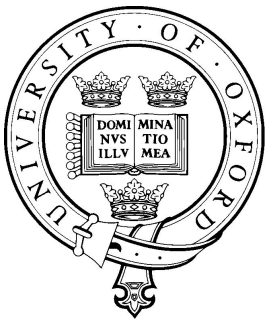
Fitness and social interactions in the great tit (*Parus major*)



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Abstract

Social behaviour is ubiquitous in vertebrate systems, but for many taxa the consequences of sociality remain unexplored, especially for non group-living species that are sometimes dismissed as nonsocial. Although studies of group-living and highly gregarious species make a major contribution to our understanding of this phenomenon, they do not allow the detection of more subtle consequences of social behaviour that may be operating in species with more cryptic social patterns.

This thesis aimed to investigate the fitness consequences of sociality in the great tit (*Parus major*). Although great tits do not live in groups, their territoriality during breeding and aggregation in large foraging flocks during winter allows the potential for social interactions in a variety of fitness-relevant contexts. Using 41 years of breeding data from the Wytham Woods great tit population I performed an analysis of between-year territorial familiarity between breeders older than one year and its effect on reproductive success. I found that familiarity with the nearest neighbour and the number of familiar neighbours had positive effects on the female's clutch size and the breeders' probability of nesting success, respectively. Both effects were robust to the inclusion of fine-scale spatial factors, and were identified to be underpinned mostly by intrinsic differences between individual breeders. The benefit of familiarity for nesting success led me to hypothesise that familiar neighbours may engage in cooperative activities such as predator nest defence – a hypothesis that I subsequently tested experimentally. To investigate the effects of between-year familiarity on nest defence I performed a field experiment using the natural variation in familiarity in territorial neighbours present in the population. The experimental manipulation revealed that familiar neighbours were more likely to join each other's nest defence than neighbours that were unfamiliar or neighbours that were first-time breeders. In the light of the importance of nest defence for predator deterrence and nesting success, it is likely that nest defence coalitions are one of the mechanisms through which individuals benefit from familiarity with neighbours.

To test the effects of sociality on a finer timescale, between winter and the subsequent breeding season, I performed a detailed analysis of the stability of relationships in winter foraging flocks and individuals fitness. Because the largest determinant of fitness is whether an individual breeds or not, I analysed the effect of social stability on the probability of breeding, as well as the effect on measures of reproductive success for individuals that were recorded breeding. I found that individuals were more likely to breed when their social stability was high, and that individuals that had more stable social relationships fledged heavier young. These effects seem to be underpinned by phenotypic plasticity of individuals in the former case, and intrinsic differences between individuals in the latter.

An analysis of within-season associations in overwintering juveniles revealed a strong spatial effect on the rate of association between juveniles in the vagrancy stage of natal dispersal. Independent of the spatial factors, the study revealed kin structure in the rate of associations driven by a high rate of association between brothers. The presence of kin structure reveals the potential for kin selection in the winter population.

Overall, this thesis reveals complex, existing and potential fitness consequences of sociality operating at different times in the life cycle and at different temporal scales. It also demonstrates that even in a species where social interactions occur much more cryptically than in some gregarious organisms, their consequences for individual fitness are still apparent, suggesting that such impacts of sociality may be more widespread than previously anticipated.

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Chapter 1

Introduction

1.1 General introduction

Sociality is an important feature of life. For example, interactions between cells underlie the origin of multi-cellularity and organismal complexity and social associations between individuals give rise to complex population structures, group living, co-operation and animal societies (West et al. 2007). Sociality can also influence the way in which selection operates. For instance, clustering of related individuals can cause selection to operate on individuals through indirect as well as direct fitness benefits (Hamilton 1964a,b). In many species, interactions with kin, as well as unrelated individuals, play an important role in creating and maintaining population structure (Platt and Bever 2009). Therefore, understanding how kin groups, and assemblages of unrelated individuals affect individual fitness is important in the context of the evolution of social behaviours driven by mechanisms such as reciprocity and kin selection, and the evolution of dispersal.

Cooperative behaviours, if driven by reciprocity (Trivers 1971), are predicted to

rely on long-term associations with the same individuals and individual familiarity. Knowing how such familiarity arises, and the time scale over which it operates, is important for our understanding of the selective forces behind cooperation. In some systems individuals may become familiar through sharing a territory boundary. At a different temporal scale, associations in groups resulting from flocking/shoaling behaviour can lead to familiarity with other group members. Cooperation can also take the form of mutualism, when the co-operator acts selfishly, but the result of the action is beneficial to the recipient. On a more basic level, neighbour recognition can mediate by-product mutualism such as the Dear Enemy Effect, which predicts that a territorial individual will be less aggressive towards neighbours than to strangers. The Dear Enemy Effect (Fisher 1954) has been reported for birds, mammals (Briefer et al. 2008; Brunton et al. 2008; Mackin 2005; Rosell et al. 2008) and other animals (Jaeger 1981). Both on a simple and more complex level of recognition, different behaviour towards familiar individuals can have potential fitness benefits. This can be mediated by reduced energy expenditure in territorial interactions (Dear Enemies spend less time on territorial contests), or through direct benefits of cooperation.

Individuals can increase their inclusive fitness by cooperating with kin. This mechanism is called kin selection and explains altruistic behaviours between relatives (Hamilton 1964a,b). Kin selection operates in many species through group living, cooperative breeding and delayed dispersal (Komdeur 1994), as well as budding dispersal (Kümmerli et al. 2009). Many studies have shown kin selec-

tion operating during breeding, when related individuals help to raise younger offspring. However, non-cooperative breeders can also benefit from associating with kin. Sibling groups may benefit from a period of sociality before they disperse. Even after dispersal, individuals may exhibit preferential treatment of relatives in structured groups consisting of mixture of kin and non-kin (Toth et al. 2009). Kin selection can select for diminished dispersal and result in spatial clustering of related individuals. Sometimes, kin clusters are created due to population viscosity alone, which results in a kin-structured population in the absence of selection or active kin discrimination (Wolf and Trillmich 2008).

1.2 Dispersal in a social context

Dispersal is an important aspect of the biology and life-history of many organisms, because it changes population density, alters population genetics and has consequences for the species' ecology. It is also relevant in the context of conservation management of endangered species. Two types of dispersal are usually recognised; natal dispersal is the

> *movement between the natal area or parental group, and the area or social group where breeding first takes place,* [whereas breeding dispersal is] *the movement between two successive breeding areas or social groups* (Clobert et al. 2001)

Dispersal behaviour is sensitive to many intrinsic (individual) and extrinsic (environmental) factors. Whether an individual disperses may depend on its genotype

(the presence of a dispersal morph), body condition (Lens and Dhondt 1994), or even maternal body condition (Massot et al. 2002). Additionally, individuals respond to habitat quality, population density and other external factors in making dispersal decisions (Parejo et al. 2007).

There is a large body of theoretical work concerning the diversity of ultimate factors affecting the evolution of dispersal (reviewed in Bowler and Benton 2005; Ronce 2007). Factors like kin competition and risk of inbreeding select for high dispersal rates. Here, for philopatric individuals, as local density rises, their risk of competing with relatives increases while the chance of breeding with a related individual also increases (Clobert et al. 2001). An opposing force selecting against dispersal is the dispersal cost. Any dispersal bears fitness costs through increased mortality, as observed for root voles (Ims and Andreassen 2000). Movement also involves allocation of resources to dispersal which could otherwise be used for reproduction, in addition to the cost of settling in an unfamiliar, sometimes suboptimal, habitat (Ronce 2007).

Limited dispersal has been pointed out as one of the conditions that create clusters of related individuals, allowing the evolution of altruism through kin selection (Hamilton 1964a,b). However, while limited dispersal may increase relatedness between potential altruists, it also increases the relatedness of competitors within the neighbourhood. When competition is completely local, the benefits of close relatedness with potential altruists are exactly canceled by the increased competition between relatives (Taylor 1992a,b; Wilson et al. 1992). One way in which

dispersal can promote the evolution of altruism is if groups of related individuals disperse together (budding dispersal) (Gardner and West 2006). In groups of cooperating relatives, dispersing in groups means the individuals still benefit from increased relatedness, but they reduce the local competition for resources between relatives. Evolution of cooperation through budding dispersal has been shown experimentally by Kümmerli et al. (2009) in siderophore-producing bacteria. Le Galliard et al. (2005) modelled the joint evolution of dispersal and altruism, showing the possibility of a positive correlation between evolutionarily stable levels of altruism and dispersal, as well as exploring the effects of the costs of dispersal and altruism on the evolutionary trajectory of those traits.

The interaction between the process of dispersal and the many facets of sociality can thus be complex. Understanding how those two factors affect each other in a wild population can supply important empirical evidence in a field dominated by theoretical studies.

1.3 Familiarity and social interactions

Familiarity affects intraspecific interactions in many species. Reported effects include increased social tolerance (Aragon et al. 2007) and the outcome of conflicts initiated against familiar versus non-familiar individuals (Hojesjo et al. 1998). Fitness benefits resulting from familiarity have been reported for many taxa, such as fish (Hojesjo et al. 1998), amphibians (Liebgold and Cabe 2008), reptiles (Aragon et al. 2007) and birds (Beletsky and Orians 1989). The way in which

familiarity arises, and the complexity of the level of recognition affect its potential social and fitness consequences.

On a basic level of association, neighbour-stranger discrimination affects territorial interactions and underlies the Dear Enemy Phenomenon (DEP). In the DEP, territorial individuals react less aggressively to neighbouring than to distant territorial or vagrant individuals (Briefer et al. 2008; Brunton et al. 2008; Rosell et al. 2008; reviewed in: Temeles 1994). According to game-theoretic approaches, territorial individuals modulate their response to the relative threat posed by neighbours versus strangers (Getty 1987; Jaeger 1981; Temeles 1990; reviewed in: Temeles 1994). In situations when a neighbour poses less threat to the defended resources (food, mates, breeding sites), reacting less aggressively to those individuals is adaptive, as the resident will expend less energy on escalating territorial contests. Treating neighbours as dear enemies is not a stable relationship and is dependent on the social context. It has been shown that territorial skylark males are dear enemies in the middle of the breeding season, when males with established territories did not pose a threat of territory overtake, but not early or late in the season, when territory boundaries were much more fluid (Briefer et al. 2008).

