	2.930	0.003
	Activity		0.177 $\pm$ 0.036	4.966	<0.001
	Age:sex (juvenile:male)		-0.003 $\pm$ 0.134	-0.024	0.981
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.060	0.246		
	Date	0.009	0.097		
	Feeder (location)	0.262	0.250		

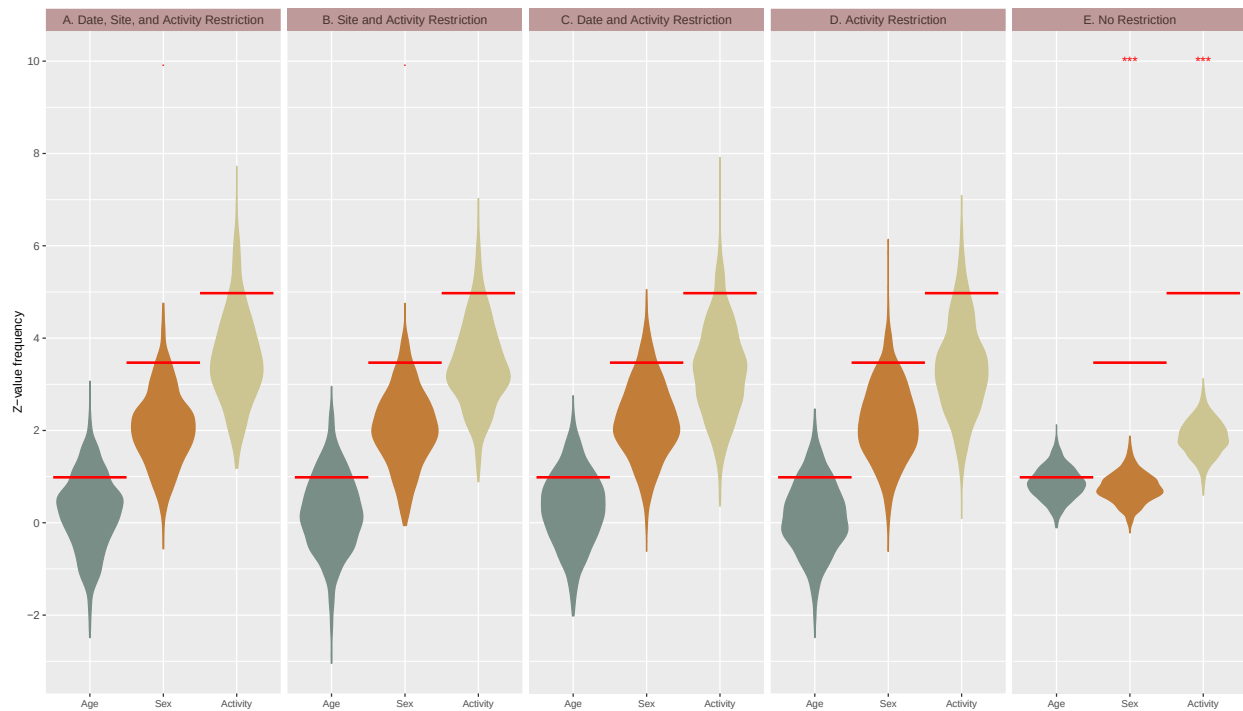


Figure S1 - violin plots displaying the results of the null models (1000 permutations) for the great tit only model (Table S13) with all five restriction types. Each panel denotes a restriction type while the fixed effects (of age, sex, and activity) are along the x axis. Solid red lines indicate the observed z-value for each effect and the stars at the top of the y axis denote significance levels, i.e. whether the observed z-value is significantly different to those derived from the null models (** = <.001,, . = .09).

Table S14 - lead or not model with blue tits only

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=152,068	Intercept		-0.240 $\pm$ 0.160	-1.499	0.134
	Age (juvenile vs. adult)		0.082 $\pm$ 0.069	1.189	0.235
	Sex (male vs. female)		0.045 $\pm$ 0.069	0.654	0.512
	Activity		0.120 $\pm$ 0.030	3.610	<0.001
	Random effects	Variance	Standard deviation		
	Ring (ID)	0.093	0.304		
	Date	0.012	0.113		
	Feeder (location)	0.140	0.374		

Table S15 - lead or not model with blue tits only and interaction of age and sex included

Dependent variable	Fixed factor/effects		Estimate $\pm$ SE	z-value	p-value
Lead or not N=152,068	Intercept		-0.193 $\pm$ 0.159	-1.219	0.223
	Age (juvenile vs. adult)		-0.029 $\pm$ 0.104	-0.277	0.782
	Sex (male vs. female)		-0.032 $\pm$ 0.088	-0.363	0.716

	Activity	0.109 ± 0.030	3.640	<0.001
	Age:sex (juvenile:male)	0.184 ± 0.134	1.376	0.169
	Random effects	Variance	Standard deviation	
	Ring (ID)	0.060	0.246	
	Date	0.009	0.097	
	Feeder (location)	0.262	0.250	

Supplementary Image 1



Image 1 - a photograph of the selective feeders. Video footage of birds using the feeders can be accessed at the following link: <https://youtu.be/DOXTM4Blfuc>

Chapter 5

Social familiarity and spatially variable environments independently determine reproductive fitness in a wild bird

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Social Familiarity and Spatially Variable Environments Independently Determine Reproductive Fitness in a Wild Bird

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ABSTRACT: The social interactions that an individual experiences are a key component of its environment and can have important consequences for reproductive success. The dear enemy effect posits that having familiar neighbors at a territory boundary can reduce the need for territory defense and competition and potentially increase cooperation. Although fitness benefits of reproducing among familiar individuals are documented in many species, it remains unclear to what extent these relationships are driven by direct benefits of familiarity itself versus other socioecological covariates of familiarity. We use 58 years of great tit (*Parus major*) breeding data to disentangle the relationship between neighbor familiarity, partner familiarity, and reproductive success while simultaneously considering individual and spatiotemporal effects. We find that neighbor familiarity was positively associated with reproductive success for females but not males, while an individual's familiarity with their breeding partner was associated with fitness benefits for both sexes. There was strong spatial heterogeneity in all investigated fitness components, but our findings were robust and significant over and above these effects. Our analyses are consistent with direct effects of familiarity on individuals' fitness outcomes. These results suggest that social familiarity can yield direct fitness benefits, potentially driving the maintenance of long-term bonds and evolution of stable social systems.

Keywords: sociality, spatial effects, reproductive success, familiarity, territorial neighbors, fitness.

Introduction

Individuals' reproductive success may depend on not only their own traits but also the external social and ecological settings they find themselves in (Snyder-Mackler et al. 2020). Social relationships can benefit fitness—for instance, when they facilitate cooperative interactions (Gokcekus et al. 2021)—but can also be costly when they lead to competition or conflict (Bebbington et al. 2017; McFarland et al. 2017; Menz et al. 2020). How and why individuals choose to tolerate, cooperate, or compete with others appear to vary across systems, but familiarity among individuals often plays a key role in shaping the balance between these phenomena (Ellis et al. 2019). Specifically, tolerance afforded through familiarity may increase rates of cooperation rather than competition and, consequently, increased fitness (Beletsky and Orians 1989; Silk 2007; Grabowska-Zhang et al. 2012a).

Across many taxa, familiarity (in a very simple sense, in terms of having previous associations) is a precursor for social tolerance and cooperation (Croft et al. 2006; Aragón et al. 2007). Having familiar associates in close proximity (socially and spatially) can increase each individual's fitness through more efficient division of labor (Griffiths et al. 2004). Familiarity is especially important for territorial species, because it can impact how much energy individuals allocate to defense of their areas and therefore how much they can allocate to reproduction (Eason and Hannon 1994). Often discussed in terms of the dear enemy effect, familiarity among neighbors allows for reduced aggression and conflict at the territory boundary and can even facilitate cooperation (Akçay et al.

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2009; Grabowska-Zhang et al. 2012a; Tumulty 2018; but see Müller and Manser 2007; Newey et al. 2010; Christensen and Radford 2018). In addition to—and possibly because of—benefits for defense, being raised among familiar individuals leads to higher fitness in various species of birds, mammals, and primates (Beletsky and Orians 1989; Seppä et al. 2001; Turner et al. 2020). Parents that have more familiar associates have been found to have higher reproductive success (Kohn 2017; Riehl and Strong 2018; Alberts 2019), and being around familiar individuals can even be more beneficial than being close to genetic relatives (Liebgold and Cabe 2008; Siracusa et al. 2020). Familiarity among parents can likewise influence reproductive success. For example, breeding with the same partner over time (pair fidelity) is associated with increased fecundity and survival probability (Black 1996; Culina et al. 2013, 2015a). Similarly, individuals who spend more time together (or are more familiar) prior to breeding have also been shown to have higher reproductive success (Martin and Shepherdson 2012; Sánchez-Macouzet et al. 2014; Culina et al. 2020). Overall, familiarity both within and among pairs seems to generally have a positive relationship with fitness outcomes, which is expected because of the supposed benefits it can bring to an individual.

As both familiarity and fitness depend on social and spatial processes, systems where individuals (1) are seasonally territorial and (2) have a constrained breeding period are particularly useful for exploring effects of familiarity on fitness, as the whole population attempts reproduction over the same season. Grabowska-Zhang et al. (2012a) simulated nest box intrusions in a great tit (*Parus major*) population during the breeding season to investigate whether neighbors would join (cooperate) in mobbing the intruder. They found that familiar neighbors (individuals that shared a territory boundary in past breeding seasons) were more likely to join in nest defense, demonstrating direct benefits of familiarity. In the same population, Grabowska-Zhang et al. (2012b) found that having familiar neighbors during the breeding season comes with fitness benefits. Males and females with more familiar neighbors or with familiar nearest neighbors had higher reproductive output. Furthermore, females with higher numbers of familiar neighbors were more likely to have larger clutch sizes (more eggs laid). Nevertheless, whether these patterns exist outside of spatial effects remained entirely unknown. Here, we expand upon this work with 15 years of additional data and a novel technique to control for spatial autocorrelation.

Although associations between familiarity and fitness appear fairly general, it is difficult to separate direct fitness benefits of familiarity (such as those hypothesized above) from other socioecological factors that may be related to these variables. For example, familiarity and suc-

cess may covary indirectly: if some areas have higher habitat quality and those areas also support greater levels of familiarity, individuals inhabiting these areas may appear to benefit from having familiar neighbors when in reality there is no direct effect of familiarity per se on fitness. Similarly, an individual's success and that of its neighbors may determine whether pairs decide to breed in the same location (site fidelity; Doligez et al. 2002; Piper 2011), allowing for a possible reciprocal relationship between familiarity, success, and consistency in territory preferences. These processes could complicate observed relationships between familiarity and fitness if they go unaccounted for.

Here, we analyze data from a long-term study of breeding great tits to investigate how having a familiar partner and having familiar neighbors (individuals sharing a territory boundary in previous years) influence fitness when directly considering spatial effects. In addition to also quantifying the effect of habitat quality, we use an approach that models two-dimensional spatial patterns in the response variable (here, components of reproductive fitness) through the use of the stochastic partial differentiation equation (SPDE), which estimates and considers spatial variation in fitness (Lindgren et al. 2011; Lindgren and Rue 2015; Krainski et al. 2018). Building on suggestions from previous work (Grabowska-Zhang et al. 2012), this approach allows the social benefits to be extricated from spatially distributed drivers of fitness, thus separating the contributions of familiarity and spatial variation in regulating sociality and fitness. We then discuss how these findings may advance our understanding of the fitness benefits of familiarity and the potential consequences in terms of selection for maintaining mutually beneficial relationships and the evolution of stable social systems.

Methods

Data Collection

This work took place within the long-term study population of great tits at Wytham Woods, Oxford, United Kingdom (51°46'N, 1°20'W). Great tits form monogamous pairs and breed during the spring (April–July) almost exclusively in the 1,020 fixed-position nest boxes that are available across the 385-ha woodland. The great tit population and their breeding behavior have been monitored since the 1960s, using a standardized procedure (Perrins 1965). Great tits are a relatively short-lived species with annual adult survival of ~50%; they typically breed once or twice (Perrins 1979). During the breeding season, nest boxes are visited to record information on the stages of each breeding attempt. Parents are identified (when nestlings are 6–14 days old) and, if previously unringed, are trapped and fitted with a unique BTO

(British Trust for Ornithology) metal leg ring. All nestlings are fitted with unique rings when they are 2 weeks old. Outside of the breeding season (September–February), extensive mist netting is carried out to additionally ring any immigrants to the woodland.

Data Analysis

Reproductive Data. Birds breeding in nest boxes were monitored throughout the breeding season. Each breeding attempt consists of building a nest, laying and incubating eggs, and rearing offspring. Territory prospecting occurs prior to egg laying, which begins in April. Once hatched, chicks must be provisioned by both parents for the first ~5 days. At the start of the breeding season, nests were monitored weekly until eggs were found in order to record (if a single egg was found) or estimate (if more than one egg were found) lay date, defined as the date the first egg of the clutch was laid (usually, one egg is laid each day). Once incubation commenced, the clutch size was defined as the maximum number of eggs within the nest (unless a larger number was recorded in future hatch checks). Nests were then visited every other day from the predicted hatch date to accurately determine the hatch date, or the day that chicks started hatching. Parents were identified and/or ringed on days 6–15 (day 1 = hatch date), and all chicks were ringed and weighed (mean chick weight) on day 15. All nests were subsequently checked to determine the number of fledglings for each breeding attempt. Earlier lay date, larger clutch size, higher chick weight, and a higher number of fledglings are likely to represent increased fitness (McCleery et al. 2004; Browne et al. 2007).

Determining Neighbors and Familiarity. We used information on the spatial arrangement of occupied nest boxes to estimate individual territories. Voronoi diagrams (Thiessen polygons) were drawn around each occupied nest box that included all of the woodland area that was closer to that nest box than to any other occupied box (Schlicht et al. 2014). We then classified individuals as first-order neighbors if they shared a territory boundary (see fig. S3). Estimating territories and neighbors in this way within this and similar systems has previously been shown to be biologically meaningful in terms of population density and breeding success and to correlate with manually determined territory sizes and neighbors (Adams 2001; Wilkin et al. 2006; Grabowska-Zhang et al. 2012b; Schlicht et al. 2014).