Territory owners benefit from a stable territorial arrangement because it lets them reduce the costs of renegotiating the territory boundary with a newcomer. In the male fiddler crab *Uca mjoebergi*, this elicits helping behaviour towards a contested neighbour (Backwell and Jennions 2004). Game-theoretic modelling of such al-

liances shows that helping neighbours can be an ESS if the costs of helping are lower than the costs of renegotiation (Mesterton-Gibbons and Sherratt 2009). Familiarity can also bring fitness benefits other than those resulting from diminished aggressive interactions. Repeated encounters between the same individuals aid the evolution of cooperative behaviours such as reciprocity. Reciprocity occurs when one individual performs a costly action that benefits another individual, with the expectation of future benefit from the current recipient (Trivers 1971). Reciprocity is best known from tight-knit groups where repeated interactions allow a degree of protection against defectors (cheats) through strategies like tit-for-tat. The tit-for-tat strategy involves cooperation on the first encounter and then repeating the partner's previous move (Axelrod and Hamilton 1981). Recently, reciprocity has been suggested in temporary territorial aggregations of a breeding passerine whereby breeding pairs of pied flycatchers *Ficedula hypoleuca* reciprocated by joining a predator mob at the nest of previously cooperating pair, but not in a mob at the nest of defectors (Krams et al. 2008). This well designed, albeit controversial (Russell and Wright 2009; Wheatcroft and Krams 2009; Wheatcroft and Price 2008), experiment suggests that reciprocity may operate in structured populations previously thought not to have stable enough associations for reciprocity to occur.

The great tit, *Parus major*, is a small passerine ecologically similar to the flycatcher in so far as both species are hole-nesting birds and both are territorial during the breeding season. However, unlike the flycatcher, the great tit is a

year-round resident in British woods. This feature makes the great tit as likely, if not more likely, to form long-term relationships with conspecifics. Great tit males have been shown to discriminate individuals by song in the laboratory (Weary and Krebs 1992), and incubating female great tits have been shown to discriminate between their mate and a neighbouring male through song recognition (Blumenrath et al. 2007). This implies the neurological capacity for individual recognition in the great tit, at least on a seasonal time-scale. Whether, and how, individuals obtain fitness benefits from social familiarity above the level of mate recognition is an important question for understanding sociality and evolution of cooperation, as well as its effects on shaping of population structure.

There is little empirical data that relates to the fitness consequences of familiarity. To assess fitness consequences directly, familiarity has to have an effect on reproductive success, the investigation of which can sometimes be difficult in a short term study. Some of the studies that have compared familiar and unfamiliar individuals have focused on variables for which the fitness consequences have to be assumed, such as social tolerance (Aragon et al. 2007) or growth (Liebgold and Cabe 2008). This thesis has an opportunity to bridge that gap thanks to good quality long term data on reproductive traits and novel approaches to quantifying social relationships.

1.3.1 Social networks

One of the important tasks in biology is linking individual-level processes and behaviour to population ecology. The structure of a population is a consequence of smaller-scale interactions of individuals with their environment, as well as interactions between the individuals that make up the population. Individuals vary greatly in their propensity to interact socially with others, and interactions are not random in natural systems (Krause and Ruxton 2002). The non-random pattern of social contacts can affect population structure (Wolf and Trillmich 2008), as well as processes such as information transfer or spread of new behaviours, including cooperative behaviours (Rand et al. 2011; van Doorn and Taborsky 2012). Social network theory (SNT) provides a tool for quantifying patterns of interactions between individuals and presents these relationships as a network. The SNT approach represents individuals as nodes connected by edges representing relationships or interactions. The position of an individual within a social network can have consequences for the amount of competition it encounters and the level of selection it experiences. House finch (*Carpodacus mexicanus*) males that change their social environment according to their level of ornamentation, effectively improve their relative attractiveness, and hence, the amount of sexual selection acting on them (Oh and Badyaev 2010). In juvenile song sparrows (*Melospiza melodia*) social network position has been linked to the ontogeny of song type and mate attraction (Templeton et al. 2012). These kind of individual effects stem from the fact that individuals differ in their social experiences, and

that different individuals may not only be exposed to different pressures based on their sociality, but also respond to them differently depending on whom they interact with and to what extent.

Social connections matter in studies of flow in natural populations. SNT has been used in several studies to assess the impact of social connections on disease transmission in natural populations (Corner et al. 2003; Cross et al. 2004; Drewe 2010). Social network structure can affect how fast the disease spreads through the population, and modulate the risk of infection for individuals depending on their position in the network (Meyers et al. 2005). Similar principles apply to the study of social learning and information flow in animal populations, but with a slight difference in the ways in which animals collect social information. Individuals gather social information directly through interacting, but also, eavesdroppers not participating in an interaction can obtain public information which can affect future interactions. For example, males that have witnessed aggressive interactions between other males tend to initiate fights with losers sooner than with winners (Earley and Dugatkin 2002; Oliveira et al. 1998). The social network approach can help to describe the structure of such information networks, which in turn can shed light on the evolution of public information use and communication strategies (Dabelsteen 2004).

SNT is a useful tool for studying the spread of novel behaviours, or cooperation in populations. One topic that has recently received a lot of attention from social network empiricists and theorists is the evolution and maintenance of cooperation

through reciprocal altruism (Trivers 1971), both in real world networks (Curry and Dunbar 2011; Santos et al. 2006) and simulated networks with different properties (van Doorn and Taborsky 2012). Simple models of the evolution of cooperation assume uniform chances of interactions between all individuals, an assumption which is rarely met in natural systems. Cooperation tends to decrease with increasing group size and uniform interactions (Berman et al. 1997; Louis et al. 2007), but dominates in substructured networks where altruists are allowed to interact predominantly with other altruists (Santos et al. 2006).

Since social network structure can affect a wide range of population and evolutionary processes, it is important to understand what forces shape connections within the network. Patterns of interactions can be influenced by partner choice based on individual characteristics. This broad class of mechanisms includes feedback loops of partner choice when interacting once changes the probability that the dyad will interact in the future, as well as positive (McPherson et al. 2001) and negative assortativity, when individuals interact predominantly with similar or different partners respectively. Thanks to recent developments in social network techniques (Franks et al. 2009; James et al. 2009), technological advances (Krause et al. 2011) and increased computational power, it is possible to increase the scale at which we study social systems and infer social structure from population-wide observations.

1.4 The study species

The great tit (*Parus major*) is a small (circa 18g) passerine bird, common in forests throughout much of Eurasia. It is a secondary cavity nester, choosing holes in old trees and stumps as nesting sites. However, great tits preferentially accept nest boxes as breeding sites (Perrins 1965). Great tits provide bi-parental care to young. In the Wytham Woods population, adults rear a single brood in a breeding season (Perrins 1979) and usually only attempt a second brood if the first one fails. The female lays on average 8.3 eggs (SD=2.0) (Wilkin 2006), incubates the eggs alone and shares chick-rearing activities with the male. Food for the young consists of small invertebrates, mainly caterpillars of the winter moth (*Operophtera brumata*) and the green tortrix (*Tortrix viridiana*). The birds time their breeding so that the nestling period coincides with the brief peak caterpillar abundance (Perrins 1991). The young fledge and leave the nest approximately 20 days after hatching.

In the autumn and winter both juveniles and adults aggregate into flocks to feed on patchy food resources. The flocks can be transient and mobile, although territorial males tend to keep close to their home range. They still defend their territory from vagrant contesters, despite territoriality being more relaxed outside of breeding season (Drent 1983). The winter flocks have a dominance hierarchy based on residency and sex. Territorial males have a higher dominance rank than non-territorial males, and males in general are dominant over females (Drent 1983). The social structure of the winter flock affects an individual's access

to food resources, with dominant individuals having priority in obtaining food. As a result, when food is scarce, subdominant individuals are at a higher risk of starvation than dominant ones (Gosler and Carruthers 1999). Social status has been shown to reflect body condition in wintering great tits (Gosler and Carruthers 1999; Gosler 1996), and body condition (flight muscle score) was a predictor of winter survival (Gosler and Carruthers 1999).

Most juveniles spend the autumn in a vagrant state and settle in stable ranges by December. Juvenile great tits disperse from their natal area, whereas adult birds exhibit breeding site fidelity. Natal dispersal distance in males is shorter than in females (Greenwood et al. 1979). Adult males are less likely to disperse between breeding years than females due to year-round territoriality (Harvey et al. 1979).

1.4.1 The study site

Wytham Woods is a large (ca. 385 ha) continuous piece of deciduous woodland located west of Oxford, UK (51°46' N, 1°20' W). Tree species dominating the woods are oak (*Quercus robur*), beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*). The woods are divided into sections reflecting their management history. Types of stands occurring in Wytham include ancient semi-natural woodland, secondary regenerations, plantations from 18th, 19th, and 20th century, as well as areas of grassland used as pasture (Gibson 1988).



Figure 1.1: Aerial photograph of Wytham Woods with the locations of data loggers (courtesy of T.A. Wilkin, modified)

The long term study of the great tit was started by David Lack in 1947, and the first nest boxes were erected between 1946 and 1950 by J.A. Gibb in Marley Wood in the East part of Wytham. Over 1,000 boxes were supplied in the rest of the woods by 1965, and they have remained at the same locations since, save minor moves due to tree falls. In 2005, T.A. Wilkin digitally mapped the locations of all nest boxes using GPS techniques (Wilkin 2006).

Since the summer of 2007, nearly every juvenile (96%) and breeding adult (97%) great tit in Wytham has been fitted with a unique Passive Integrated Transponder (PIT) tag, placed on a plastic leg ring. A total of 1,815 adult and 6,702 nestling

great tits were tagged between spring of 2007 and spring of 2010. Detection loggers attached to column bird feeders have been put at fixed locations (Figure 1.1) around the woods to allow the detections of individuals outside the breeding season. PIT tag detection occurred through the induction of voltage in the inert tag by the electro-magnetic field of the antenna when the bird perched on an antenna to obtain a sunflower seed from the feeder. The identity was transmitted by the tag and a time stamp logged by the data logger. The dataset therefore consisted of the identities of the birds, the place, date and time of their detection. Data were collected outside the breeding season when the food is scarce enough for the feeders to attract birds, between August and early March. A total of fifteen loggers were rotated in a random sequence every three to four days between 61 fixed locations within the eight areas of Wytham (denoted by numbers in Figure 1.1) in the first two winters, and every seven days in the third winter of the study. The rotation allowed a thorough coverage of the study site without the birds gaining access to a predictable, reliable food source.

1.5 Familiarity and networks in great tits

With historical data on the locality of breeding birds, and new approaches to identifying social interactions at a fine temporal scale, this thesis has an opportunity to expand our understanding of how familiarity may arise and the time-scale on which it can affect the life of individuals.

Although the great tit does not rank high on the scale of sociality, its ecology and

life-history provides frequent opportunities to interact repeatedly with the same individuals, and hence create stable relationships. As outlined above, the importance of familiarity in a territorial context has a strong backing in behavioural ecology literature. The long-term study of the Wytham population provides a unique opportunity to look into effects of familiarity over a long period of time and includes a great number of individuals, which is often not possible for shorter studies.

PIT tag winter data allows insight into large-scale patterns of social behaviour that are difficult to observe by human observers, particularly on a population-wide scale. Because these patterns need to be inferred from the temporal co-occurrence of individuals in the logging data, I shall refer to such events as associations, rather than using the term interactions, which is common in social behaviour literature. While associations at feeding stations imply potential for interaction, interacting at the feeder cannot be confirmed, and should not be assumed, from logging data. What associations can tell us about the social environment of individuals without having to rely on confirmed interactions includes information about spatial proximity of individuals, as well as the strength of individual relationships based on the frequency of associations.

It is uncertain whether winter associations lead to familiarity in the same way territorial interactions do. However, by analysing patterns of individual associations it is possible to determine whether social behaviour in the winter affects individuals in a similar way to interactions in a more stable, territorial context.

I will also try to ascertain what determines the patterns of associations between juveniles, which, unlike older birds, do not have the familiarity from previous territorial context. Juveniles also undergo natal dispersal in their first winter, therefore their patterns of sociality may be governed by different factors to those important for the more sedentary adult individuals. I will use Social Network Theory (SNT) approach to quantify winter associations. In the winter, great tits forage in flocks, but due to their transient nature, group analysis classically applied in studies of social behaviour is not appropriate. The classic "gambit of the group" approach assumes that the large majority of, or all, interactions happen within the same group; that the type of interaction is similar within the group, and that the rate of interactions is the same for all dyads in the group (Whitehead and Dufault 1999). Analysis of individual dyadic associations instead avoids the problem of unstable group membership, and weighing the associations with the use of association indices helps to quantify the strength of the association and disentangle strong relationships from accidental contact (James et al. 2009).

1.6 Outline of the thesis

The aim of my thesis is to address questions about social interactions in the Wytham great tit population. I intend to investigate social behaviour at decreasing temporal scales that occur between the form of behaviour and its individual consequences. These are summarised in Table 1.1,

Chapter	Behaviour	Scale	Consequences	Previous work
Chapter 2	Territorial familiarity	Between years	Direct fitness	red-winged blackbirds (Beletsky and Orians 1989)
Chapter 3	Mobbing and territorial familiarity	Between years and within season	Potential direct fitness	Familiarity aspect: ravens (Fraser and Bugnyar 2012); Mobbing aspect: pied flycatchers (Krams et al. 2008)
Chapter 4	Stability in winter associations	Between seasons	Direct fitness	house finches (Oh and Badyaev 2010); cowbirds (White et al. 2010)
Chapter 5	Social structure and kin affiliation in juveniles	Within season	Potential indirect fitness	none in non-cooperative breeding species

Table 1.1: Summary of chapter themes in order of decreasing time-scale of consequences of social behaviour

with reference to previous work done on taxonomically similar species. The effect of social interactions on life-history traits and characteristics of sociality outside of breeding season are of particular importance, because there is still little empirical data on interactions between individuals in those periods of the year when birds are not closely tied to the breeding site and are therefore much more difficult to observe.

In Chapter 2, I investigate the effect of stable territorial relationships on the reproductive performance of adult (older than 1 year) great tits. Familiarity with neighbouring conspecifics could be advantageous as it increases the amount of information about the competitive ability of rivals, quality of prospective mates or the cooperative inclination of local residents. This is similar to the way in which

familiarity with habitat benefits an individual as it increases the knowledge of available resources and predator danger. There has been rather little empirical work on direct fitness consequences of familiarity. The only reported effects were the positive influence of familiar neighbours on reproductive performance in red-winged blackbirds (Beletsky and Orians 1989); no effect was found in the females of the same species (Weatherhead 1995). The analysis investigates the effects of familiarity along the reproductive time-line, separating the influence of familiarity at several stages in the reproductive cycle.

Following on from results identified in Chapter 2 that familiarity with neighbours benefits breeders, I experimentally test whether experienced breeders behave differently towards neighbours familiar from previous year's territorial context. In Chapter 3 I hypothesise that familiar neighbours will join in each other's nest defence, a mechanism that could be responsible for the increased nesting success of breeders with familiar neighbours identified in Chapter 2. Using existing variation in the territory occupancy of first-year and older birds in May 2011, I designed an experiment to test whether territorial neighbours will join in the nest defence of a neighbour challenged with a simulated predator intrusion based on sharing a territory boundary (being neighbours) the previous year.

In chapter 4 I investigate the stability of associations in the winter and their relationship with reproduction the following spring. I use the strongest ties in an individual's pool of associates and quantify turnover in that pool to assess the level of stability in an individual's social environment. Associations in the

winter when food is scarce can potentially affect the survival and body condition of individuals through differential access to food depending on the dominance hierarchy in the flock. I look into the relationship between social stability in winter and the probability that an individual will breed in the study population the following spring, and for those individuals that do, I analysed the relationship between stability and measures of reproductive performance.

In the final chapter I investigate the factors affecting patterns of associations in juvenile great tits. I look into the effects of natal origin of individuals on the rate at which they associate, and ask whether siblings from the same nest associate more than is expected from the effect of their shared origin. The breeding population of great tits in Wytham has non-random mating structure (Szulkin et al. 2009) and bears the signs of incomplete population mixing. I investigate social factors affecting individuals in the vagrancy stage of natal dispersal and identify the signs of population viscosity in winter associations. I also identify the degree of kin structure in the winter population. The presence of kin associations is relevant for the potential for fitness-related interactions between kin that can be kin-selected. Understanding such social population structuring is relevant for the understanding of the evolution of sociality.

This thesis deals with different aspects of social behaviour in the great tit. I look at familiarity between territorial neighbours and its effect on fitness of experienced breeders. I also analyse patterns of sociality in the winter and quantify their effects on subsequent breeders. Finally, I characterise the factors governing

winter sociality between juveniles during vagrancy and identify kin structure in the winter population.

Authors' contributions:

Main contributors

Ada M. Grabowska-Zhang. Collected two years of logger data; conceived, analysed and wrote first drafts of each manuscript; corrected subsequent drafts and submitted manuscripts to journals.

Ben C. Sheldon. Provided overall guidance in research techniques, advice on statistical approaches, analysis methods and writing; gave detailed comments on all drafts.

Camilla A. Hinde. Provided co-supervision in the last two years of my DPhil project; co-author in Chapter 3 and 4; provided advice on writing and statistical approaches; gave detailed comments on subsequent drafts of Chapter 2, and first and subsequent versions of all other drafts.

Teddy A. Wilkin. Set up logger locations and collected two years of logger data; provided co-supervision in the first two years of my DPhil project; provided GIS data for spatial analyses; co-author in Chapter 2.

Additional contributors

Colin Garroway. Co-author in Chapter 5. ; provided advice and statistical input into randomisation techniques in Chapter 5; commented on drafts of Chapter 5.

The EGI. Collected great tit life-history data over the past 60 years.

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Chapter 2

Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*)

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Supplementary material can be found in Appendix A.

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Original Article

Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*)

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Social interactions can often affect the fitness of individuals. Territorial animals frequently interact with their neighbors, and long-term familiarity might lead to the development of cooperative relationships, which might influence the fitness of neighboring individuals. Here we test the hypothesis that familiarity with neighbors positively affects reproductive success in the great tit (*Parus major*). We used data from a 41 year long-term study of the great tit to quantify neighbor familiarity and its relationship with different stages in the great tit reproductive cycle. Breeding birds had from 0 to 11 neighbors with whom they were familiar by sharing a territory boundary the year before; although owing to low annual survival, the mean proportion of familiar neighbors (0.1) was quite small. Despite the low average proportion of familiar neighbors, we found evidence suggesting positive effects of increased familiarity: females with more familiar individuals in their neighborhood laid larger clutches. We also found that both males and females with more familiar neighbors had a greater chance of successfully fledging offspring. These results suggest that long-term familiarity can benefit territorial breeding birds. Future work is needed to address the underlying mechanisms of how neighbor familiarity influences individual fitness. *Key words:* familiarity, *Parus major*, reproductive success, sociality, territorial neighbors. *[Behav Ecol]*

INTRODUCTION

In many organisms, individuals retain a relatively stable home range or territory over the long term. Benefits of territory fidelity include the accumulation of information about the local habitat, available resources, and the presence of predators, for example, local familiarity improved territory acquisition in juvenile lizards (Stamps 1987), and territory relocation was shown to cause short-term costs in damselfish (McDougall and Kramer 2007). Birds have been shown, when displaced, to prefer to pay the costs of finding the way back to their home territory rather than to settle in an unfamiliar area (Pärt 1995). The importance of the territory to territorial species may depend not only on the characteristics of their habitat but also on the social context of the neighborhood. Territory defense is costly, and renegotiating the boundary with an unfamiliar newcomer tends to incur more cost than defending the territory against an established neighbor (Eason and Hannon 1994). Storing information about the competitive ability of territorial rivals and retaining stable social relationships may be an additional benefit of site fidelity observed in many species.

At a basic level of association, neighbor–stranger discrimination affects territorial interactions and underlies the dear enemy phenomenon (DEP). In the DEP, territorial individuals react less aggressively to neighboring than to distant territorial or vagrant individuals (Briefer et al. 2008; Brunton et al. 2008; Rosell et al. 2008; reviewed in Temeles 1994). In agreement with game-theoretic predictions, territorial individuals modulate their response to the relative threat posed by neighbors versus strangers (Jaeger 1981; Getty 1987; Temeles 1990; reviewed in Temeles 1994). In situations when a neighbor poses less threat to the defended resources (food, mates, and breeding sites), reacting less aggressively to those individuals is adaptive, as the resident will expend less energy on escalating territorial contests. Treating neighbors as dear enemies is not an invariant relationship and is dependent on the social context. For example, it has been shown that territorial male skylarks are dear enemies in the middle of the breeding season (when males with established territories did not pose a threat of territory overtake) but reverse their strategies early or late in the season, when territory boundaries are much more fluid (Briefer et al. 2008).

Familiarity can bring fitness benefits other than those resulting from diminished aggressive interactions. Repeated encounters between the same individuals aid the evolution of cooperative behaviors, such as reciprocity. Reciprocity is best known from tight-knit groups where repeated interactions allow a degree of protection against defectors (cheats) through strategies like tit for tat. The tit for tat strategy involves cooperation on the first encounter and then repeating the partner's previous move (Axelrod and Hamilton 1981). Recently, reciprocity has been suggested to occur in temporary territorial aggregations of a breeding passerine bird whereby breeding pairs of pied flycatchers (*Ficedula hypoleuca*) reciprocated by joining in a predator mob at the nest of previously cooperating pair but not in a mob at the nest of defectors (Krams et al. 2008). This widely discussed experiment (Wheatcroft and Price 2008; Russell and Wright 2009; Wheatcroft and Krams 2009) suggests that reciprocity can operate in structured populations previously thought not to have stable enough associations for reciprocity to occur.