We then determined whether individuals were neighbors in previous years and classified them as familiar neighbors accordingly (following methods from Grabowska-Zhang et al. 2012b). We excluded yearlings from analyses

since they could not have familiar neighbors from previous years (but see sec. 1 in the supplemental PDF for independent analysis of the effect of age—adult vs. juvenile—on fitness). We created a variable denoting the number of male familiar neighbors and the number of female familiar neighbors each individual had; males and females of each pair were always considered separately, aligning with common practice in this study system and similar systems. If an individual in a neighboring box had not been identified, this could mean that some neighbors were wrongly assigned as unfamiliar. Consequently, our measures are conservative, as neighbors that were familiar could be assigned as unfamiliar but not the other way around (see fig. S3 for an illustrative explanation). It is known, however, that birds breeding for the first time are more likely to be unidentified in this population (Kidd et al. 2015), and these individuals, by definition, cannot have familiar neighbors. To conduct additional sensitivity analysis, we reran all of the models with the proportion of familiar neighbors out of all identified neighbors rather than the number of neighbors (table S4) and by limiting the analysis to individuals who have at least three (~50%) identified neighbors of each sex (sec. 4 in the supplemental PDF), which produced similar results. We also controlled for familiarity within the pair bond by including a binary pair familiarity variable indicating whether individuals bred together in the previous year.

We additionally included a count of the number of oak trees within 75 m of each nest box as a measure of habitat quality. Great tits provision their nestlings with caterpillars (found most abundantly on oak trees) and other insects, and variation in caterpillar availability has been associated with clutch size, growth rate, and fledging success (Tinbergen and Boerlijst 1990; Perrins 1991; Keller and van Noordwijk 1994; Nour et al. 1998; Rytönen and Krams 2003; Tremblay et al. 2003; Lambrechts et al. 2004). Previous studies have also shown that broods raised close to oak trees have a better physical condition (Wilkin et al. 2009), and individuals in deciduous woodlands (with more oak trees) provision broods more often and more appropriately in terms of the size of the brood (Blondel et al. 1991).

Finally, we calculated the distance that each individual had traveled from the previous year by taking the distance of the most direct path between the nest box that they bred in for each year.

Statistical Analysis. We analyzed data on 8,823 individual adults that bred in the 58 years between 1965 to 2022. We first ran two generalized linear models (GLMMs) to understand the predictors of familiarity within the pair and among neighbors. The neighbor familiarity model included pair familiarity, age (numeric), sex, and distance traveled from the previous year as fixed effects and focal

ID, box, and year as random effects. The pair familiarity model included age (numeric), sex, and distance traveled from the previous year as fixed effects and focal ID, box, and year as random effects. To investigate the association between familiarity and reproductive success, we fitted GLMMs using the integrated nested Laplace approximation (INLA) R package, which allows for the fitting of a SPDE random effect to quantify and control for spatial autocorrelation in the response variable (Rue et al. 2009; Bakka et al. 2018; Albery et al. 2019, 2021; Martino and Riebler 2020). The SPDE effect models the distance between points to calculate spatial autocorrelation (Lindgren et al. 2011); nest box point locations and their associated reproductive output data were used to approximate spatial variation in the fitness variables. Continuous variables were scaled to have a mean of 0 and standard deviation of 1. We ran two sets of models, one with the females and another with the males, with the model structure detailed in table 1. Year is included as both a continuous fixed effect and a categorical random effect to account for any trend that has occurred over time as well as categorical yearly differences in reproductive success (Albery et al. 2019). To investigate the effect of different familiarity metrics, we iteratively added these social effects (number of familiar neighbors, number of familiar female neighbors, number of familiar male neighbors, and pair familiarity) to the base model, investigating which indicators best fit the data. We used deviance information criterion (DIC) to distinguish between models, as is often used for this analytical approach (Albery et al. 2019). In each round, we added each social effect individually and then kept the best-fitting one, until all had been added or their addition did not improve the model, using a cutoff of 2 DIC. Because the neighbor variables (overall number, male number, and female number familiar) were well correlated ($R > 0.5$), we did not allow more than one neighbor variable as explanatory variables in the same model; the models therefore sought the single best-fitting neighbor effect. In other words, we specified a separate model for each of the social fixed effects while keeping the base fixed and random effects consistent and then compared the resulting models using DIC. Fixed effect estimates were provided by the mean and 95% credibility intervals of the posterior

estimate distribution. Significance was determined by examining each effect's overlap of the 2.5% and 97.5% posterior estimates with zero.

Results

Familiarity Effects

We analyzed data on individuals from 6,079 pairs. On average, each pair had five neighbors ($SD = 1.53$; fig. 1A); 82.1% of them were of known identity ($SD = 19.37\%$), and 10.3% were familiar ($SD = 15.7\%$). Figure 1B is a visual example of territories, numbers of neighbors, and familiarity in a single year (2008).

Our measures of familiarity (either within pairs or among neighbors) influenced three of the five fitness variables (i.e., were retained by the model selection process for these models; fig. 2). The models for mean chick weight and binary success were not improved by the addition of information about familiarity (tables S8, S9). Different variables were retained (through the model selection process) for males and females, leading to slightly different coefficients.

Pair Familiarity Effects

Females with a familiar partner had significantly earlier lay dates (-0.109 [95% credible interval (CI), -0.155 to -0.063]) and more fledglings (0.068 [95% CI, 0.003 – 0.132]). Males with a familiar partner similarly had significantly earlier lay dates (-0.198 [95% CI, -0.244 to -0.152]) and more fledglings (0.075 [95% CI, 0.009 – 0.140]) and additionally had larger clutch sizes (0.116 [95% CI, 0.053 – 0.180]). These effects remained significant when controlling for spatial autocorrelation (fig. 2).

Neighbor Familiarity Effects

Females with more familiar neighbors (of both sexes) had significantly earlier lay dates (-0.036 [95% CI, -0.056 to -0.015]). Females with more male familiar neighbors had significantly larger clutches (0.052 [95% CI, 0.026 – 0.077]; fig. 2). These effects remain when controlling for spatial

Table 1: Model structure

Response (fitness) variables	Base fixed effects	Social fixed effects	Random effects
Lay date	Year	Number of familiar neighbors	Focal ID
Clutch size	Focal age	Number of familiar female neighbors	Year
Mean chick weight	Habitat quality (oaks)	Number of familiar male neighbors	SPDE (for spatially corrected models)
Number of fledglings		Pair familiarity	
Binary success			

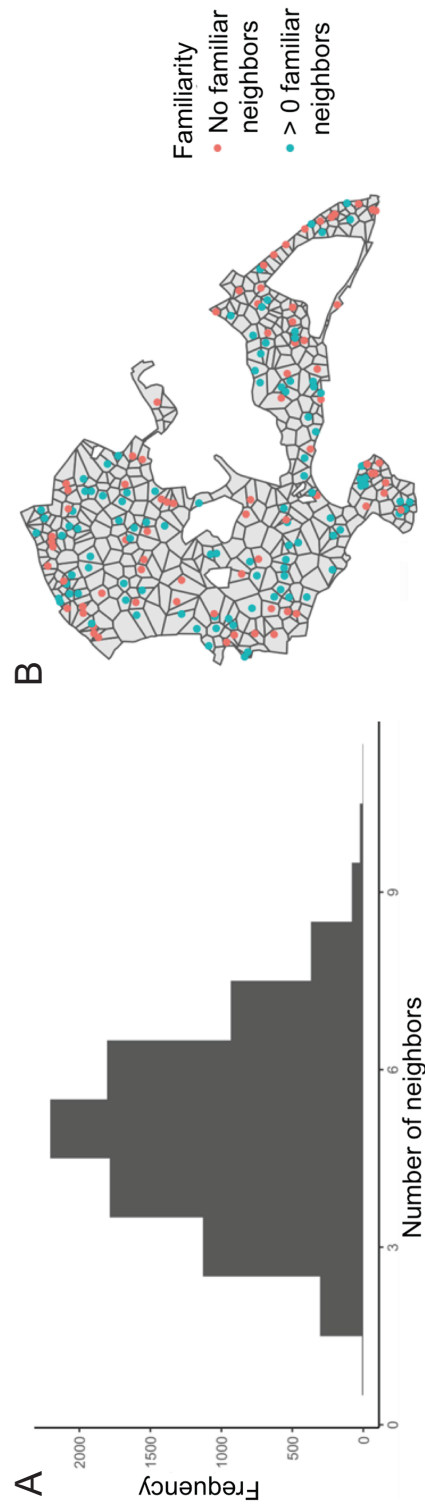


Figure 1: A, Distribution of number of neighbors pairs had. B, Example map from one breeding season (2008) illustrating territories, neighbors, and familiarity for individuals of known identity (by necessity restricted to birds in second year or older).

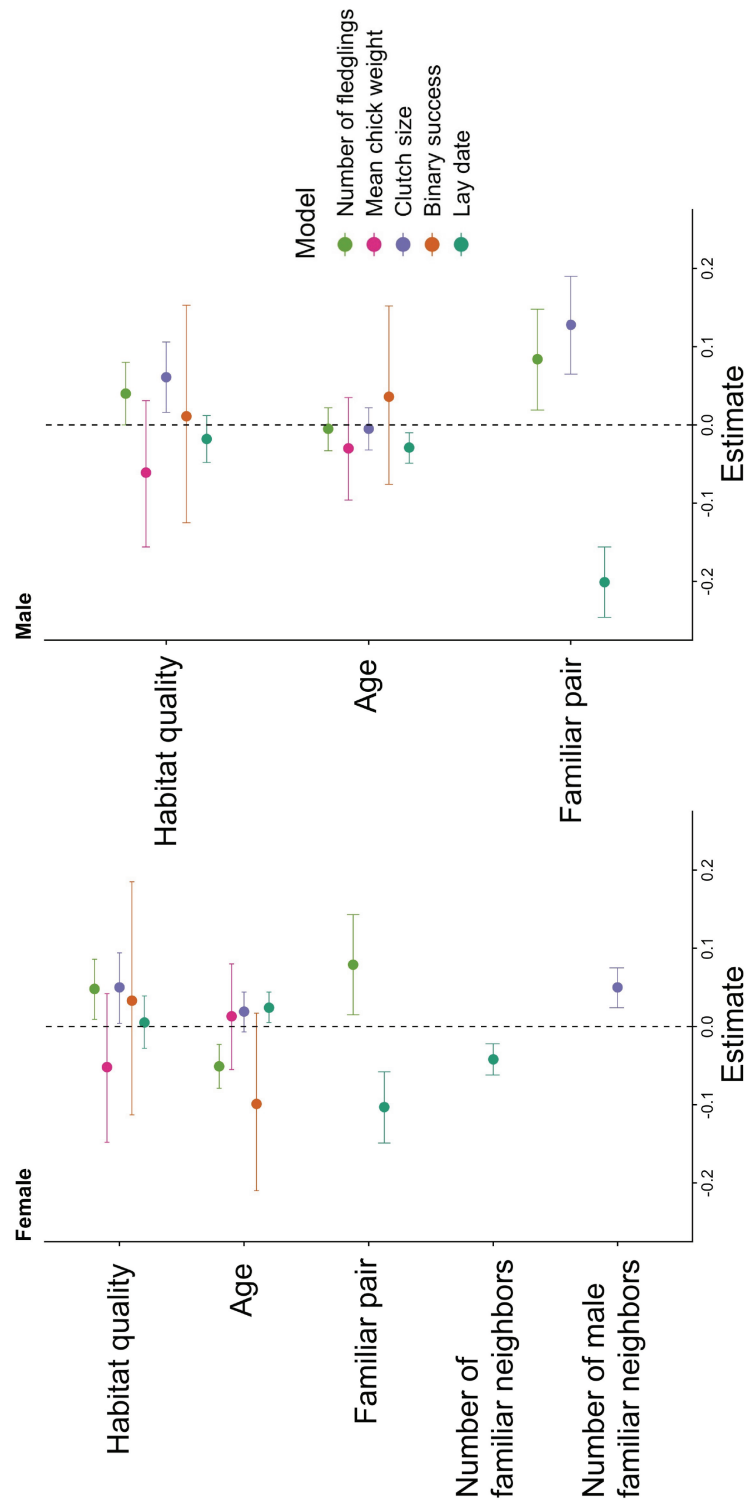


Figure 2: Summary (excluding intercept and year effect) of all 10 models for females and males, with SPDE spatial autocorrelation correction. Circles represent the estimate for each effect that was retained in the model selection process, and error bars denote 95% credible intervals. The same figures with the year effect included are presented in section 7 of the supplemental PDF.

autocorrelation. Further, all of the same neighbor familiarity effects are observed when considering the proportion (rather than number) of familiar neighbors (fig. S5; table S3).

Predictors of Familiarity

The number of familiar neighbors an individual had was influenced by the distance that it had moved from the box it bred in during the previous year, with those that traveled further having fewer familiar neighbors ($z = -19.99$, $P < .001$; table 2, pt. A). It was rare for familiarity to arise from individuals just remaining in identical breeding locations in successive years. Specifically, overall only 1.92% (SD = 1.41%) of dyads were familiar because neither move boxes from the previous year. Furthermore, when the models are run with the additional control variable of whether individuals stayed in the same box as the previous years, the results largely hold (sec. 5 in the supplemental PDF). As expected, familiar pairs also had more familiar neighbors ($z = 3.01$, $P < .001$). In terms of familiarity within the pair, older individuals ($z = 3.36$, $P < .001$) and those that traveled shorter distances ($z = 18.81$, $P < .001$) from their box in the previous year were more likely to be familiar with their partner (table 2, pt. B).

Environmental Drivers

For females, better habitat quality was associated with significantly earlier lay dates (-0.069 [95% CI, -0.091 , -0.047], larger clutches (0.062 [95% CI, 0.031 – 0.092], heavier mean chick weight (0.058 [95% CI, 0.014 – 0.131], and more fledglings (0.049 [95% CI, 0.020 – 0.079], but the effect remained significant only for number of fledglings

in the spatially corrected models (0.048 [95% CI, 0.009 – 0.086 ; fig. 2). For males, better habitat quality was associated with significantly earlier lay dates (-0.077 [95% CI, -0.098 to -0.057], larger clutch size (0.065 [95% CI, 0.037 – 0.094], and a higher number of fledglings (0.045 [95% CI, 0.017 – 0.074], but once spatial autocorrelation was controlled for, the effect remained significant only for clutch size (0.063 [95% CI, 0.016 – 0.109 ; fig. 2).

To graphically illustrate the spatial distribution of each of the fitness variables when accounting for the fixed and random effects in each model, we projected the SPDE random effect onto a two-dimensional plane (figs. 3, S8; method explained further in sec. 5 in the supplemental PDF). The projections for females (fig. 2) and males (fig. S8) differ slightly but follow the same pattern. Generally, fitness metrics are lower in the southern part of the woods. When considering the northern portion of the woods, those in the western part have earlier lay dates (2A), larger clutches (2C), and a higher number of fledglings (2E). The entire northern portion has relatively high chick weight (2D), while binary success has a more patchy distribution (2B). Accounting for spatial autocorrelation improves all of the models substantially (table 3).

Base Model Effects

In all 10 of the models (tables S8, S9), year was a significant predictor of all of the fitness variables, and this was still the case once spatial autocorrelation was controlled for (fig. 2). There were several significant effects of age: older females had later lay dates (0.022 [95% CI, 0.002 – 0.042] and fewer fledglings (-0.049 [95% CI, -0.077 to -0.020], while older males had earlier lay dates (-0.034 [95% CI, -0.054 to -0.014]). When accounting for spatial autocorrelation, the effects remained the same.

Without accounting for the effects of familiarity, we also compared adult versus juvenile success (figs. S1, S2; tables S1, S2). For females, adults had significantly earlier lay dates (-0.096 [95% CI, -0.110 to -0.083] and larger clutches (0.099 [95% CI, 0.081 – 0.116]). Adult males had significantly earlier lay dates (-0.084 [95% CI, -0.098 to -0.070], larger clutches (0.056 [95% CI, 0.036 – 0.076], more fledglings (0.034 [95% CI, 0.014 – 0.054], and a higher chance of success (0.084 [95% CI, 0.005 – 0.166]). When accounting for spatial autocorrelation, the effects remained the same but adult females also had significantly more fledglings (0.022 [95% CI, 0.002 – 0.041]).

Discussion

Using 58 years of data documenting breeding success and territorial neighbor familiarity in a wild bird population, we demonstrate how pair and neighbor familiarity

Table 2: GLMM results for predictors of pair familiarity and number of familiar neighbors, with individual ID, box, and year included as random effects

Response and variable	Estimate	SE	Z	P
A. Number of familiar neighbors:				
Intercept	.050	.050	.999	.318
Pair familiarity (true)	.076	.025	3.011	<.001
Age	.010	.011	.854	.393
Sex (male)	.004	.023	.166	.868
Distance traveled from previous year	-.478	.024	-19.991	<.001
B. Pair familiarity:				
Intercept	-1.381	.114	-12.169	<.001
Age	.102	.030	3.360	<.001
Sex (male)	.124	.061	2.016	.044
Distance traveled from previous year	-1.400	.074	-18.813	<.001

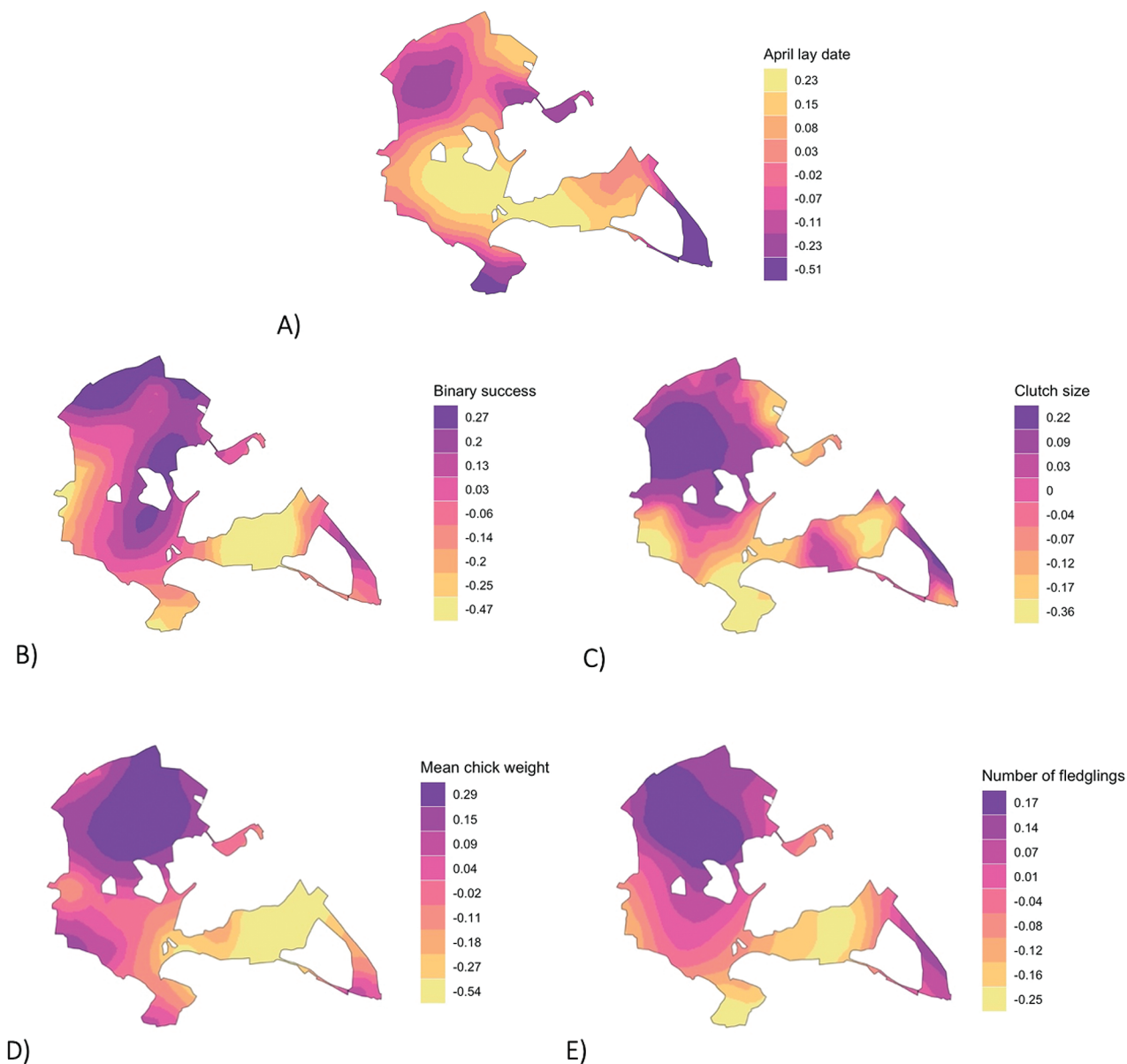


Figure 3: Two-dimensional projection of spatial distribution of each fitness variable (with z-scores) for females, when accounting for fixed and random effects in each model, onto actual map of study area. The method for projection is further explained in section 5 of the supplemental PDF.

influence reproductive success and how this operates over space. We find that familiarity within pairs and among neighbors increases reproductive success, confirming benefits of neighbor familiarity for females in terms of earlier lay dates and larger clutches. This work builds on previously established findings in this population (Grabowska-Zhang et al. 2012b), which had previously suggested these patterns but could not separate the potentially confounding effects of spatial autocorrelation and pair familiarity. Here,

by replicating these findings using more than a decade of additional data, additionally considering familiarity within the pair, and accounting for a variety of environmental confounders, we provide evidence for the standalone importance of neighbor familiarity. Importantly, we largely replicate the results (particularly for clutch size) while additionally accounting for spatial heterogeneity in our fitness variables. Expanding upon these previous findings, we highlight that this relationship is not just the product

Table 3: DIC for base and SPDE models

Sex and model	Base	SPDE	Δ DIC
Male:			
Lay date	8,314.272	8,165.894	−149.377
Binary success	2,347.758	2,337.212	−10.545
Clutch size	11,647.945	11,525.877	−122.067
Mean chick weight	2,215.621	2,165.770	−49.851
Number of fledglings	12,013.903	11,929.604	−84.299
Female:			
Lay date	7,626.573	7,479.224	−147.349
Binary success	2,156.470	2,143.878	−12.593
Clutch size	10,214.466	10,143.980	−70.487
Mean chick weight	2,050.142	2,022.038	−28.104
Number of fledglings	11,291.936	11,245.623	−46.312

of an indirect covariation in space but also due to a direct benefit.

Overall, pair familiarity influenced lay date, clutch size, and number of fledglings, and neighbor familiarity was related to lay date and clutch size. Pair familiarity was associated with higher reproductive success for both sexes; females additionally benefited from having familiar neighbors, while males did not. Although all fitness distributions were heavily autocorrelated in space, the effects of familiarity persisted over and above this spatial heterogeneity. Our results demonstrate the importance of social factors as well as spatial factors in determining reproductive outcomes. It is well documented that social instability can come with negative effects in terms of survival (Herzog et al. 2009; Capitanio and Cole 2015; Maldonado-Chaparro et al. 2018); here we show that maintaining stable social relationships, particularly for females, is important for reproductive success.

The strongest fitness effect we identified was that of pair familiarity, with familiar pairs being more successful overall and both males and females in familiar pairs having a higher number of fledglings than those in unfamiliar pairs. This may be in part driven by the propensity of unsuccessful individuals to divorce or change their breeding partner (Culina et al. 2015b). Previous work has shown that pairs in this population also benefit from spending more time with each other in the winter prior to the breeding season, because this behavior allows for earlier lay dates (Culina et al. 2020). This is the first time that other ecological variables that could create these patterns have been considered; our findings likewise demonstrated earlier lay dates (and increased fitness) in familiar pairs, suggesting that stronger bonds both within and between years contribute to increased reproductive success, partially by facilitating earlier laying. Similar results have been found in other monogamous avian species (Black 2001; Van De Pol et al. 2006; Griggio and Hoi 2011; Gabriel and Black 2013; Sánchez-

Macouzet et al. 2014; Wiley and Ridley 2018; Leach et al. 2020; Maldonado-Chaparro et al. 2021) but not in others (Naves et al. 2007; Hatch and Westneat 2008). It is possible that previously observed effects of neighbor familiarity on fledging success in this population (that we do not find here) may have been driven by a lack of accounting for familiarity within the pair (Grabowska-Zhang et al. 2012).

A variety of proximate mechanisms of neighbor familiarity could underlie their observed fitness effects. Because traits like lay date and clutch size are predominantly controlled by the female (Browne et al. 2007; Evans et al. 2020), it is perhaps unsurprising that females rather than males benefit from having familiar neighbors. Females with more familiar neighbors have earlier lay dates, which may arise from their ability to avoid disputes and acquire territories earlier in the season. Females with more male familiar neighbors lay larger clutches; this was also found by Grabowska-Zhang et al. (2012). This may be due to a perception of increased food security in terms of the ability to forage more widely (Nicolaus et al. 2009). Females may also have extrapair copulations with those familiar males (Beck et al. 2020). Importantly, higher-quality females may acquire more familiar neighbors while also producing larger broods, driving apparent between-individual correlations between neighbor familiarity—for example, if individuals choose associates on the basis of their apparent quality. Although extrapair paternity is estimated to be relatively low in this populations (13%–14%; Blakey 1994; Patrick et al. 2012), further work considering genetic paternity and rates of extrapair copulations is needed to gain a better understanding of the relationship between neighbor familiarity, extrapair copulations, and fitness outcomes.

Accounting for the structure of spatial autocorrelation significantly improved all of the models. Different fitness components had slightly different distributions, but the northern portion of the woods tended to feature higher fitness than the others (fig. 2). This pattern may be driven by the fact that the southern portion has a higher number of nest boxes available or because it is slightly closer to roads and urban areas (rather than farmland), but further work is necessary to determine the precise drivers of this spatial variation (Perrins and Jones 1974). There were also strong effects of habitat quality on some variables (clutch size and number of fledglings) that were in addition to the spatial variation observed. This suggests that habitat quality or spatial effects alone cannot account for the observed benefits of familiarity. Similarly, it is encouraging that the social effects we observed were likewise robust to accounting for spatial effects, particularly given that social structure and behavior are themselves dependent on environmental drivers (He et al. 2019).

The benefit that comes with maintaining social relationships may contribute to cooperation among nonkin. This

becomes more pertinent as individuals age, as favoring relationships with familiar individuals can counter the negative effects of senescence on survival and reproduction (Roper et al. 2021) within (Nicolai et al. 2012; Culina et al. 2013) and/or outside of (Silk et al. 2010; Kohn 2017; Siracusa et al. 2020) the pair. As is the case for other studies on the relationship between familiarity and fitness, our findings are limited to the particular context and environment that is investigated. The costs and benefits of familiarity are likely to vary across species and across different environments in terms of climate, density, or predation risk (Brask et al. 2019; Liu et al. 2020; Capilla-Lasheras et al. 2021). Future similar studies across different populations could help to tease apart these effects. Furthermore, while current analytical techniques (such as INLA SPDE effects employed here) often assume that spatial effects are consistent over time, further work could examine the temporal stability of spatial effects and how they may vary with other ecological factors. Understanding temporal patterns of changes in spatial effects and covariation with ecology would further develop our understanding of the relationship between time, space, and sociality. Finally, it is unclear whether individuals actively choose to stay in similar areas so that they have familiar neighbors or whether individuals that stay close to their initial breeding location just happen to have more familiar neighbors (although birds in this population do have stronger overwinter bonds with their future neighbors; Firth and Sheldon 2016). To unravel causality in this setting, future studies could examine reproductive success while manipulating (by either limiting or encouraging) dispersal distances and/or the ability to recouple with one's mate. Identifying the fitness benefits of familiarity and delineating it from its spatial correlates in this way will further inform the factors driving the evolution of sociality and cooperation.