Previous studies of the consequences of familiarity between individuals have analyzed the effects of familiarity on a number of traits in a variety of species. Reported effects include higher social tolerance in male lizards (Aragon et al. 2007), faster growth rate in wild sea trout (*Salmo trutta*) (Hojesjo

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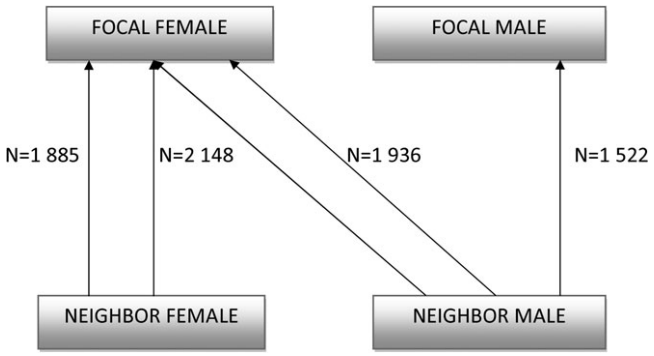


Figure 1
Summary of the investigated relationships between sexes of territorial neighbors. Few studied the influence on focal females of their female or male neighbors as well as neighbors irrespective of sex. Males were investigated for influence of their male neighbors. Numbers on arrows represent the number of focal individuals used in each data set.

et al. 1998) and juvenile salamanders (*Plethodon cinereus*) (Liebgold and Cabe 2008), and better survival and growth in the Arctic char (*Salvelinus alpinus*) (Seppa et al. 2001). Preference for familiar shoal-mates and its benefits have been widely studied in fish (Griffiths et al. 2004; Bhat and Magurran 2006; Lee-Jenkins and Godin 2010). However, most studies that have compared familiar and unfamiliar individuals focused on variables for which the fitness consequences have to be assumed: There has been rather little empirical work on direct fitness consequences of familiarity. The only reported effects were the positive influence of familiar neighbors on reproductive performance in male red-winged blackbirds (Beletsky and Orians 1989), but no effect was found in the females of the same species (Weatherhead 1995). Familiarity had no effect on the reproductive success of translocated New Zealand robins (*Petroica australis longipes*) (Armstrong 1995) or North Island saddlebacks (*Philesturnus carunculatus rufusater*) (Armstrong and Craig 1995); although, in these studies, small sample sizes might have limited the power to detect any effects.

The great tit (*Parus major*) is a small passerine bird common in European broad-leaved forests (Perrins 1979). It is a secondary cavity nester, choosing holes in old trees, and stumps as nesting sites but preferentially accepts nest-boxes as breeding sites in our study population (Perrins 1965). Males defend multipurpose territories on which they feed, mate, and rear young. The amount of time spent defending the territory depends on how often the male is contested by other males (Slagsvold et al. 1994). Previous work on this species reveals that once they have settled in a breeding territory, adults show very limited breeding dispersal in subsequent years (Harvey et al. 1979); hence, there is the potential for long-term familiarity to arise between neighboring individuals. Familiarity with males from neighboring territories could benefit the defender, as familiar males are more likely to have prior information about each other's condition and are therefore less likely to challenge each other or escalate in territorial display. Both parents participate in chick rearing, but it remains untested whether social environment affects their success as breeders.

The aim of this study was to explore hypotheses about familiarity with neighbors and its effect on reproductive performance in great tits. The 2 sexes are likely to be affected differently or to a different degree by the presence of familiar individuals in the neighborhood. Familiarity can be defined in a variety of ways. We use a measure of familiarity with individuals from surrounding territories to assess its effect on different measures of reproductive success, from the onset of breeding to the recruitment success of the reproductive event. Defining familiar neighbors as individuals that shared a territory boundary in the previous year is a straightforward measure, and one for which there is a large quantity of data available. We use the number of familiar neighbors and a simpler, one-dimensional binary variable, the familiarity status of the nearest neighbor, with familiarity defined in the same way.

MATERIALS AND METHODS

Study population

The analysis was performed on data from a great tit population in Wytham Woods, Oxfordshire. The site is described in more detail by Wilkin (2006). This piece of continuous woodland has over 1000 nest-boxes that have been kept at fixed localities throughout the study period. Breeding events from 1965 to 2005 were used in this study. Life-history traits (date of laying the first egg [laying date, where 1 = April 1], clutch size, fledging success, fledgling mass, and number of offspring recruited to the local breeding population) were recorded for all breeding attempts using a field protocol standardized throughout the study. Details of the methods have been described by Perrins (1965); the major sources of variation in these life-history traits are described by McCleery et al. (2004) and Browne et al. (2007). The identities of breeding individuals were established from British Trust for Ornithology rings by trapping adult birds in the nest-box. All fledglings born in Wytham are ringed in the nest-box, and the immigration status (resident or immigrant) of the breeder can be established from the ring. Immigration status of the breeding female has a documented

Table 1
Variable abbreviations used in global model formula

Response variables	Covariates	Parameter symbols
LD—laying date	AC—spatial autocorrelation covariate	β_0—intercept
CS—clutch size	ALT—altitude	β_w—within-individual component of variance
FM—mean fledgling mass	DIS—distance moved from previous year	β_b—between-individual component of variance
NS—nest success	EDG—distance from the woodland edge	u_0—random intercept
RS—number of recruits	FAM—number of familiar neighbors	u_1—random slope
	FS—female status, resident or immigrant	$\varepsilon_{(Gaussian)}$—error term$_{(distribution)}$
	NN—familiarity with the nearest neighbor	
	TER—territory size	
	WRM—the sum of maximum daily temperatures from 1st to 25th April	
	ID—breeder identity	
	YEAR—year	

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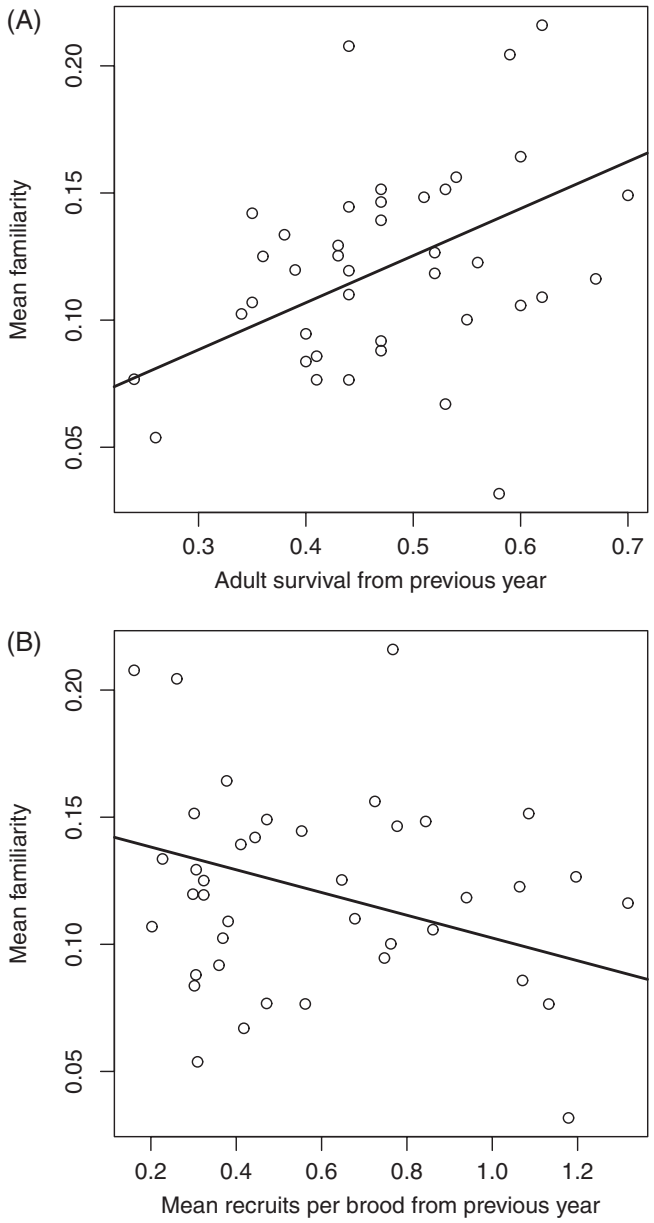


Figure 2
Effects of annual variation in demographic variables on mean proportion of familiar neighbors in great tits using model averaging; (A) adult survival from previous year and (B) mean number of recruits per brood from previous year.

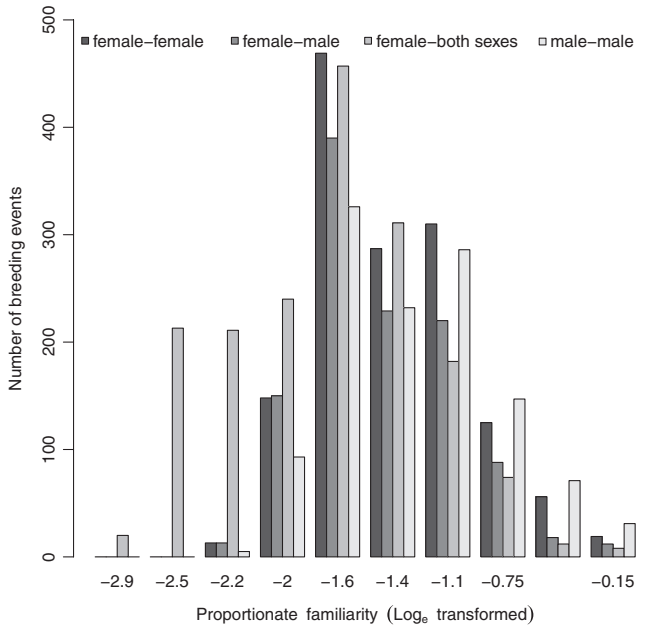


Figure 3
The distribution of proportionate familiarity across data sets of 4 focal breeder-neighbor combinations (log$_e$ transformed).

effect on life-history traits (McCleery et al. 2004; Bouwhuis et al. 2010). Recruitment success was measured as the number of young recruited to the Wytham population (Perrins and McCleery 1985); local recruitment only reflects fitness if natal emigration is independent of the state of individuals, which, as far as we are aware, is the case in our population (Verhulst et al. 1997; Bouwhuis et al. 2009). Distance moved between breeding attempts by adults (breeding dispersal), although usually shorter than the width of a territory (Harvey et al. 1979), was also recorded due to its potential to decrease the familiarity with surrounding individuals.

Environmental variables

We included a number of environmental variables as covariates based on previous work in this population. The effect of territory size on reproduction was described by Wilkin et al. (2006). The measure of spring temperature in each year was recorded as warmth sum (after McCleery and Perrins 1998), which is the sum of maximum day temperatures from 1 March to 25 April. This measure was included as it is known to influence the timing of breeding through changes in food abundance. Altitude, as well as distance to forest edge, was previously shown to affect reproductive traits (Wilkin, Perrins, et al. 2007), as it affects plant phenology and the timing of food supply.