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Statement of Authorship

S.G., J.A.F., and B.C.S. were responsible for conceptualization. J.A.F. and B.C.S. acquired the funding. Data analysis, model analysis, and visualization were carried out by S.G. and G.F.A. S.G. wrote the original draft, and all other authors provided supervision and reviewed and edited the manuscript.

Data and Code Availability

All data and code have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.7m0cfxpzc>; Gokcekus et al. 2023).

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Chapter 6

Different types of social links differentially shape reproductive success in a multi-level society of wild songbirds

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Different types of social links differentially shape reproductive success in a multi-level society of wild songbirds

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Abstract: The social environment has direct consequences for individuals' health, reproductive success, and survival. This environment consists of different kinds of dyadic bonds that exist at different levels; in many social species, smaller social units come together in larger groups, creating multilevel societies. In great tits (*Parus major*), individuals have four major types of dyadic bonds: pair mates, breeding neighbors, flockmates, and spatial associates, all of which have been previously linked to fitness outcomes. Here, we show that these different types of dyadic bonds are differentially linked with subsequent reproductive success metrics in this wild population and that accounting for spatial effects can alter these relationships. Specifically, individuals with stronger bonds with their pair mate had earlier lay dates, while generally more social individuals had a higher number of fledglings. Further, when controlling for spatial breeding effects, strong prior winter bonds with breeding neighbors were not beneficial and individuals with increased winter spatial associates had smaller clutch sizes. Our study highlights the importance of considering different types of dyadic relationships when investigating the relationship between fitness and sociality, and the need for future work aimed at experimentally testing these relationships, particularly when the population is spatially structured.

Introduction

Many animals live in complex societies (Ward & Webster, 2016). The social behavior of individuals within populations gives rise to structured social systems, and social interactions

have an inevitable influence on many of the decisions and behaviors that animals engage in throughout their lives, including foraging activity, mate choice, survival, and reproduction (Snyder-Mackler et al., 2020). Consequently, variation in sociality throughout the lifespan is an important determinant of overall fitness (Bond, Lee, Farine, Ozgul, & König, 2021; Ellis, Snyder-Mackler, Ruiz-Lambides, Platt, & Brent, 2019; Menz et al., 2020; Siracusa et al., 2020; Turner, Robitaille, Bills, & Holekamp, 2020). While social relationships come in many forms, sociality is often quantified using a single type of dyadic bond between individuals, for example by quantifying the strength of the bond between reproductive pairs, foraging partners, or breeding neighbors. A key remaining question is how individual variation in different types of dyadic relationships simultaneously shapes fitness outcomes in these complex societies.

Different kinds of dyadic relationships within populations can pave the way for hierarchically nested social relationships that form multilevel societies (Papageorgiou & Farine, 2021). Indeed, all representations of social relationships are ultimately built upon dyadic units. Multi-tiered social structures often consist of breeding pairs or families that are nested within higher-order groups, allowing for flexibility in social interaction (Grueter, Qi, Li, & Li, 2017). Smaller, more stable units may come together to form larger fluctuating groups, such that individuals may maintain and keep track of relationships at multiple levels (Papageorgiou et al., 2019).

Assessing the effects of different layers of social associations on fitness is crucial to gaining a more complete understanding of how different types of social relationships differentially shape the various aspects of fitness (i.e. different measures of survival and reproductive output). Further, the differential effects of social associations are also important when

considering how different social systems evolve, as they ultimately outline the overall costs and benefits of the diverse forms of social relationships that may exist within a society. However, quantifying these effects in wild populations can be difficult, as it requires data not only from different social contexts (breeding vs. non-breeding) across years but also with associated data on spatial effects and fitness outputs. Long-term, individual-based studies with high-resolution data on social associations between individuals are necessary for gaining a more complete understanding of sociality and fitness (Clutton-Brock & Sheldon, 2010; Sheldon, Kruuk, & Alberts, 2022).

The long-term study system of great tits (*Parus major*) at Wytham Woods provides a unique opportunity to link different kinds of social relationships with fitness outcomes. Individuals are monitored both over the winter and during the spring (breeding season) over multiple years and in different contexts, with associated data being collected on reproductive success. As detailed below, four broad types of associations exist within this population that are known to be biologically meaningful: pair mates (Culina, Firth, & Hinde, 2020; Culina, Lachish, & Sheldon, 2015; Culina, Radersma, & Sheldon, 2015; Firth, Cole, et al., 2018; Firth & Sheldon, 2016), breeding neighbors (Gokcekus et al., 2023; Grabowska-Zhang, Sheldon, & Hinde, 2012; Grabowska-Zhang, Wilkin, & Sheldon, 2012), winter flockmates (Firth, Verhelst, Crates, Garroway, & Sheldon, 2018; Firth et al., 2017; Firth, Voelkl, Farine, & Sheldon, 2015), and winter spatial associates (Farine et al., 2015; Firth & Sheldon, 2016; Firth, Verhelst, et al., 2018).

In this monogamous species, **pair mates** bond and defend their territory during the breeding season, while also staying close during the non-breeding season (Firth et al., 2015). Pair bonds can be understood as the core unit of this multilevel society (Grueter et al., 2020).

Spatial and social associations often have an influence on mate choice (Beck, Farine, & Kempenaers, 2020), and mate choice will in turn have an influence on fitness (Fayet, Shoji, Freeman, Perrins, & Guilford, 2017; Griffith, Pryke, & Buttemer, 2011; Ihle, Kempenaers, & Forstmeier, 2015). Stronger associations within the pair bond, often assessed in terms of familiarity over time, seem to come with fitness benefits in many species (Ausband, 2019; Sánchez-Macouzet, Rodríguez, & Drummond, 2014; Van De Pol, Heg, Bruinzeel, Kuijper, & Verhulst, 2006). In this population, pairs who meet earlier in the winter have higher reproductive success (Culina et al., 2020), pairs that stay together longer are more likely to survive (Culina, Lachish, et al., 2015), and individuals that are unsuccessful are more likely to divorce (Culina, Radersma, et al., 2015; Gokcekus et al., 2023).

During the breeding season, territorial great tits have **breeding neighbors**, and these neighbors often also coexist in winter flocks (Firth & Sheldon, 2016). Studies have shown that familiarity among neighbors can lead to mutual tolerance and decreases in aggression and energy required for territorial defense, potentially optimizing the timing of reproduction and facilitating coordination and cooperation (Bebbington et al., 2017; Beletsky & Orians, 1989; Booksmythe, Hayes, Jennions, & Backwell, 2012; Grabowska-Zhang, Sheldon, et al., 2012; Liebgold & Cabe, 2008; Riehl & Strong, 2018; Siracusa et al., 2020) (but see Müller & Manser, 2007; Temeles, 1994). Great tits in Wytham Woods benefit from having familiar neighbors (individuals that were neighbors in previous years), through increases in cooperation (Grabowska-Zhang, Sheldon, et al., 2012) and, presumably consequentially, higher reproductive success (Grabowska-Zhang, Wilkin, et al., 2012). Females with familiar neighbors have earlier lay dates, and females with familiar male neighbors lay larger clutches (Gokcekus et al., 2023).

Outside of the breeding season, individuals also have **flock mates** that they forage with in winter flocks, but ultimately hold little or no association with them in the breeding season (Massen, Sterck, & De Vos, 2010). Studies in mammalian and avian species have demonstrated that having more (Cameron, Setsaas, & Linklater, 2009; Ellis et al., 2019; McFarland et al., 2017; Turner et al., 2020) or stronger (Cheney, Silk, & Seyfarth, 2016; Kohn, 2017; Silk et al., 2010) social associations can come with fitness benefits (but see Menz et al., 2020; Sabol, Lambert, Keane, Solomon, & Dantzer, 2020). It is possible that more/stronger bonds allow for more appropriate individual or group responses to social and environmental stressors (Campbell, Tkaczynski, Lehmann, Mouna, & Majolo, 2018; Micheletta et al., 2012; Young, Majolo, Heistermann, Schülke, & Ostner, 2014), higher rates of cooperation (Berghänel, Ostner, Schröder, & Schülke, 2011; Samuni, Crockford, & Wittig, 2021; Samuni et al., 2018), and/or increases in dominance that lead to more successful reproduction (Bray, Feldblum, & Gilby, 2021; Feldblum, Krupenye, Bray, Pusey, & Gilby, 2021; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Strauss & Holekamp, 2019). In this system, the average flock size is 7.5 individuals (range 2-80 birds), and an individual's flock mates influence patterns of social information acquisition (Aplin et al., 2015; Culina et al., 2020; Firth, Sheldon, & Farine, 2016).

During the winter, individuals are also **spatially associated** with others while foraging, which may indicate some form of social association and familiarity but not necessarily a positive social interaction. The effects of such associations can vary based on factors such as predation risk and competition (Alberts, 2019). The configuration and constraints of the external environment can also influence spatial proximity, and therefore associations, between individuals (He, Maldonado-Chaparro, & Farine, 2019; Papageorgiou et al., 2019). Partitioning out these purely spatial associations (by calculating similarity in space use

without requirements for social association) can help to gain a clearer understanding of how different dyadic relationships contribute to the formation of multi-level societies and their fitness consequences.

Although the link between sociality and fitness has been considered for several types of dyadic relationships separately, considering them together and in concert with spatial effects is necessary to gain a better understanding of how natural selection operates on individual social behavior, how this varies for different types of relationships, and therefore how evolution shapes social organization. What are the consequences of different types of sociality? Here, we examine how these four types of relationships contribute to multiple components of fitness within a multi-level society of wild songbirds, while considering spatial effects based on breeding position.

Methods

a. Study system

Our study was conducted in Wytham Woods, Oxford, UK (51°46'N, 1°20'W) on the long-term study population of great tits (*Parus major*). These 385ha of mixed deciduous woodland house ~1018 fixed nest boxes, with known GPS coordinates, that are monitored yearly to record breeding attempts and performance (Perrins, 1965). Either during the breeding season (at the nest) or throughout the year (through mist netting) individuals are caught, fitted with a unique BTO (British Trust for Ornithology) metal leg ring and a plastic leg ring with a passive integrated transponder (PIT) tag, aged and sexed, and measured to record standard morphometric information. It is estimated that 90% of the population is tagged (L. M. Aplin et al., 2013).

b. Data collection

i. Winter social network data collection

During the winter, great tits feed from patches of resources that are distributed throughout the woodland. Sunflower seed feeding stations with two opposing access holes equipped with RFID antennae (Dorset ID, Aalten, The Netherlands) were placed in a stratified grid at 65 fixed locations approximately 250m apart. Feeders opened automatically every weekend over the winter (December-February, 2011-2014) from pre-dawn to after dusk. When birds used one of these feeders, tags allowed the detection of the time and date of their visit, creating a spatio-temporal data stream consisting of each individual visit to a feeder.

ii. Breeding season data collection

1. Fitness measures

During the breeding season (March-June), birds breeding in nest boxes were monitored through the stages of nest building, egg laying, incubation, and rearing offspring. Nests were checked weekly until eggs were found. Based on the assumption that one egg is laid each day, lay date was recorded (if one egg was found) or estimated (if more than one eggs were found) as the date the first egg of the clutch was laid. After incubation began, clutch size was recorded as the maximum number of eggs within the nest. Parents were either identified or ringed a week after eggs hatched, and all chicks were ringed and weighed a week later. Subsequently, nests were checked to determine the number of chicks that had fledged in each breeding attempt.

2. Labelling neighbors

In order to label territorial neighbors during the spring, we used the spatial arrangement of occupied nest boxes to estimate individual territories and their boundaries. For each occupied box, a Voronoi diagram (Thiessen polygon) was drawn to include all of the points that were closer to the focal box than any other occupied box (Adams, 2001; Schlicht, Valcu, & Kempenaers, 2014). This method of estimating territories and neighbors accurately accounts for population density and is highly correlated with territory sizes and boundaries that are manually determined (Grabowska-Zhang, Wilkin, et al., 2012; Schlicht et al., 2014; Wilkin, Garant, Gosler, & Sheldon, 2006) as well as with the winter social structure (Farine & Sheldon, 2015; Firth & Sheldon, 2016).

iii. Calculating the four measures of dyadic associations

Each of the four measures of dyadic bonds was calculated based on the social interactions of individuals during the winter. In the spatio-temporal data stream created by the feeder visits, intermittent bursts of clustered activity can be detected which denote flocks that are arriving to feed together. These flocks were detected using a Gaussian mixture model (GMM) that statistically assigns each individual visit to the group that it is most likely to belong to (Psorakis, Roberts, Rezek, & Sheldon, 2012). We created a social network (association matrix) for each winter based on co-occurrences in flocks using the simple ratio index (SRI). The SRI values range from 0 to 1 and can be defined by the following equation: $SAB = x / (x + yAB + yA + yB)$, where:

- SAB is the strength of association between A and B
- x is the number of times A and B were in the same flock
- yAB is the number of times A and B were detected at the same time but not together
- yA is the number of times A was detected in a flock without B
- yB is the number of times B was detected in a flock without A

To quantify the relationship between **pair mates**, we only retained records where the identity of both individuals in the breeding pair was known. Based on the winter social network, we calculated the strength of each pair's bond during the winter prior to the breeding season (following Culina et al., 2020; Firth, Cole, et al., 2018).

The relationship between **breeding neighbors** was quantified based on the territory and neighbor estimates described above and winter social networks. For every focal and each of their first-order neighbors, we calculated the bond strength between them from the previous winter (following Firth & Sheldon, 2016). For each individual, we calculated the average bond strength to their male neighbors, female neighbors, and all neighbors (male and female combined).

To represent **flockmate** associations, we used two social network metrics, weighted degree (the number of connections an individual had weighted by the strength of those connections i.e. the sum of their SRI scores to others) and average bond strength (the average strength of connections i.e. the mean of their non-zero SRI scores to others). In other words, these metrics are based on co-occurrence within the foraging groups identified through the GMMs described above.