Territory boundaries

Nest-boxes occupied by great tits each year were mapped using Map Info Professional 8.5, using methods described in Wilkin et al. (2006). Breeding territory boundaries were estimated by Dirichlet tessellation, which constructs a polygon that contains all points that are closer to the focal reference point (nest-box) than to any other reference point, with edges equidistant to closest neighboring points. This measure of territory size assumes the use of all available space between the nest-boxes. Although this may be true for small territories, larger ones may contain space that is not frequently used by breeders. Consequently, breeders may have fewer interactions with neighbors on large territories, as there will be unused space between areas most frequented by territory holders. We acknowledge that this method provides a very simple model of space use, but it has the advantage that it is objective and can be applied at a large scale and can thus be applied retrospectively over large sample sizes. Previous work using this measure on this population has shown that it generates estimates of local population density, which are related in the expected way to a range of life-history traits, and that the measure is comparable to territories mapped from observation (Wilkin et al. 2006).

Identities of the focal individuals breeding at a particular nest-box and their first-order neighbors were analyzed from year to year to establish previous year territory holders. The resulting database contained reproductive attempts from 1965 to 2005, each row containing a focal and neighbor territory pair of

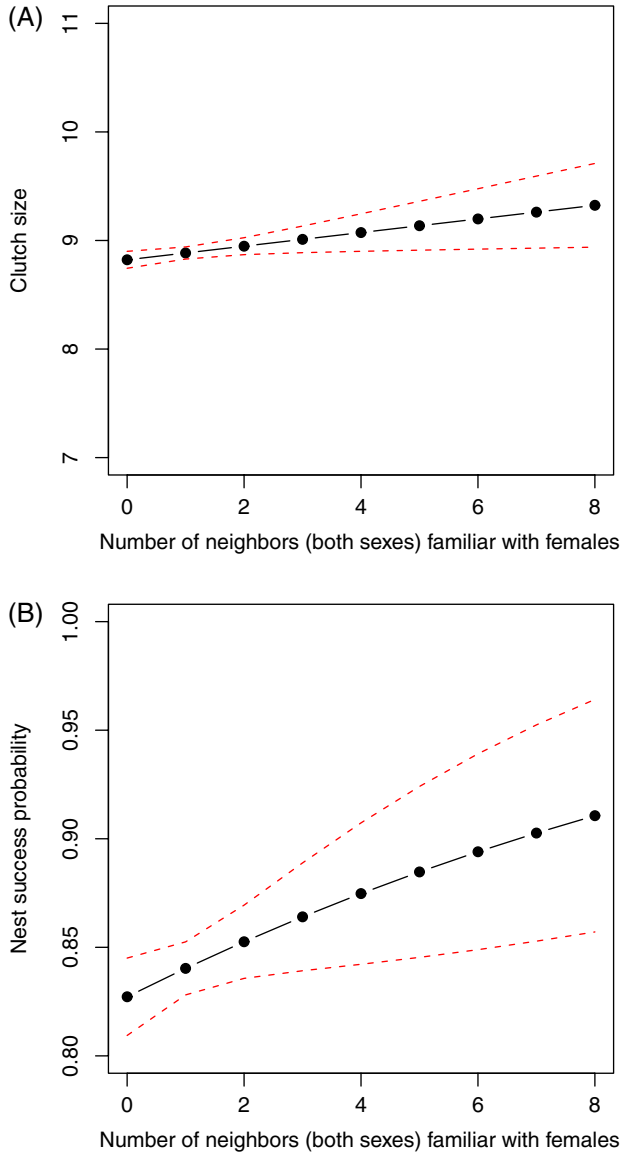


Figure 4
The effect of between-individual variation in familiarity with neighbors of either sex on (A) clutch size and (B) nest success probability. *x* axis contains the entire range of values of familiar neighbors; *y* axis contains ±1 standard deviation variation in clutch size. The figure was derived from the averaged model.

breeders. Familiar neighbors were defined as individuals that shared a territory boundary with the focal bird in the previous year. Identities of breeders were matched to territories, and the database was queried to extract those neighbors in year t that were also neighbors to the focal individual in year $t - 1$.

Data selection

The analysis was performed on birds breeding for the second or subsequent time, as it is clearly impossible for first time breeders to have neighbors familiar from the previous breeding season, in this context. Four classes of neighbors were analyzed in this study. They are summarized in Figure 1. First, the female neighbors of the focal female were assessed for familiarity, that is, a shared territory boundary in the previous year. The same procedure was performed for male neighbors of the focal female. Next, neighbors of either sex of the focal female were analyzed. We also performed the same analysis of the effects of male–male familiarity. We counted the number of familiar individuals surrounding the territory and assessed the familiarity status of the nearest neighbor for each of those categories of breeders.

The data set comprised different numbers of breeding events and individuals for different analyses, as both identity of the focal individual and the neighbor had to be known. Any breeding attempts in which the identity of the focal individual was not known were also excluded from the analysis. The reason for this was that in such cases, it is impossible to determine an individual's social environment, and data on phenotypic characteristics are unavailable. In cases where some of the focal or previous-year neighbors remained unidentified, focal year neighbors might have been wrongly assigned unfamiliar status, which renders our analysis conservative, that is, we might assign familiar neighbor as unfamiliar but not the other way round. Cases that include unidentified neighbors when the focal identity was known amounted to up to 14% of all investigated neighbor pairs. Some individuals appear in the data set more than once, and breeder identity was therefore used as a random factor in our analyses to account for multiple breeding attempts by the same individuals across years. Across data sets, between 945 and 1297(59–63%) individuals appear once, 390–570 (about 25%) appear twice, and 187–356 (23–26%) individuals appear in the data set more than twice. We used within-subject centering (van de Pol and Wright 2009) to separate the variation in familiarity into between-individual and within-individual components, as they generate 2 different hypotheses; the former relates to inherent differences between individuals (variation in the population) and the latter indicates differential responses in the same individual (phenotypic plasticity). Individuals appear in the data set as focal breeders and are also included in the count of neighbors in data points where their neighbors appear as focals. This reappearance of individuals in 2 contexts in the data set does not affect the analysis; removal of a random subset of repeating pairs does not change the result.

Different classes of individuals may be familiar in different contexts; for example, first-year individuals cannot be familiar for as long as older individuals. Our measure provides a simple way of ensuring all measured individuals have the same scope for familiarity between years. All investigated individuals needed to have bred in the population at least 2 years in a row, which excludes first-year individuals and first-time immigrants to the population. The primary interest was to establish whether individuals with long-term neighbors differ in their reproductive performance from those without familiar neighbors. We divided the reproductive attempt into measures derived at 5 sequential stages, so that measures of reproductive performance included in the analyses are 1) egg-laying date, 2) clutch size, 3) mean fledgling mass, 4) fledging success, and 5) recruitment success. We analyzed fledging success as a binomial measure of whether the nest produced at least one fledgling or failed before the young fledged.

Males who have stable neighbors are expected to positively influence offspring traits, such as fledgling mass and recruitment success, whereas female familiarity with neighbors may also affect the sex-specific traits of laying date and clutch size. If the effect on laying date is negative, it suggests familiarity benefits the females, as selection strongly favors early laying in the majority of years in this population (Charmantier et al. 2008). A female's long-term familiarity with neighbors might affect her reproductive decisions based on her perception of local density or competitor quality, leading to effects on laying date or clutch size or both.

Statistical methods

We used an information theoretic approach with corrected Akaike's information criterion (AIC_C) to first explore the

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Table 2
Averaged models examining the correlates of reproductive success in focal females

Response: LD	Estimate†	Variance	SE	Unconditional SE	Lower CI	Upper CI	Relative importance
(Intercept)	27.1	1.01	1	1	25.2	29.1	
FS	−1.26	0.00502	0.266	0.266	−1.78	−0.741	1
ALT	1.24	0.00469	0.262	0.262	0.723	1.75	1
DIS	1.35	0.00438	0.257	0.257	0.843	1.85	1
FAM_W	0.258	0.00388	0.25	0.25	−0.231	0.747	0.28
Response: CS							
(Intercept)	−3.8	9.23	1.74	na	−7.22	−0.385	na
AC	1.44	0.0016	0.198	na	1.05	1.83	na
FAM_B	0.176	0	0.062	na	0.0543	0.297	na
LD	−0.745	0	0.0677	na	−0.877	−0.612	na
Response: FM							
(Intercept)	15.3	0.0867	0.543	0.543	14.3	16.4	
ALT	−0.865	0.00299	0.234	0.234	−1.32	−0.406	1
CS	1.11	0.00285	0.231	0.231	0.661	1.57	1
FAM_B	0.357	0.00252	0.224	0.224	−0.0822	0.797	0.38
LD	−0.419	0.00576	0.275	0.276	−0.959	0.122	0.37
NN_B[a]	0.271	0.0024	0.221	0.221	−0.163	0.705	0.12
TER	0.715	0.00333	0.24	0.24	0.244	1.19	1
Response: NS							
(Intercept)	2.78	12.1	1.35	1.35	0.138	5.43	
AC	−3.42	168	3.6	3.6	−10.5	3.64	0.22
ALT	−0.408	0.0003	0.125	0.126	−0.654	−0.162	1
CS	0.724	0.0002	0.115	0.115	0.498	0.949	1
FAM_B	0.177	0.0002	0.122	0.122	−0.0618	0.417	0.49
FAM_W	0.0345	0.0001	0.108	0.108	−0.178	0.247	0.06
LD	−0.106	0.0003	0.129	0.129	−0.359	0.148	0.20
NN_B[a]	0.147	0.0002	0.124	0.124	−0.096	0.391	0.31
NN_W[a]	−0.0288	0.0001	0.107	0.107	−0.239	0.181	0.06
TER	0.264	0.0002	0.12	0.12	0.0288	0.5	1
Response: RS							
(Intercept)	−0.615	0.0001	0.102	0.102	−0.814	−0.415	
CS	0.405	0.0000	0.0562	0.0562	0.295	0.515	1
FAM_B	0.0588	0.0000	0.0574	0.0575	−0.0538	0.171	0.28
FM	1.56	0.0001	0.0931	0.0932	1.38	1.74	1
LD	−0.389	0.0000	0.0704	0.0705	−0.527	−0.251	1
NN_B[a]	0.127	0.0000	0.0533	0.0533	0.0222	0.231	1
NN_W[a]	−0.0344	0.0000	0.0344	0.0344	−0.102	0.033	0.27
TER	0.18	0.0000	0.0498	0.0498	0.0826	0.278	1

Variable abbreviations in all tables: LD, laying date; CS, clutch size; FM, mean fledgling mass; RS, number of recruits; FS, female status, resident or immigrant; AC, spatial autocorrelation covariate; ALT, altitude; DIS, distance moved from previous year; FAM_B, between-individual component of the number of familiar neighbors; FAM_W, within-individual component of the number of familiar neighbors; NN_B, between-individual component of familiarity with the nearest neighbor; NN_W, within-individual component of familiarity with the nearest neighbor; EDG, distance from the edge of the forest; TER, territory size; RS, number of recruits; WRM, warmth sum, the sum of maximum daily temperatures from 1st to 25th April; †, estimates have been standardized to 2 standard deviations (Gelman 2008), with the exception of AC variable, estimates of which cannot be directly compared with other parameters within the models. The variables of interest are the number of familiar neighbors of either sex and the familiarity status of the nearest neighbor of either sex. SE, standard error; CI, confidence interval; na, not applicable.