To estimate winter **spatial associations**, we calculated the spatial overlap for every possible dyad by accounting for the number of times individuals were observed at each feeder (following Firth, Cole, et al., 2018). So, for example, if two individuals spent equal proportions of time in the same location on the same day (not necessarily at the same time), they would be assigned a 1; if they were never at the same location on the same day, they

would be assigned a 0. Proportions for each focal individual were summed to create a single variable accounting for both the number of individuals each focal was in the same location as and the amount of time they each spent there. In contrast to the flockmate associations, this measure is based only on spatial overlap in location.

To quantify winter spatial associations in another way, we additionally calculated two spatial density metrics. Using the *adehabitathr* package in R, we created space use distribution kernels and assigned each individual a local density measure based on the rasterized usage distribution of the individual's location during the winter. From this, we calculated lifetime density, or the density of the individuals' centroids across the study period, and annual density – which was the same measure but restricted to each sampling year.

c. Data analysis

We analyzed three years (2011-2014) of data from 754 individuals. We ran separate models for males and females for each of the five fitness variables derived from the breeding data (binary success, clutch size, lay date, mean chick weight, and number of fledglings), as each individual has different social characteristics (following Gokcekus et al., 2023). We fitted Generalized Linear Mixed Models (GLMMs) using the Integrated Nested Laplace Approximation (INLA) R package and fitted the SPDE random effect (for breeding season locations). This models the distance between points in order to account for spatial autocorrelation in the response variable (Albery, Becker, Kenyon, Nussey, & Pemberton, 2019; Rue, Martino, & Chopin, 2009); we used locations of nest boxes. Continuous variables

were scaled to have a mean of 0 and a standard deviation of 1. The base model included year (as a categorical fixed effect), categorical age (juvenile vs. adult), and habitat quality (the number of oak trees within a 75m radius of the nest box). Individual identity was additionally included as a random effect.

To investigate the effect of each of the dyadic relationship measures, we iteratively added the social effects (one measure of the social pair bond, three measures of breeding neighbor bonds, two measures of flockmate bonds, and three measures of spatial associations; correlation matrix in Supplementary Figure 1) to the base model, and used Deviance Information Criterion (DIC) to identify the best fit. In each round, social effects were individually added until all had been included or their addition did not improve the model, using a cutoff of 2 DIC (following Albery et al., 2022; Gokcekus et al., 2023). Fixed effect estimates were provided by the mean and 95% credibility intervals of the posterior estimate distribution. Significance was determined by examining each effect's overlap of the 2.5% and 97.5% posterior estimates with zero.

Results

We analyzed data on 754 individuals embedded within 377 mated pairs with a total of 4,498 neighbor bonds and flockmate associations for each individual determined from 204,838 winter foraging flocking events. Our measures of sociality (in terms of the four types of dyadic bonds) influenced three of the five fitness-related variables (i.e. were retained by the model selection process for these models; lay date, clutch size, and number of fledglings).

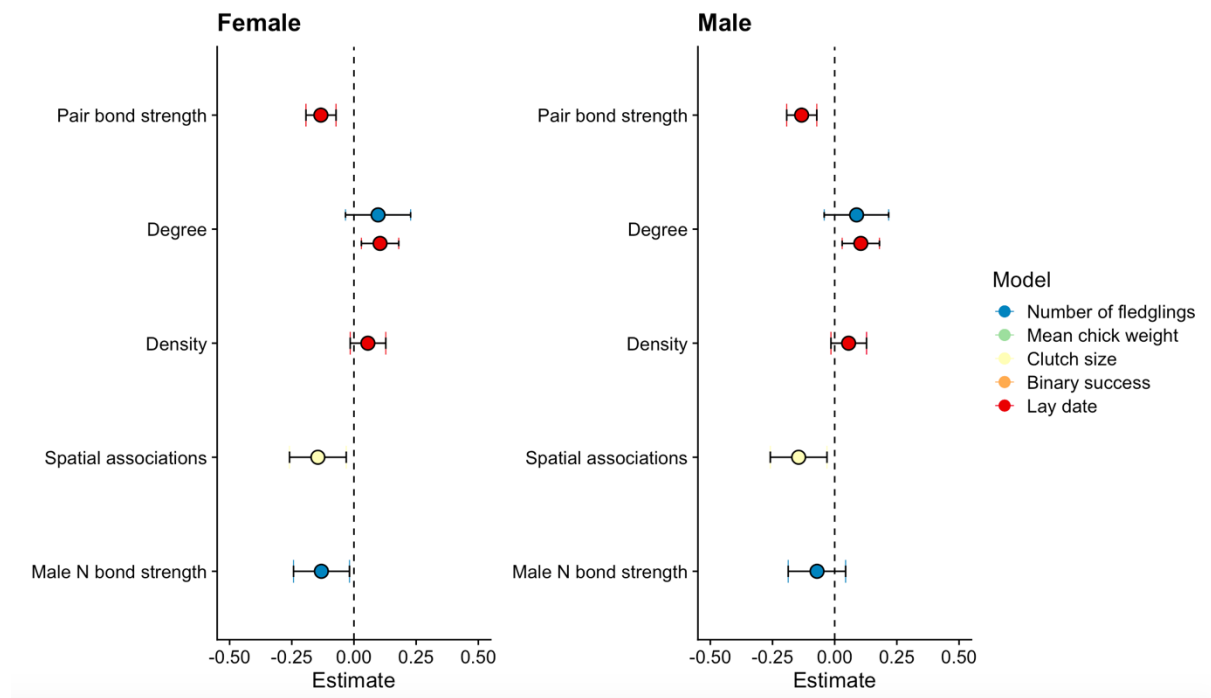


Figure 1 – Summary of the social effects for all ten models, for females and males, with the SPDE spatial autocorrelation correction. Points represent the estimate for each effect that was retained in the model selection process and error bars denote 95% credibility intervals. ‘Male N bond strength’ refers to the focal individual’s average bond strength to their male neighbors.

Four levels of dyadic bonds

Individuals with stronger winter bonds to their pair mate had earlier lay dates, and this effect remained significant when controlling for breeding spatial autocorrelation (Figure 1; Female: -0.13 , CI: $-0.19, -0.07$; Male: -0.13 , CI: $-0.19, -0.07$).

Individuals with stronger bonds to their male breeding neighbors had fewer fledglings. This effect was not significant after controlling for breeding spatial autocorrelation for males (-0.08 , CI: $-0.19, .04$), but remained significant for females (-0.13 , CI: $-0.24, -0.02$; Figure 1).

Individuals with more bonds to flock mates (higher degree) had a higher number of fledglings ($F: .19$, $CI: .07, .31$; $M: .18$, $CI: .06, .29$), but this effect was not significant after controlling for spatial autocorrelation ($F: .10$, $CI: -.03, .23$; $M: .09$, $CI: -.04, .22$). Individuals with more bonds to flock mates had later lay dates, and this effect remained significant after controlling for breeding spatial autocorrelation ($F: .10$, $CI: .03, .18$; $M: .10$, $CI: .03, .18$; Figure 1).

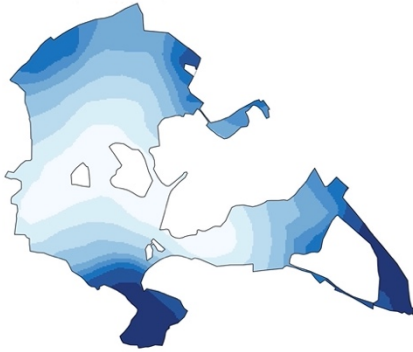
Individuals with more winter spatial associates had smaller clutches, but this effect was only significant after controlling for breeding spatial autocorrelation ($F: -.14$, $CI: -.26, -.03$; $M: -.14$, $CI: -.26, -.03$; Figure 1). Although it was retained in the models, there were no significant effects of density on lay date ($F: .06$, $CI: -.01, .13$; $M: .05$, $CI: -.02, .13$).

Non-social spatial drivers

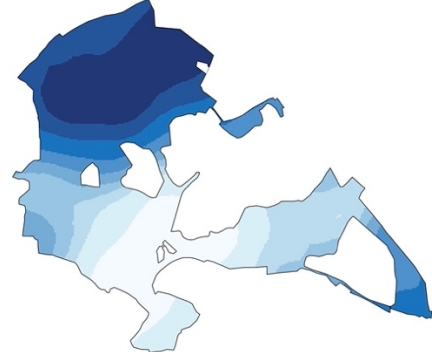
Individuals who bred in areas with a better habitat quality had earlier lay dates ($F: -.09$, $CI: -.16, -.02$; $M: -.09$, $CI: -.16, -.02$) and larger clutches ($F: .11$, $CI: .01, .21$; $M: .11$, $CI: .01, .21$; Figure 3), but this effect was no longer significant after controlling for breeding spatial autocorrelation.

The spatial distribution of each of the response (fitness) variables is graphically illustrated by projecting the SPDE random effect onto a two-dimensional plane (Figure 2). Overall, the southern part of the woods has lower reproductive success than the northern part, and lay dates are the latest in the central portion of the woods. Adding the SPDE random effect (accounting for breeding spatial autocorrelation) improves all of the models substantially, with the exception of the binary success model (Table 1).

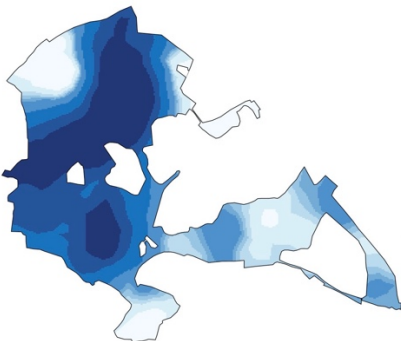
A)



B)



C)



D)



Figure 2 - 2D projection of the spatial distribution of the z-scores for each fitness variable (for females), when accounting for both the fixed and random effects in each model. For a) lay date, b) clutch size, c) mean chick weight, and d) number of fledglings. Darker shading denotes higher success.

Table 1 - DIC for base and SPDE models

Model	Base	SPDE	DeltaDIC
Lay date	570.145	550.329	-19.816
Binary success	1046.171	1045.140	-1.030
Clutch size	933.781	906.790	-26.991
Mean chick weight	901.932	880.485	-21.447
Number of fledglings	1028.322	1007.455	-20.867

Other non-social drivers

Year had an influence on all of the variables except for mean chick weight (see Fig x). There were no significant differences in terms of numeric age. However, juveniles had significantly later lay dates than adults (F: .35, CI: .21, .48; M: .35, CI: .17, .54). All social and non-social drivers were included in the same models (Table 2).

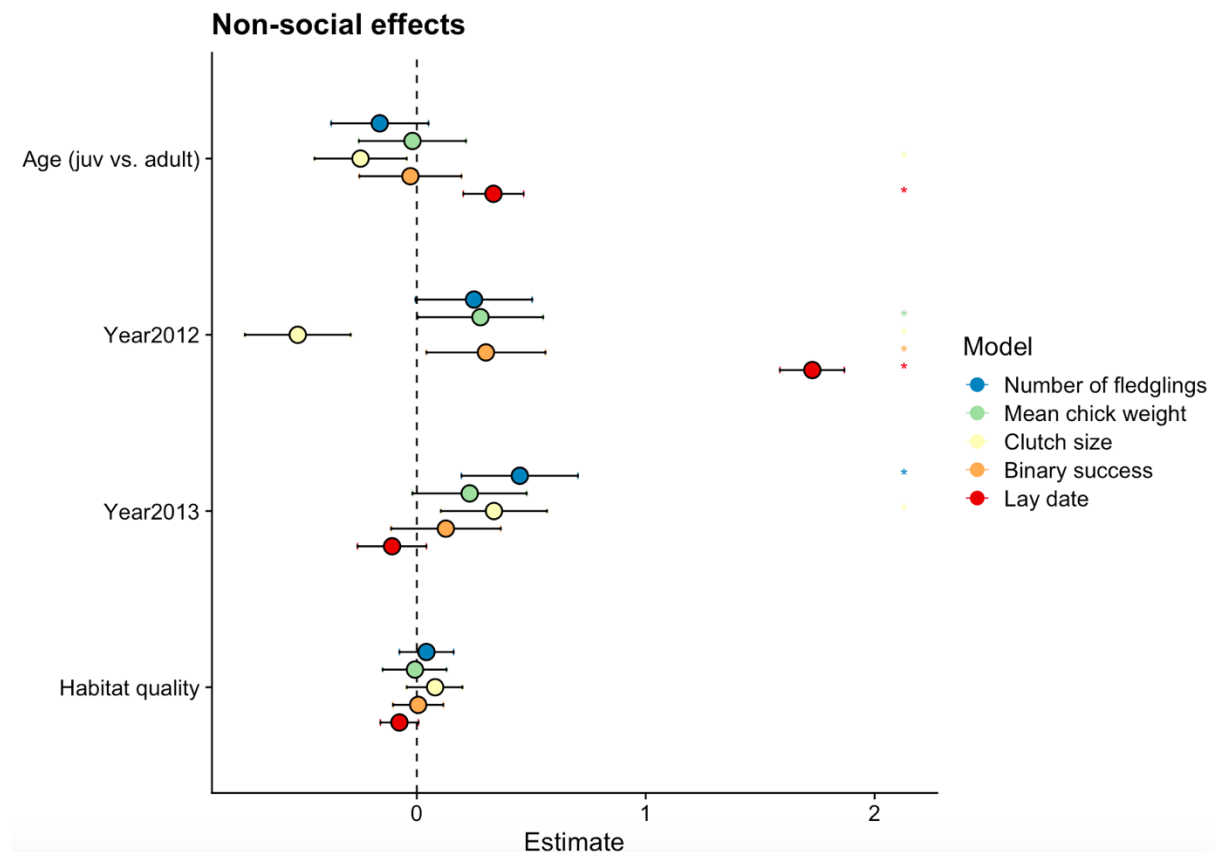


Figure 3 - Summary of the non-social effects with the SPDE breeding spatial autocorrelation correction. Points represent the estimate for each effect that was retained in the model selection process and error bars denote 95% credibility intervals. Years are in comparison to 2014.

Table 2 - model statistics for female main models (same information for males can be found in Supplementary Table 1); bold variables are significant in both models, italic variables are only significant before controlling for breeding spatial autocorrelation, * variables are only significant after controlling for breeding spatial autocorrelation

Response	Variable	Estimate	Lower	Upper	SPDE Mean	SPDE Lower	SPDE Upper
Lay date	<i>(Intercept)</i>	-0.52	-0.64	-0.40	-0.52	-1.17	0.13
	Age (juv. vs. adult)	0.35	0.21	0.48	0.34	0.20	0.47

	Year 2012	1.72	1.58	1.87	1.73	1.59	1.87
	Year 2013	-0.12	-0.27	0.03	-0.11	-0.26	0.04
	<i>Habitat quality</i>	-0.09	-0.16	-0.02	-0.08	-0.16	0.01
	Pair bond strength	-0.13	-0.19	-0.07	-0.13	-0.19	-0.07
	Degree	0.12	0.05	0.19	0.10	0.03	0.18
	Density	0.04	-0.02	0.11	0.06	-0.01	0.13
Binary success	(Intercept)	-0.12	-0.30	0.06	-0.12	-3.58	3.34
	Age (juv. vs. adult)	0.01	-0.21	0.23	-0.03	-0.25	0.20
	Year 2012	0.30	0.04	0.56	0.30	0.04	0.56
	Year 2013	0.12	-0.12	0.36	0.13	-0.11	0.37
	Habitat quality	0.01	-0.09	0.11	0.01	-0.10	0.12
Clutch size	(Intercept)	0.09	-0.09	0.27	0.12	-1.03	1.26
	Age (juv. vs. adult)	-0.21	-0.41	-0.01	-0.25	-0.45	-0.04
	Year 2012	-0.46	-0.69	-0.23	-0.52	-0.75	-0.29
	Year 2013	0.39	0.16	0.62	0.34	0.10	0.57
	<i>Habitat quality</i>	0.11	0.01	0.21	0.08	-0.04	0.20
	Spatial associations*	-0.08	-0.19	0.03	-0.14	-0.26	-0.03
Mean chick weight	(Intercept)	-0.14	-0.34	0.06	-0.18	-0.60	0.21
	Age (juv. vs. adult)	0.03	-0.21	0.27	-0.02	-0.25	0.21

	Year 2012	0.25	-0.04	0.53	0.28	0.00	0.55
	Year 2013	0.19	-0.07	0.45	0.23	-0.02	0.48
	Habitat quality	0.02	-0.09	0.13	-0.01	-0.15	0.13
Number of fledglings	(Intercept)	-0.19	-0.38	-0.01	-0.17	-1.20	0.85
	Age (juv. vs. adult)	-0.09	-0.31	0.12	-0.16	-0.37	0.05
	<i>Year 2012</i>	0.28	0.01	0.54	0.25	-0.01	0.50
	Year 2013	0.47	0.22	0.73	0.45	0.20	0.70
	Habitat quality	0.05	-0.05	0.15	0.04	-0.08	0.16
	<i>Degree</i>	0.19	0.07	0.31	0.10	-0.03	0.23
	Male neighbor bond strength	-0.20	-0.31	-0.09	-0.13	-0.24	-0.02

Discussion

Although individuals exist in complex multi-level societies, much work exploring the relationship between sociality and fitness has focused on a single type of dyadic bond. Using three years of behavioral and reproductive data in wild songbirds, we demonstrate the fitness consequences of four types of dyadic relationships that are found within multilevel societies. Individuals with a stronger bond to their pair mate had earlier lay dates, consistent with previous findings (Culina et al., 2020). Although more social individuals (higher winter network degree) had later lay dates, they also had a higher number of fledglings, suggesting

that social associations with flock mates influence fitness outcomes in multiple dimensions, rather than simply improving fitness overall. When controlling for other social and spatial effects, bonds with breeding neighbors were not beneficial: having stronger bonds with neighboring males was associated with having slightly fewer fledglings. Finally, individuals with more winter spatial associates had smaller clutch sizes – suggesting that it is important to control for spatial relationships when considering other, more traditionally studied, aspects of sociality. Accounting for breeding position spatial autocorrelation in fitness outcomes improved nearly all of the models, highlighting the importance of accounting for spatial effects.

Our results demonstrate support for a consistent finding in this population - the importance of the pair bond in determining lay dates, with individuals that met earlier in the winter (Culina et al., 2020) or had bred together in the past (Gokcekus et al., 2023) having earlier lay dates. Historically, many external factors have been used to predict lay dates (Perrins & McCleery, 1989), including temperature (Noordwijk, McCleery, & Perrins, 1995; Visser, Van Noordwijk, Tinbergen, & Lessells, 1998), habitat quality (Wilkin, Perrins, & Sheldon, 2007), caterpillar growth (Visser, Holleman, & Gienapp, 2006), and presence of parasites (Oppliger, Richner, & Christe, 1994) among others. Yet the strength of the pair bond seems to consistently be an important predictor that is not usually examined. Lay date has often been considered as an individual trait, but these results suggest that it may also be a social trait (and therefore dependent on others in the social system; see discussion below on flock mate relations and lay date)(Evans, Postma, & Sheldon, 2020).

Previous studies in this population have shown that individuals breed close to their highly associated former flock mates (Firth & Sheldon, 2016) and that neighbors who are socially

familiar (due to year-to-year territory sharing) have higher fitness (Gokcekus et al., 2023). However, when controlling for other types of dyadic bonds, having strong winter bonds to subsequent breeding neighbors was not actually beneficial in this sample. Females with stronger bonds to neighboring males had fewer fledglings. It is possible that tolerating males may actually come at a cost if it leads to having fewer resources. Additionally, if females with stronger bonds to male neighbors are more likely to have extra-pair copulations, males may subsequently provide less parental care in the nest or spend more time investing in other females (Eliassen & Jørgensen, 2014; Magrath & Komdeur, 2003).

This finding on breeding neighbors raises the possibility that the previously observed positive effect of neighbor familiarity (Gokcekus et al., 2023; Grabowska-Zhang, Wilkin, et al., 2012) is actually due to general sociality and/or early establishing of territories and not the result of cooperation that arises due to specific bonds with particular individuals. However, it is also possible that breeding neighbor familiarity is most important for an aspect of fitness that we cannot measure: whether individuals are able to establish a territory at all. In support of this possibility, a previous study on this population showed that immigrants are more likely to fail in establishing a territory (and therefore establishing a breeding attempt) than integrated members (Kidd, Sheldon, Simmonds, & Cole, 2015). Furthermore, it is possible that individuals that are familiar over multiple years are easier to identify because they become associated with territory boundaries. If there is a limit on the number of individuals that great tits can identify, it is possible that having stronger bonds with neighbors is not as beneficial as having neighbors that are familiar over the years simply because birds are more likely to be aware of this between-year familiarity (Gokcekus, Firth, Regan, & Sheldon, 2021).

Individuals with a higher degree during the winter have more fledglings, which is in line with the general idea that being more social comes with fitness benefits (Snyder-Mackler et al., 2020). However, this effect is weakened when considering breeding location spatial effects, raising the possibility that part of this relationship may be explained by higher-quality areas supporting stronger bonds. On the other hand, individuals with higher-degree also had later lay dates, which may represent that dedicating social time to other flockmates reduces the social bond with their pair mate and thus potentially pushes back the lay date. When considering winter spatial relations, we find that individuals with more winter spatial associates have smaller clutches. Individuals who spent the winter in higher-density areas had slightly later lay dates but this effect was not significant. Females who spend the winter in areas with higher numbers of individuals might anticipate greater competition and lay smaller clutches accordingly to avoid overstretching the available resources. This result also highlights the importance of explicitly testing and controlling for spatial associations when investigating more apparent measures of sociality.

In this multi-level society, four types of social relationships measured across seasons influenced breeding success when tracked over multiple years. However, future experimental work is necessary to understand the causation behind these effects. For example, sociality's influence on reproductive success could be investigated by manipulating the ability of some individuals to form social bonds. Detailed data on different kinds of social associations across multiple circumstances and years is necessary for a more thorough knowledge of the fitness consequences of sociality within multi-level societies. Disentangling the effects of different types of dyadic bonds within such societies and separating them from spatial patterns is crucial to gaining a more thorough understanding of the factors that drive the evolution of social stability within populations.

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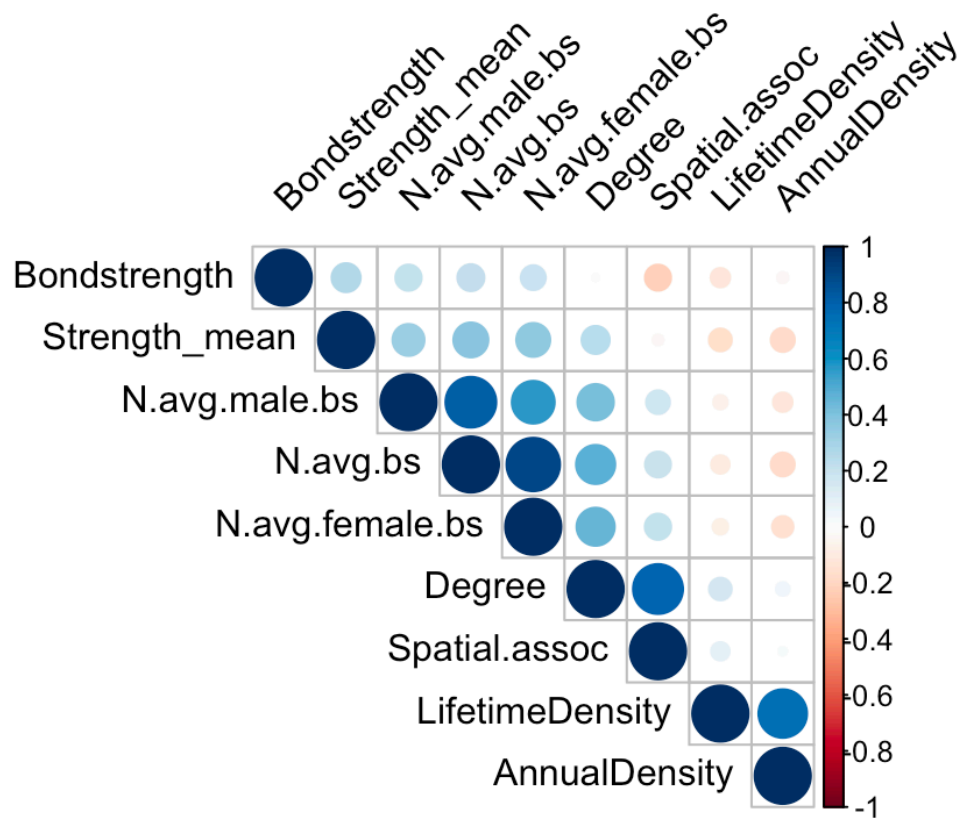
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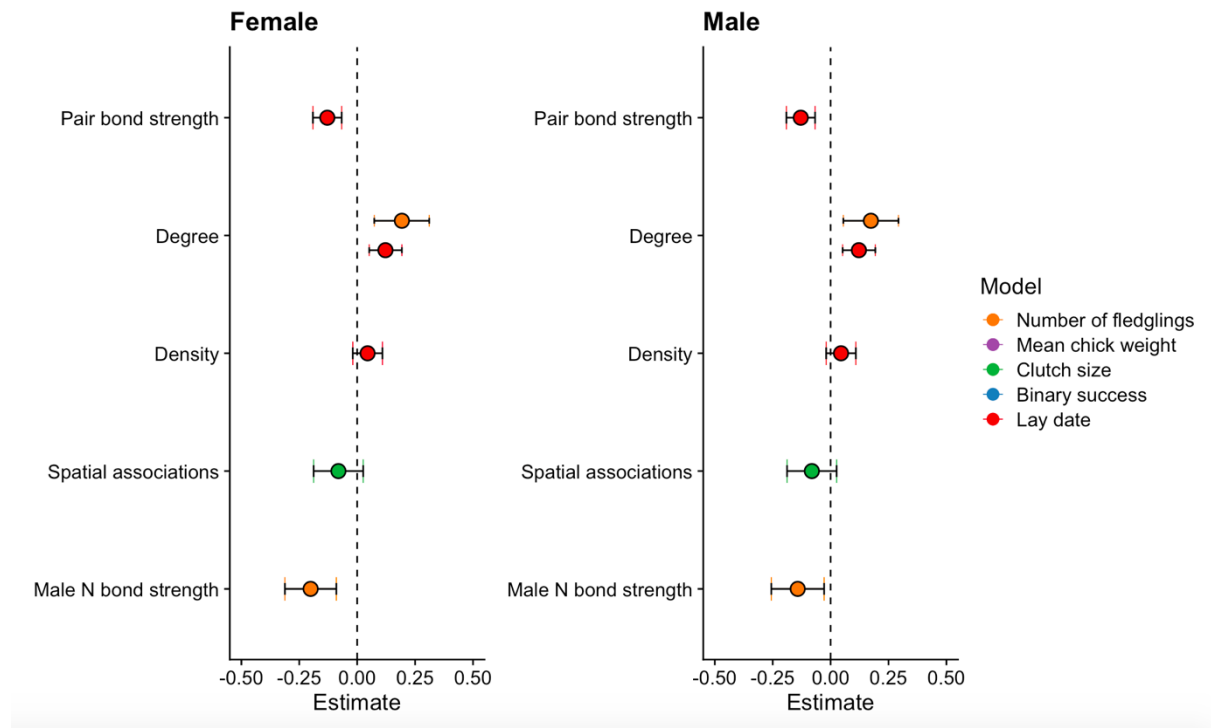
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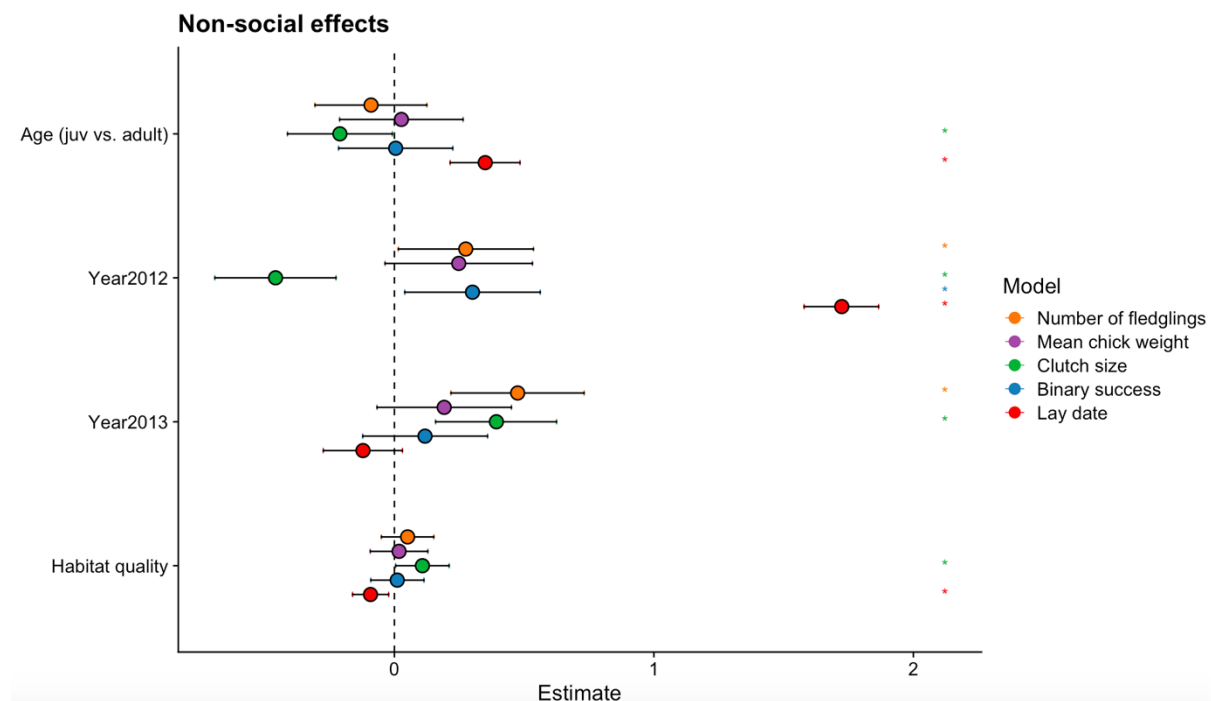
Supplementary material