[a] Unfamiliar as the reference category.

predictors of familiarity at the population level and then to generate hypotheses about the effects of familiarity on measures of reproductive success. We used the MuMIn package (Bartoń 2010) in the R environment (R Development Core Team 2005) to perform all subset selection and model averaging based on AIC_C value. The input variables were standardized using the "arm" package (Gelman et al. 2010), so that parameter estimates can be easily and correctly interpreted (Gelman 2008). Models with $\Delta AIC_C \leq 2$ (i.e., for which there is no strong indication that one model has the best fit) were averaged to obtain parameter estimates. We used the natural average method, where parameters are averaged only across models they occur in. We used a single best model as our source of inference if the second best model had a value of $\Delta AIC_C \geq 2$.

In order to understand the behavior of familiarity as a variable, we performed model selection analysis in order to determine predictors of mean yearly familiarity in the population for the years used in the study. We explored the effects of demographic variables such as adult survival, recruitment, and population size on the annual levels of familiarity present in the population. Population size was estimated from nest-box occupancy rates, the proxy for recruitment rate was the number of recruits per brood, and survival rate was estimated from a capture-mark-recapture analysis, which controls for variation in resighting probability (Bouwhuis et al. forthcoming). Our global model was:

$$y = \beta_0 + \beta_1 \mathrm{SRV} + \beta_2 \mathrm{REC} + \beta_3 \mathrm{POP} + \varepsilon,$$

where y is average familiarity in a given year, SRV is adult survival, REC—recruitment as the average number of recruits per brood, and POP—population size. Error term ε was drawn from

Table 3
Averaged models examining the correlates of reproductive success in focal females

Response: LD	Estimate†	Variance	SE	Unconditional SE	Lower CI	Upper CI	Relative importance
(Intercept)	−1.63	2760	7.24	7.24	−15.8	12.6	
FS[a]	−1.37	0.0107	0.322	0.322	−2	−0.736	1
AC	1.08	0.007	0.288	0.289	0.513	1.64	1
ALT	0.638	0.0155	0.353	0.353	−0.0534	1.33	0.81
DIS	1.51	0.0102	0.318	0.318	0.886	2.13	1
FAM_B	−0.32	0.0119	0.331	0.331	−0.969	0.328	0.22
FAMw	0.522	0.0088	0.306	0.307	−0.0786	1.12	0.58
NN_B[b]	−0.472	0.01	0.316	0.316	−1.09	0.147	0.35
WRM	−11.7	2.22	1.22	1.22	−14.1	−9.3	1
Response: CS							
(Intercept)	−4.03	8.06	1.68	1.69	−7.33	−0.726	
AC	1.47	0.0014	0.192	0.192	1.09	1.85	1
FAM_B	0.217	0.0000	0.0673	0.0674	0.0848	0.349	1
LD	−0.723	0.0000	0.0746	0.0746	−0.87	−0.577	1
NNw[b]	0.111	0.0000	0.0493	0.0493	0.0145	0.208	0.36
Response: FM							
(Intercept)	7.66	5620	8.64	8.64	−9.27	24.6	
AC	0.769	0.0659	0.507	0.507	−0.225	1.76	0.64
ALT	−1.09	0.0036	0.245	0.245	−1.57	−0.606	1
CS	1.14	0.0036	0.244	0.244	0.661	1.62	1
FAM_B	0.636	0.0033	0.239	0.239	0.168	1.1	1
NN_B[b]	0.25	0.0031	0.236	0.236	−0.213	0.713	0.12
NNw[b]	0.328	0.0021	0.214	0.214	−0.0907	0.747	0.34
TER	0.773	0.0044	0.258	0.258	0.268	1.28	1
Response: NS							
(Intercept)	2.4	4.64	0.798	0.798	0.834	3.96	
AC	−2.86	305	4.18	4.18	−11.1	5.33	0.12
ALT	−0.484	0.0003	0.131	0.131	−0.741	−0.227	1
CS	0.738	0.0002	0.124	0.124	0.495	0.981	1
FAM_B	0.363	0.0003	0.136	0.136	0.095	0.63	1
FAMw	0.0628	0.0003	0.132	0.132	−0.196	0.322	0.11
LD	0.021	0.0004	0.142	0.142	−0.257	0.299	0.10
NN_B[b]	0.153	0.0004	0.143	0.143	−0.128	0.434	0.27
NNw[b]	0.13	0.0003	0.128	0.128	−0.122	0.382	0.26
TER	0.3	0.0003	0.132	0.132	0.041	0.559	1
Response: RS							
(Intercept)	−0.0294	0.0339	0.421	0.421	−0.855	0.797	
AC	−0.696	0.0153	0.352	0.352	−1.39	−0.00665	0.87
CS	0.415	0.0000	0.0636	0.0636	0.29	0.54	1
FAM_B	0.101	0.0000	0.0574	0.0574	−0.0117	0.213	0.80
FAMw	−0.0105	0.0000	0.0363	0.0364	−0.0817	0.0608	0.13
FM	1.62	0.0001	0.109	0.109	1.41	1.83	1
LD	−0.323	0.0000	0.0782	0.0782	−0.476	−0.17	1
NNw[b]	−0.0666	0.0000	0.037	0.037	−0.139	0.00604	0.81
TER	0.188	0.0000	0.0558	0.0558	0.0783	0.297	1

Models inspect the familiarity with male neighbors. The variables of interest are the number of familiar male neighbors and the familiarity status of the nearest male neighbor; abbreviations of variables as for Table 2. SE, standard error; CI, confidence interval; †, estimates have been standardized to 2 standard deviations (Gelman 2008), with the exception of AC variable, estimates of which cannot be directly compared with other parameters within the models.

[a] Immigrant as the reference category.

[b] Unfamiliar as the reference category.

a normal distribution. We also explored predictors of familiarity at the level of individual reproductive attempt. We looked for predictors of familiarity measured as the number of familiar neighbors (successes) and the number of unfamiliar neighbors (failures) in a model with binomial error structure. We examined the following global model with binomial error structure:

$$y_{\text{bin}} = \beta_0 + \beta_1\text{DIS} + \beta_2\text{EDG} + \beta_3\text{TER} + \beta_4\text{AGE} + \beta_5\text{ALT} + \beta_6\text{AC} + \varepsilon,$$

where DIS is the breeding dispersal distance, EDG is the distance between the nest-box and the woodland perimeter, TER is territory size, AGE is breeder age, ALT is altitude, and AC is a spatial autocovariate controlling for autocorrelation. Finally, we examined the effects of 2 measures of familiarity on different aspects of reproductive success. The measures adopted in all models are 1) the number of neighbors that also shared a territory boundary the year before and 2) the familiarity status of the nearest neighbor. Those 2 variables of interest measure the overall level of familiarity within a territory and the importance of being familiar with the closest territorial neighbor, respectively. All global models contain TER—a measure of territory size, to control for density effects. In order not to overparameterize our global models, we only included variables (for details, see Table 1) that have been documented to affect the dependent variable (as recommended by Burnham and Anderson

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Table 4
Averaged models examining the correlates of reproductive success in focal females

Response: LD	Estimate†	Variance	SE	Unconditional SE	Lower CI	Upper CI	Relative importance
(Intercept)	8.55	2440	7.03	7.03	−5.24	22.3	
AC	0.716	0.0061	0.279	0.279	0.169	1.26	1
FS[a]	−0.883	0.0092	0.309	0.309	−1.49	−0.277	0.98
ALT	1.05	0.0159	0.355	0.355	0.349	1.74	1
FAM_B	0.133	0.0118	0.33	0.33	−0.513	0.78	0.02
NN_B[b]	−0.483	0.0092	0.309	0.309	−1.09	0.123	1
Response: CS							
(Intercept)	−2.92	9.1500	1.74	1.74	−6.33	0.49	
AC	1.34	0.0015	0.197	0.197	0.952	1.73	1
LD	−0.695	0.0000	0.0679	0.0679	−0.828	−0.561	1
TER	0.141	0.0000	0.063	0.063	0.0179	0.265	0.42
Response: FM							
(Intercept)	17.3	287	3.49	3.49	10.5	24.2	
AC	−0.403	0.0116	0.328	0.328	−1.05	0.241	0.31
ALT	−0.871	0.0043	0.256	0.256	−1.37	−0.369	1
CS	1.24	0.0031	0.235	0.235	0.783	1.7	1
LD	−0.41	0.0061	0.279	0.279	−0.958	0.137	0.40
NN_B[b]	0.502	0.0032	0.238	0.238	0.036	0.968	0.79
NNw[b]	0.351	0.0016	0.201	0.201	−0.0424	0.744	0.43
TER	0.959	0.0039	0.249	0.249	0.47	1.45	1
Response: NS							
(Intercept)	11.4	132	3.39	3.39	4.74	18	
AC	−10.9	257	4	4	−18.8	−3.06	1
ALT	−0.532	0.0004	0.138	0.138	−0.803	−0.261	1
CS	0.828	0.0002	0.119	0.119	0.595	1.06	1
FAM_B	−0.15	0.0002	0.123	0.123	−0.39	0.0911	0.33
FAM_W	0.0438	0.0002	0.113	0.113	−0.177	0.265	0.10
LD	−0.0973	0.0003	0.132	0.132	−0.356	0.161	0.12
NN_B[b]	0.307	0.0003	0.129	0.129	0.0537	0.56	1
NNw[b]	0.199	0.0002	0.12	0.12	−0.0354	0.434	0.67
TER	0.451	0.0003	0.131	0.131	0.195	0.708	1
Response: RS							
(Intercept)	−0.571	0.0005	0.127	0.127	−0.82	−0.321	
AC	−0.0812	0.0079	0.298	0.298	−0.666	0.504	0.11
CS	0.433	0.0000	0.057	0.057	0.321	0.545	1
FAM_B	0.147	0.0000	0.0557	0.0558	0.0375	0.256	1
FAMw	0.0106	0.0000	0.0386	0.0386	−0.0651	0.0862	0.11
FM	1.58	0.0001	0.095	0.0951	1.39	1.76	1
LD	−0.369	0.0000	0.0709	0.071	−0.508	−0.23	1
NN_B[b]	0.0755	0.0000	0.0618	0.0619	−0.0458	0.197	0.34
NNw[b]	0.0659	0.0000	0.0362	0.0362	−0.00501	0.137	0.73
TER	0.167	0.0000	0.0499	0.05	0.0686	0.264	1

Models inspect the familiarity with female neighbors. The variables of interest are the number of familiar female neighbors and the familiarity status of the nearest female neighbor; abbreviations of variables as for Table 2. SE, standard error; CI, confidence interval; †, estimates have been standardized to 2 standard deviations (Gelman 2008), with the exception of AC variable, estimates of which cannot be directly compared with other parameters within the models.