Supplementary Figure 1 - Correlation matrix of social variables



Supplementary Figure 2 - model results (only social effects) without SPDE spatial autocorrelation correction



Supplementary Figure 3 - model results (only non-social effects) without SPDE spatial autocorrelation correction

Supplementary Table 1 - Male model results

Response	Variable	Estimate	Lower	Upper	SPDE Mean	SPDE Lower	SPDE Upper
Lay date	<i>(Intercept)</i>	-0.52	-0.64	-0.40	-0.52	-1.24	0.18
	Age (juv. vs. adult)	0.35	0.17	0.54	0.37	0.19	0.55
	Year 2012	1.72	1.58	1.87	1.73	1.58	1.86
	Year 2013	-0.12	-0.28	0.04	-0.12	-0.28	0.04
	<i>Habitat quality</i>	-0.09	-0.16	-0.02	-0.08	-0.16	0.01
	Pair bond strength	-0.13	-0.19	-0.07	-0.13	-0.19	-0.07
	Degree	0.12	0.05	0.19	0.10	0.03	0.18
	Density	0.04	-0.02	0.11	0.05	-0.02	0.13
Binary success	(Intercept)	-0.11	-0.30	0.09	-0.11	-3.21	2.99
	Age (juv. vs. adult)	-0.04	-0.36	0.28	-0.07	-0.39	0.24
	Year 2012	0.30	0.04	0.57	0.30	0.04	0.56
	Year 2013	0.13	-0.12	0.37	0.14	-0.11	0.38
	Habitat quality	0.01	-0.09	0.12	0.01	-0.10	0.12
Clutch size	(Intercept)	0.08	-0.11	0.26	0.11	-0.87	1.09
	Age (juv. vs. adult)	-0.17	-0.45	0.11	-0.21	-0.49	0.07
	Year 2012	-0.46	-0.70	-0.23	-0.52	-0.76	-0.29
	Year 2013	0.38	0.14	0.62	0.33	0.09	0.56

	<i>Habitat quality</i>	0.11	0.01	0.21	0.08	-0.05	0.20
	Spatial associations*	-0.08	-0.19	0.03	-0.14	-0.26	-0.03
Mean chick weight	(Intercept)	-0.18	-0.40	0.03	-0.23	-0.66	0.17
	Age (juv. vs. adult)	0.17	-0.18	0.52	0.17	-0.17	0.51
	Year 2012	0.24	-0.04	0.53	0.27	-0.00	0.54
	Year 2013	0.17	-0.10	0.43	0.20	-0.06	0.45
	Habitat quality	0.02	-0.09	0.13	-0.01	-0.15	0.13
Number of fledglings	(Intercept)	-0.17	-0.38	0.03	-0.18	-1.24	0.88
	Age (juv. vs. adult)	-0.09	-0.41	0.24	-0.11	-0.42	0.21
	<i>Year 2012</i>	0.24	-0.02	0.51	0.22	-0.04	0.47
	Year 2013	0.45	0.20	0.71	0.43	0.18	0.68
	Habitat quality	0.06	-0.04	0.16	0.06	-0.06	0.18
	Male neighbor bond strength	0.18	0.06	0.29	0.09	-0.04	0.22
	<i>Degree</i>	-0.14	-0.26	-0.03	-0.07	-0.19	0.04

Chapter 7

General discussion

General discussion

Thesis aims and motivations

Social interactions have fitness consequences for many species and are a crucial component of ecology and evolution (Snyder-Mackler et al. 2020). How individuals navigate their social environments to maximize benefits and reduce costs is influenced by social, cognitive, and environmental factors. Cooperation, where individuals engage in behaviors that confer a direct fitness benefit on others, is an important social process, a key factor in the success of many species, and often is essential for survival in social environments (Axelrod and Hamilton 1981; Sachs et al. 2004; Nowak 2006; Clutton-Brock 2009). The social network approach, which quantifies social relationships through the use of networks, is an increasingly utilized tool for studying social behaviors and processes like cooperation, while simultaneously considering the factors that may influence them (Croft et al. 2015; Brask et al. 2019). Because social interactions, cooperative relationships, and social network structure are all mutually affecting each other, considering cooperation through a social network approach can help to uncover insights in to how all three of these phenomena interact to determine an individual's fitness.

In this thesis, I focused on a number of distinct aspects of cooperation and examined the influence of motivation, dominance, familiarity, and spatial effects on different types of social interactions and relationships. I used both long-term population data and social network data to assess the relationship between familiarity and breeding success to gain a better understanding of how social support and different types of dyadic bonds influence fitness. I highlight several important components of understanding social behavior, including

creating clear conceptual frameworks, making use of the social network approach, and explicitly controlling for and understanding spatial and temporal factors that influence social processes. My thesis provides important groundwork, both theoretically and empirically, for future research that investigates cooperation and other social behaviors while accounting for spatial, temporal, and ecological effects.

Summary of main findings

This thesis explores how social phenomena such as cooperation, individual recognition and leadership in non-human animals can be investigated using quantitative social approaches, and considers the causes of different social behaviors, as well as their fitness consequences. In the first part of this thesis, I conducted a thorough literature review to bring together our understanding of cooperation and individual recognition using a social network approach (**Chapters 2 & 3**). To gain a more complete empirical understanding of complex concepts like cooperation, it is necessary to have clear definitions. I carried out a comprehensive review of what is already known, and what remains to be understood, about cooperation (**Chapter 2**) and individual recognition (**Chapter 3**) in non-human animals, and highlighted the use of a social network approach for gaining insights into both of these phenomena. Understanding the causes and consequences of cooperation requires an investigation of the characteristics of social interactions at the dyadic, group, and population level; all of which can be explored through a social network approach (**Chapter 2**). By using the social network approach alongside experimental manipulations of social structure or cooperative interactions, and fine-scale observational data collected from natural populations, we can uncover the mechanism behind and consequences of cooperation. Studying cooperation in this way can also give insights into social network structures and positions themselves, and how varying levels or forms of cooperation may be associated with different social structures.

I argue that future work looking at the covariation of cooperation with social structure in natural populations may provide insights into how cooperation and social structure are related and improve our understanding of the structural diversity of animal societies.

The integration of social network analysis with research on individual recognition can also improve our understanding of how individual recognition interacts with other social processes, such as cooperation, and can reveal the influence of individual recognition on social dynamics in group formation and social structure (**Chapter 3**). Individual recognition may be important for the emergence and spread of cooperation, especially in settings with repeated interactions among multiple individuals with different goals. Tracking the cooperative or uncooperative behaviors of others can maintain group cohesion and prevent cheating. Bystanders and social eavesdropping, which require individual recognition, can also increase the benefits of engaging in cooperative behaviors. It is also possible that individual recognition allows for more fine-tuned cooperation in some species, while other species rely on more simple, conditional rules. I argue that a better understanding of individual recognition can help to uncover the mechanisms that allow for cooperation in different populations. Through these complementary reviews, I endeavored to provide the conceptual basis for a more holistic understanding of these social behaviors and processes.

After establishing this background and thoroughly reviewing the possibilities for future work, I took a closer look at passive leadership behavior, by considering the dynamics of feeder use in my study population (**Chapter 4**). I looked at which individuals initially approach a selective feeder and unlock it (taking on the cost of waiting for it to open), which can be understood as a form of passive leading behavior. I found that great tits, males, and individuals with high activity levels (feeders visits) are more likely to be “leaders” than blue

tits, females, and individuals with low activity levels. However, these characteristics also interact with spatial and temporal dynamics. In the null model approach, the behavioral variable is randomized, but spatial and temporal patterns are retained; this allows us to consider patterns of non-independence within data and compare observed results to what we would expect at random. Using this approach, I show that the effects of sex and activity can be explained by where and when individuals choose to feed, highlighting the importance of accounting for these factors properly.

In the future, devices such as these feeders could be linked together to study cooperation. Using RFID tags, sets of feeders can be programmed so that two individuals must be present for the feeders to open (to gain a food reward). Furthermore, these feeders can be programmed so that only pairs of a particular composition (male-female, great tit-blue tit, etc.) can access the food. The relative reward (amount of food) that each individual in the pair receives can also be manipulated. These types of experimental studies would allow for a deeper understanding of how cooperative relationships are formed and how they persist over time. My work makes way for future studies on cooperative behavior using these technologies by establishing a baseline understanding of how individuals approach food resources and how spatial and temporal effects may play a role in these dynamics.

In the final part of this thesis, I focused in on specific types of social relationships and trying to understand their fitness consequences while simultaneously accounting for the spatial and temporal effects that we know are important in this population. Using 58 years of data, I showed that familiarity across years both within, and among, breeding pairs has consequences for reproductive success (**Chapter 5**). Although previous work provided evidence for a relationship between familiarity and fitness, whether these patterns existed

outside of spatial effects remained unknown (Grabowska-Zhang et al. 2012). Here, I expanded upon this work with 15 years of additional data and a novel technique to control for spatial autocorrelation. I found that individuals with a familiar partner had earlier egg laying dates and a higher number of fledglings while females with familiar neighbors additionally benefited from earlier lay dates and larger clutches. These results were robust even when considering spatial factors.

I then wanted to look at how dyadic relationships (including the one between pair mates and the one between breeding neighbors) measured using social networks based on the non-breeding season (winter) influence fitness (**Chapter 6**). Using three years of high-resolution social and spatial data, I found that the strength of the pair bond is an important predictor for determining lay dates. Social associations with flock mates influenced fitness outcomes in a complex way, with more social individuals having later lay dates but also a higher number of fledglings. Having strong bonds with neighbors was not related to increased reproductive output, and strong bonds with neighboring males was associated with fewer fledglings. Individuals with more winter spatial associates had smaller clutch sizes; highlighting the importance of considering different types of dyadic relationships when investigating the relationship between fitness and sociality.

The fitness consequences of social relationships

As discussed above, familiarity is often a precursor for social tolerance and cooperation, which can lead to higher fitness as familiarity transfers across time and settings to impact reproductive success (Beletsky and Orians 1989; Croft et al. 2006; Aragón et al. 2007; Silk 2007; Liebgold and Cabe 2008; Kohn 2017a; Riehl and Strong 2018; Alberts 2019). This seems to be the case particularly for neighbors, or individuals that share territory boundaries.

For example, red squirrels with more familiar neighbors sired more pups and were more likely to survive (Siracusa et al. 2020). However, separating the influence of spatial and social factors can be difficult (Albery et al. 2021). It can be unclear if particular behaviors and outcomes are linked to individual differences, social characteristics, or spatial factors (**Chapter 4**). Long-term data from natural populations, where spatial factors are measured and known, are well suited to answering these questions as the role of spatio-temporal factors can be explicitly considered (Firth and Sheldon 2016; Albery et al. 2021). Even when accounting for spatial heterogeneity in fitness outcomes, I found that familiar pairs have higher reproductive success overall, with both males and females in familiar pairs having earlier lay dates and more fledglings than those in unfamiliar pairs. Neighbor familiarity is only related to reproductive success in females, with those with familiar neighbors having earlier lay dates and larger clutches. This is the case even when accounting for habitat quality and spatial autocorrelation in fitness outcomes (Figure 1). The mechanisms behind these effects are not fully understood, but could be related to direct benefits through reduced aggression and increased cooperation, or indirect effects on reproductive timing. Future work that manipulates the ability of individuals to cooperate or to control the timing of breeding can help to further elucidate causality in this context.

Although establishing these fitness consequences is important, this measure of familiarity only focuses on a single kind of social association, namely breeding together (for pairs) or at a shared boundary (for neighbors) over multiple years. Many different kinds of dyadic bonds exist. Hierarchically nested levels of social relationships, known as multilevel societies, are composed of smaller units such as breeding pairs or families that are part of larger groups (Grueter et al. 2020; Papageorgiou and Farine 2021). These multi-tiered structures allow for flexibility in social interaction and require individuals to maintain and track relationships at

multiple levels. Examining the impact of different layers of social associations on fitness is crucial for understanding the relationship between social relationships, social processes (like cooperation), and success, as well as the evolution of different social systems (**Chapter 2**). However, studying these phenomena in the wild can be challenging as it requires long-term, individual-based data from various social contexts, including breeding and non-breeding periods, as well as information on spatial effects and fitness outcomes.

In **Chapter 6**, I used three years of social, spatial, and reproductive data to examine the fitness consequences of four types of dyadic relationships (between pair mates, breeding neighbors, flock mates, and spatial associates) while again considering spatial effects. Here, social relationships were assessed based on winter associations rather than the breeding season in the previous year. As was the case of for familiar pairs, I found that individuals with a stronger winter bond to their future breeding pair mate had earlier lay dates, while those with more social bonds with winter flock mates subsequently had later lay dates but also had a higher number of fledglings. Individuals with more winter spatial associates had smaller clutch sizes upon breeding. Surprisingly, prior winter bonding with subsequent breeding neighbors was not beneficial and having stronger winter bonds with neighboring males was associated with fewer fledglings.

These conflicting results regarding the importance of relationships with breeding neighbors may be related to the role of individual recognition (**Chapter 3**). It is possible that individuals that are familiar over multiple breeding seasons are easier to identify (Godard 1991). If a neighbor is repeatedly observed on a territory boundary over the course of the breeding season, it may be easier to form an association between that individual and the territory boundary which would then lead to a “labelling” of that individual as familiar. This

can also be understood as a form habituation to that individual (neighbor) and their song, particularly when they are in that specific location. If great tits have a limit on the number of individuals they can recognize, it may be that across year familiarity is more important. Hearing the same song from the same location from the same individual over the course of the entire breeding season is likely to be a stronger cue for individual recognition than the various vocalizations, locomotor cues, and chemical cues that individuals perceive over the winter. Furthermore, individuals have many more social associates in the winter than they have neighbors in the breeding season, making it more likely that familiar breeding neighbors can be more easily identified and consequently more likely to lead to cooperation and fitness benefits. This is related to the idea that individual recognition and cooperation evolve together (Crowley et al. 1996), which has gained attention in recent years (Tumulty et al. 2021).

The importance of how the social environment is perceived is also highlighted by the result that females with more winter spatial associates then subsequently lay smaller clutches. It is possible that females that spend the winter in areas with a larger number of individuals perceive higher levels of competition overall and adjust their clutch size accordingly, and it has been shown that individuals in higher density areas have smaller clutches (Wilkin et al. 2006). This finding also emphasizes the importance of controlling for, or explicitly testing, spatial associations when studying other kinds of social relationships.

Considering spatial and temporal effects on social foraging and fitness

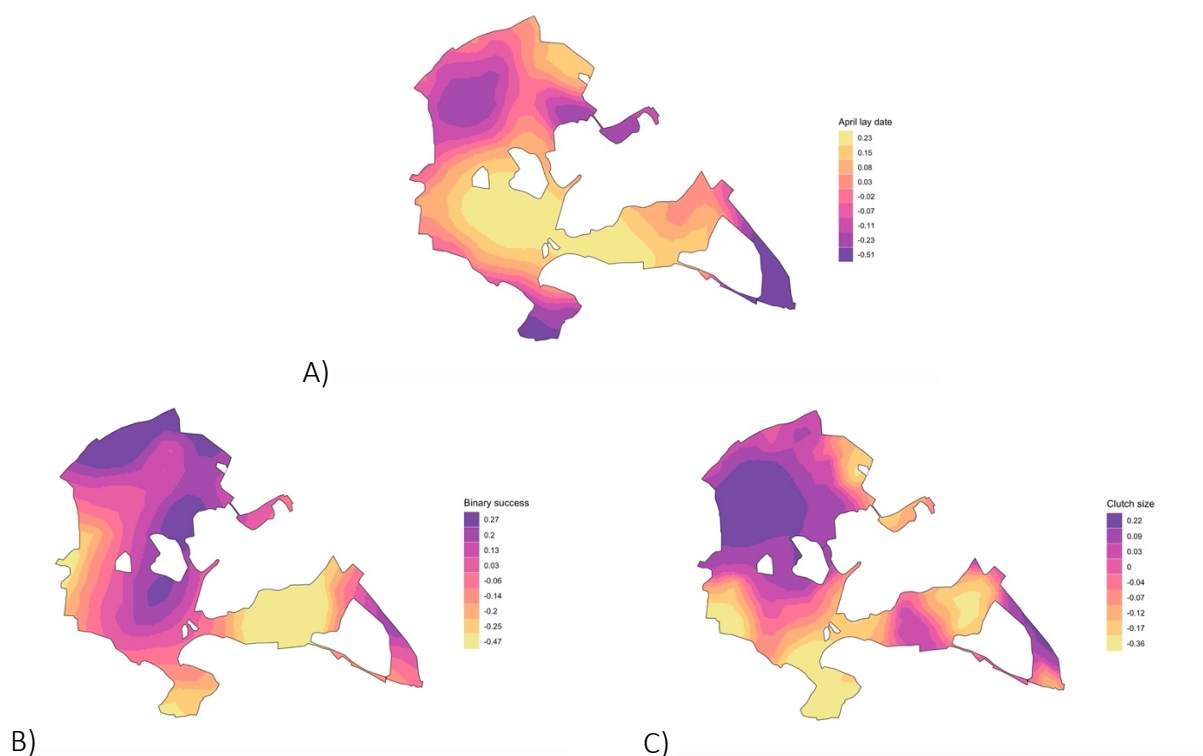
For most social interactions to occur, it is necessary for individuals to be present in the same location at the same time. This shared physical presence is an inherent aspect of a majority of social interactions and makes the separation of spatial and social factors difficult.

Understanding the relationship between social preferences and spatial patterns, and uncovering where they diverge and overlap, is challenging (He et al. 2019; Sosa et al. 2021). Variation in behavior at the intersection of spatial and social interaction can impact ecological and evolutionary processes including the development of social systems (Webber et al. 2023). Spatio-temporal patterns may drive observed differences in social behaviors (**Chapter 4**) and spatial autocorrelation in observed outcomes (like fitness measures, Figure 1) may make results hard to interpret (**Chapters 5 & 6**). Because of the fundamental relationship between social interactions and spatio-temporal effects, having a complete understanding of sociality necessitates the consideration of spatial factors.

Individuals may attempt to strategically alter the timing and location of their movements in order to manipulate their social interactions and alter their position within the physical and social landscape. For example, although the effects of sex and activity on passive leadership are dependent on spatio-temporal effects, it is possible that individuals choose to feed at certain location and at certain times precisely because it increases (or decreases) their chance of being the leader (**Chapter 4**). This could be explored further by manipulating the ability of individuals to be leaders in certain areas and observing subsequent rates of feeding in those locations.

If some areas are more desirable, both in the social (types of social interactions) and/or physical (resource availability and habitat quality) sense, it is possible that individuals attempt to spend more time in those locations. Individuals choose their locations based on their social preferences; for example, great tits are more likely to breed near individuals that they associated with during the previous winter (Firth and Sheldon 2016). The strategies that individuals employ to decide where and when to spend time may change based on both internal and external characteristics. For example, individuals may choose to avoid particular

locations even if they are high quality because they are more likely to encounter particular individuals or types of social interactions. Aging red deer (*Cervus elaphus*) spend more time in areas that are lower quality, lower density, and on the periphery of the population's range which leads to lower social connectedness overall (Albery et al. 2022). It is possible that these older, and therefore less competitive, individuals alter their location to avoid the possibility of negative social interactions. However, movement patterns and where individuals choose to spend their time will also be dependent on group and population dynamics. For example, the movement of one individual within a high density area can have a direct influence on the movement of others (Couzin et al. 2002). These complex interactions between sociality and spatial position need to be untangled to gain a more complete understanding of the ecology and evolution of social processes.



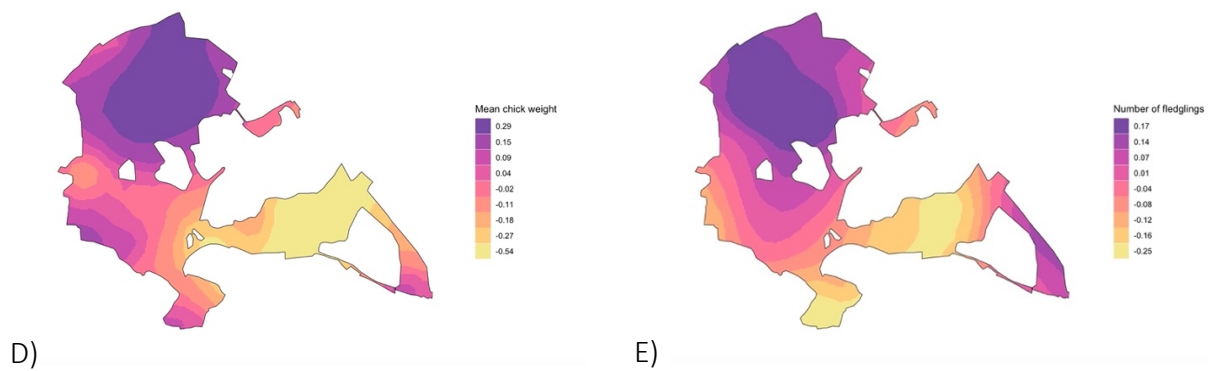


Figure 1 – A 2D projection of the spatial distribution of five fitness variables (lay date, binary success, clutch size, chick weight, number of fledglings; with z-scores) over 58 years, on to the actual map of the study area (from Chapter 5). Different fitness components had slightly different distributions, but the northern portion of the woods tended to feature higher fitness than the others. Despite strong spatial heterogeneity, the social effects (of neighbor familiarity) on fitness that we observed were robust to accounting for spatial effects.

Recognizing the importance of sociality

The influence of biotic factors on animal survival and various characteristics of reproduction have been studied extensively but it is now becoming clear that social characteristics are also important. For example, historically, biotic factors have been the main focus in trying to predict laying dates, including external characteristics like temperature (Noordwijk et al. 1995; Visser et al. 1998), habitat quality (Wilkin et al. 2007), caterpillar growth (Visser et al. 2006), and the presence of parasites (Oppliger et al. 1994) among others. However, pair familiarity and the strength of the pair bond also seem to be important factors (Chapters 5&6). Social factors, in addition to individual and environmental ones, should be considered in the future when considering various aspects of reproduction and reproductive success.

To further uncover the influence of social vs. non-social effects, future work can manipulate social factors while other characteristics of the environment stay the same. For example, selective feeders can be used to disrupt social interactions between individuals in wild tit

flocks (Firth and Sheldon 2015). Through constant changes to which individuals can access each feeder, birds in disrupted areas will have fewer opportunities to form strong bonds with their pair mate, social partners, and future neighbors. The relationships between sociality and fitness can then be examined in these areas and in other control areas where birds could go on as normal. This can help to uncover the extent to which the relationship between sociality and fitness is causal.

Long term data can also be used to look at how social factors may increase or decrease in importance over time and throughout the lifespan. In great tits (**Chapters 5 & 6**) and across other species of birds, mammals, and fish, individuals have higher fitness if they grow up, reproduce, age, and endure periods of scarcity with strongly-bonded associates (Beletsky and Orians 1989; Seppä et al. 2001; Riehl 2011; Kohn 2017b; Alberts 2019; Siracusa et al. 2020; Turner et al. 2020; Gerber et al. 2022). What remains to be understood is how the consequences of sociality change over the course of the lifespan. Evidence is now emerging which suggests that individuals become more socially selective and decrease their social network sizes over time, in primates (Almeling et al. 2016; Rosati et al. 2020; Rathke and Fischer 2021) and other mammals (Wey and Blumstein 2010; Kroeger et al. 2021; Weiss et al. 2021; Albery et al. 2022). For example, older rhesus macaque (*Macaca mulatta*) females become more “selective” : they reduce their network sizes and focus on the most beneficial partnerships (Siracusa et al., 2022), and these stronger bonds may help to mitigate the negative effects of aging (Siracusa et al. 2020). Future work examining the social interactions and relationships of individuals over the entire course of their lifespan can help to better understand how sociality, age, and fitness interact.

Concluding remarks

We have come a long way in understanding the social behaviors that individuals engage in, with new insights in to the causes and consequences of negative, neutral, and beneficial social interactions (Silk 2007; Bebbington et al. 2017; McFarland et al. 2017; Menz et al. 2020; Siracusa et al. 2020). Advances in automated tracking technologies have allowed for the collection of precise, detailed, and large data sets on the social interactions of individuals in natural populations. Although stemming from different causes or leading to different outcomes, various aspects of sociality and ecology are fundamentally related. To collect and analyze the right information, and to make full use of these resources, clear conceptual frameworks must be established (**Chapters 2 & 3**), and spatial and temporal factors must be accounted for (**Chapters 4-6**). By studying sociality through a social network approach, we can further analyze the relationships between properties of individuals and group level processes and, in-turn, uncover how network positions, group connectivity measures, and social structure may relate to individual or group levels of cooperative (and other social) behaviors.

Advances in automatic tracking, the compilation of long-term data sets, and novel methods for accounting for spatial patterns have provided a unique opportunity to gain a deeper understanding of sociality, the mechanisms behind social processes, and the fitness consequences of social interactions and relationships. My work adds to a foundation of fundamental information on how individuals approach food resources, which paves the way for future studies of cooperation using automated devices (e.g. those that dispense food while simultaneously tracking various kinds of interactions). I also demonstrate how familiarity and sociality over time can positively impact fitness and raise the possibility that individual recognition plays a role in these processes. The theoretical and empirical advances that I have made provide the groundwork for future research on cooperation and the

biological processes that allow for social behaviors that accounts for spatial, temporal, and ecological factors.

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