[a] Immigrant as the reference category.

[b] Unfamiliar as the reference category.

2002). Global models used across all 4 data sets were performed in lme4 package (Bates and Maechler 2009):

$$y_{LD} = \beta_0 + \beta_B NN + \beta_W NN + \beta_B FAM + \beta_W FAM + \beta_2 ALT + \beta_3 TER + \beta_4 FS + \beta_5 DIS + \beta_6 AC + u_0 ID + u_0 YEAR + u_1 YEAR + \varepsilon_{(Gaussian)}$$

$$y_{CS} = \beta_0 + \beta_B NN + \beta_W NN + \beta_B FAM + \beta_W FAM + \beta_2 LD + \beta_3 TER + \beta_4 EDG + \beta_5 AC + u_0 ID + u_0 YEAR + u_1 YEAR + \varepsilon_{(Gaussian)}$$

$$y_{FM} = \beta_0 + \beta_B NN + \beta_W NN + \beta_B FAM + \beta_W FAM + \beta_2 LD + \beta_3 CS + \beta_4 TER + \beta_5 ALT + \beta_6 AC + u_0 ID + u_0 YEAR + u_1 YEAR + \varepsilon_{(Gaussian)}$$

$$y_{NS} = \beta_0 + \beta_B NN + \beta_W NN + \beta_B FAM + \beta_W FAM + \beta_2 LD + \beta_3 CS + \beta_4 TER + \beta_5 ALT + \beta_6 AC + u_0 ID + u_0 YEAR + u_1 YEAR + \varepsilon_{(binomial)}$$

Table 5

Averaged models examining the correlates of reproductive success in focal males

Response: LD	Estimate†	Variance	SE	Unconditional SE	Lower CI	Upper CI	Relative importance
(Intercept)	8.35	670	5.09	5.09	−1.62	18.3	
FS[a]	−0.735	0.0114	0.327	0.327	−1.38	−0.0941	1
AC	0.675	0.0018	0.206	0.207	0.27	1.08	1
ALT	1.39	0.015	0.35	0.35	0.701	2.07	1
FAM_B	−0.231	0.0113	0.326	0.326	−0.871	0.408	0.14
FAM_W	−0.339	0.0103	0.318	0.318	−0.963	0.286	0.19
NN_W[b]	−0.225	0.0102	0.317	0.318	−0.848	0.398	0.14
TER	−0.237	0.0164	0.358	0.358	−0.938	0.464	0.15
WRM	−11.4	2.1	1.2	1.21	−13.8	−9.03	1
Response: CS							
(Intercept)	−4.84	26.6	2.27	2.27	−9.29	−0.389	
AC	1.55	0.0043	0.256	0.256	1.05	2.05	1
LD	−0.583	0.0000	0.0797	0.0798	−0.739	−0.426	1
TER	0.137	0.0000	0.0688	0.0688	0.00249	0.272	0.31
Responce: FM							
(Intercept)	−1.81	235	3.91	3.91	−9.47	5.85	
AC	1.1	0.0027	0.228	0.228	0.651	1.54	1
ALT	−0.318	0.0025	0.224	0.224	−0.756	0.121	0.36
TER	0.323	0.0029	0.231	0.231	−0.13	0.776	0.36
Response: NS							
(Intercept)	−10.2	176	3.64	3.64	−17.3	−3.06	
AC	14.4	253	3.99	3.99	6.56	22.2	1
ALT	−0.227	0.0011	0.183	0.183	−0.586	0.131	0.25
CS	0.359	0.0011	0.181	0.182	0.00304	0.715	0.91
FAM_B	0.0885	0.0013	0.189	0.189	−0.283	0.46	0.08
FAM_W	0.0674	0.0009	0.171	0.171	−0.269	0.403	0.08
LD	0.207	0.0018	0.205	0.205	−0.194	0.608	0.22
NN_B[b]	−0.0859	0.001	0.179	0.179	−0.436	0.265	0.08
NN_W[b]	0.0848	0.0007	0.165	0.165	−0.239	0.409	0.09
Response: RS							
(Intercept)	−0.261	0.0001	0.103	0.103	−0.463	−0.059	
CS	0.31	0.0000	0.062	0.062	0.188	0.431	1
FAM_B	0.0897	0.0000	0.0617	0.0617	−0.0313	0.211	0.54
FAM_W	0.0437	0.0000	0.0436	0.0436	−0.0417	0.129	0.36
FM	0.97	0.0001	0.0896	0.0897	0.794	1.15	1
LD	−0.407	0.0000	0.0783	0.0783	−0.561	−0.254	1
NN_B[b]	−0.0382	0.0000	0.0672	0.0673	−0.17	0.0936	0.07
NN_W[b]	−0.0557	0.0000	0.0408	0.0408	−0.136	0.0242	0.46
TER	0.211	0.0000	0.0541	0.0542	0.105	0.317	1

Models inspect the familiarity with male neighbors. The variables of interest are the number of familiar male neighbors, and the familiarity status of the nearest male neighbor. SE, standard error; CI, confidence interval. Abbreviations of variables as for Table 2; †, estimates have been standardized to 2 standard deviations (Gelman 2008), with the exception of AC variable, estimates of which cannot be directly compared with other parameters within the models.

[a] Immigrant as the reference category.

[b] Unfamiliar as the reference category.

$$y_{NS} = \beta_0 + \beta_B NN + \beta_W NN + \beta_B FAM + \beta_W FAM + \beta_2 LD + \beta_3 CS + \beta_4 FM + \beta_5 TER + \beta_6 AC + u_0 ID + u_0 YEAR + u_1 YEAR + \varepsilon_{(poisson)}.$$

We fitted random intercepts in our models (as recommended by Grueber et al. 2011); a random slope was fitted to year. Summary of random effects for global models can be found in Supplementary Table 1. In order to statistically eliminate any spatial autocorrelation that may be present in our models, we included an autocorrelation variable as a fixed covariate in all our global models, as recommended by Dormann et al. (2007). The covariate was calculated with autocov_dist function in spdep package (Bivand et al. 2010).

RESULTS

Characterizing familiarity

Mean familiarity varied across years. The mean ratio of the number of familiar to the total number of neighbors varied from 0.03 to 0.22 (median = 0.12, interquartile range [IQR] = 0.009–0.15). Model selection with AIC_C resulted in the following best model:

$$y = \beta_0 + \beta_1 SRV + \beta_2 REC + \varepsilon.$$

The second best model had $\Delta AIC_C = 2.24$ (for details of model selection, see Supplementary Material). Adult survival and recruitment had the expected effects on familiarity, positive, and negative, respectively (Supplementary Table 3), such that familiarity was higher in years when a larger proportion of adults had survived from the previous year and lower following high rates of juvenile recruitment. The effects

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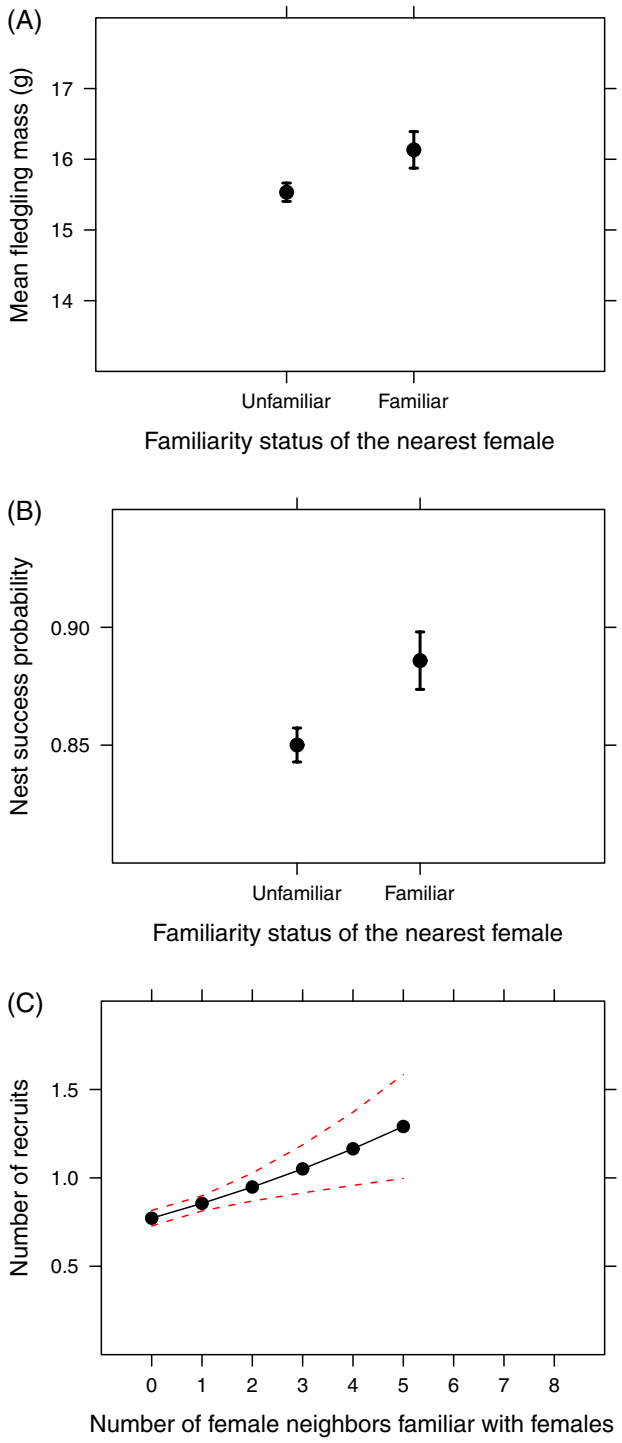


Figure 5
The between-individual effect of nearest female neighbor familiarity on female reproductive traits. (A) Mean fledgling mass. (B) Probability of nest success. (C) The effects of the number of familiar female neighbors on the number of recruits. Effects are predictions from averaged models.

in the table are standardized to 2 standard deviations and are therefore on a comparable scale. Untransformed slopes are visualized in Figure 2. We further aimed to identify the correlates of familiarity in the individual's environment to be aware of their effects in further analysis. Across data sets, territory size had a negative effect on familiarity (for details, see Supplementary Tables 4–7). Distance moved between years was negatively correlated with familiarity level of focal females but not focal males. Distance from the forest edge was positively correlated with familiarity of females but was not an important predictor for focal males.

Neighboring individuals

For females, the total number of female neighbors ranged from 1 to 12, with median of 5 neighbors (IQR = 4–6). The number of familiar female neighbors was between 0 and 5, with median of 0 (IQR = 0–1). Females had from 1 to 12 male neighbors (median = 5, IQR = 4–6) and from none to 5 familiar male neighbors (median = 0, IQR = 0–1). Females' neighbors of both sexes ranged from 2 to 24 (median = 10, IQR = 8–12) and from none to 8 were familiar (median = 0, IQR = 0–2). Males had from 1 to 11 male neighbors (median = 5, IQR = 4–6) and none to 5 familiar male neighbors, with median of 1 (IQR = 0–1). Hence, although the majority of neighbors in any single year were unfamiliar, there is considerable spread in the proportion of prior familiarity among breeding neighbors (Figure 3). Distributions of the number of familiar neighbors as well as the total number of neighbors in a territory were similar for all analyses. The total number of neighbors did not differ between males and females (two-sample *t*-test: $t = -1.12$; $P = 0.262$), but females had on average 0.18 familiar neighbors fewer than males ($t = 7.25$; $P < 0.001$); this is expected given slightly higher rates of breeding dispersal in female great tits compared with males (Harvey et al. 1979).

Familiarity and reproductive success

Our results show positive between-individual effect of the number of familiar neighbors on clutch size for focal females with familiar neighbors of both sexes and a positive within- and between-individual effect for focal females with familiar male neighbors (Figures 4A and 6A, respectively). In both of those cases, the confidence interval did not contain zero, indicating that number of familiar neighbors is a useful predictor of clutch size (Tables 2 and 3, respectively). Our measures of familiarity did not appear in the set of top models for this variable for female neighbors of females and male neighbors of male (Tables 4 and 5, respectively).

The between-individual component of familiarity (with nearest neighbor for female–female data set and number for other data sets) improved the nest success probability (Figure 5B). The direction of the effect was consistently in the direction such that the benefit of familiarity for producing a successful brood, but for female–both sexes (Table 2) and male–male (Table 5) data sets the confidence intervals included zero. There was a positive between-individual effect of nearest neighbor familiarity for female–both sexes data set. Within-individual effects contained 0 in their confidence intervals, except for female–male neighbors data set, where there was a within-individual positive effect on clutch size.

Familiarity with the nearest female neighbor was also associated with the focal female fledging heavier young (Figure 5A). Nearest neighbor familiarity was more informative than the number of familiar neighbors for fledgling mass and nest success in this data set, whereas number of familiar neighbors had an effect on the number of recruits. Confidence intervals of our estimates did not include 0.

Familiarity was not a useful predictor of laying date in any of the data sets or average fledgling mass for female–both sexes and male–male data sets (Tables 2 and 5, respectively), however, between-individual variation in number of familiar neighbors had a positive effect on fledgling mass for female–male data set (Figure 6C).

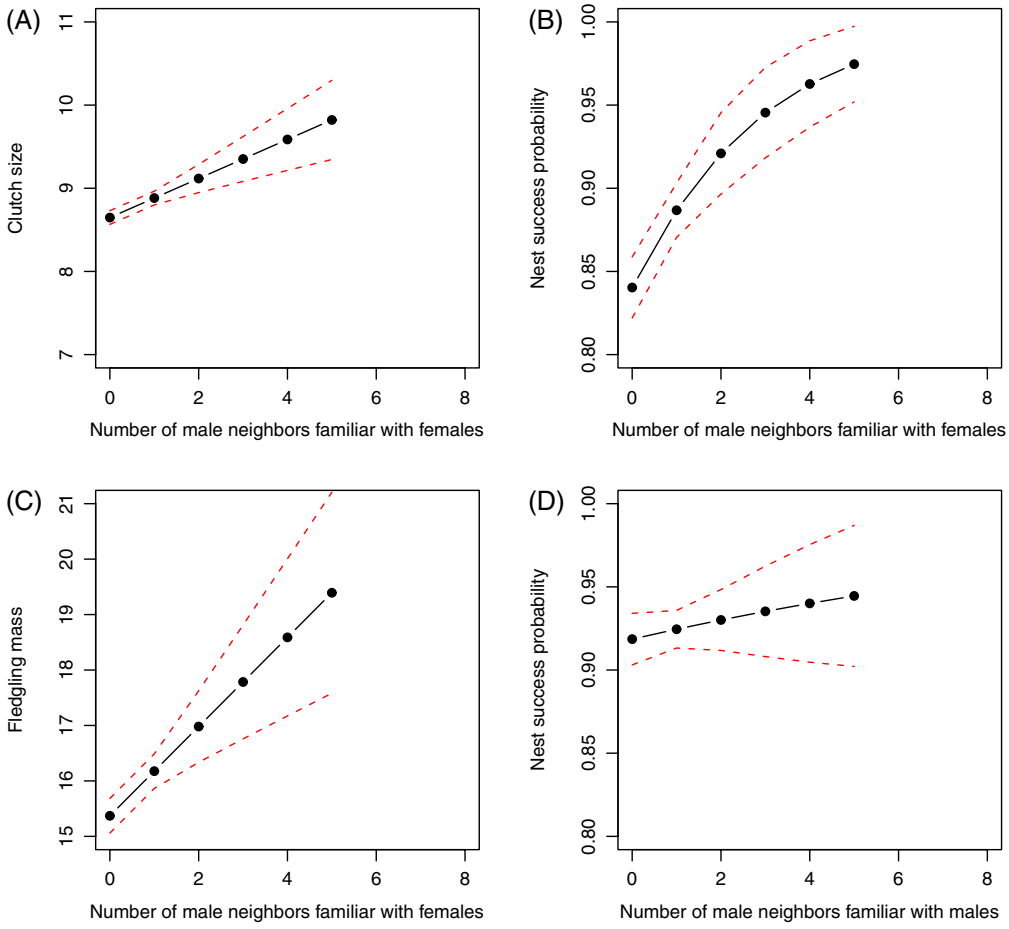


Figure 6
The between-individual effect of the number of familiar neighbors on (A) clutch size of females with familiar male neighbors, (B) probability of nest success (females with familiar male neighbors), (C) mean fledgling mass (females with familiar male neighbors), and (D) nest success probability for males with familiar male neighbors (note confidence interval includes 0 here).

These analyses suggest that there are effects of neighbor familiarity on reproductive success but that these occur predominantly at the between-individual level rather than the within-individual level.

DISCUSSION

We characterized long-term familiarity between breeding great tits and used this to explore hypotheses about the effects of familiarity between territorial neighbors on reproductive success. We found that females with a larger number of familiar neighbors laid larger clutches and that for both sexes of breeders, the probability of breeding successfully was higher when surrounded by more familiar individuals or if the nearest neighbor was familiar.

In our characterization of interannual variation in familiarity, we found the expected effect of annual variation in adult survival rate (positive) and recruitment success (negative), which suggests that our measure of individual familiarity captures real differences in the extent to which long-term associations could arise. Adult survival had a positive effect on mean familiarity independent of juvenile recruitment and population size, which is captured in a multiple regression analysis. There was a small but significant difference in the mean number of familiar neighbors between sexes, with females having fewer familiar neighbors than males. This is likely to be due to the fact that males defend territories and are less likely to disperse if they are territory owners (Harvey et al. 1979). Few great tits disperse from year to year, and dispersal distance is short (mean = 66.1 m, IQR = 27.7–121.5 m for females; median = 51.4, IQR = 0–87.8 m for males); in many cases, these dispersal distances are insufficient to move to a different group of neighboring individuals. However, there was evidence that breeding dispersal distance, territory size, and distance from edge influenced the level of individual familiarity. Breeding dispersal between years had the expected negative effect on familiarity, although territory size had a negative effect on familiarity. Larger territories may themselves result from subdominant first-year breeders settling in the vicinity and may result in both the focal male being able to defend a larger area and a decreased familiarity level. Distance of the focal nest-box from the edge of the wood had a positive effect on familiarity, which may be caused by immigrants from outside the population settling to breed closer to the edge (Wilkin, Garant, et al. 2007), thereby decreasing the chance of an adult breeder having neighbors familiar from the previous year.

Our results show that familiarity with neighbors is related to increases in some, although not all, aspects of the reproductive success of great tits. It also suggests that familiarity with neighbors mostly benefits the female at that stage, as it has been shown previously that traits like clutch size are predominantly controlled by the female of the breeding pair (Browne et al. 2007). The female decision to lay a larger clutch is unlikely to be influenced by altered territorial behavior between her partner and neighboring males, as her mate's familiarity with neighboring males showed no effect on clutch size (Table 5). The fact that the familiarity of the nearest neighbor, rather that familiarity among all neighbors, was more informative for the female neighbor data set (Table 4) may reflect differences

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in social relationships or habitat use between the sexes. It is possible that females do not venture to the edges of their territory as much as males, as they do not routinely defend the territory, and therefore may have far fewer interactions with neighbors occupying more distant nest-boxes compared with the nearest neighbor.

We separated the effect of familiarity in our analysis, into between- and within-individual effects, and found that in general, there is more evidence for an effect of familiarity at the between-individual level than within individuals. This suggests that the effect of familiarity is due to different individuals reacting differently to their social environment. The within-individual effect, while suggesting effects in the same direction, in most cases, overlapped 0 in its confidence interval (but see clutch size analysis in Table 3). However, due to the fact that only a small proportion of individuals appear in the data more than once and hence that there are few individuals for which within-subject effects could be estimated, it is likely that our analysis lacks the power to identify different responses within individuals across years (Martin et al. 2011), and hence, most of the effect is attributed to the between-individual term. The between-individual analysis might suggest that spatial effects on productivity drive an association, if individuals were to remain resident for longer in areas where they had been more successful. For example, Doligez et al. (2002) showed experimentally that birds use public information in breeding habitat selection and base their decisions about emigrating from a habitat patch on the perceived local reproductive success. However, because we fitted terms for spatial autocorrelation in the models and the familiarity effects is robust to their inclusion, we suspect that habitat-driven effect is not the case in our study. One alternative is that individuals differ in their propensity to form stable long-term relationships. Variation in behavioral traits such as exploration behavior or problem solving ability (e.g., Quinn et al. 2009; Cole et al. 2011) is well documented for this species. It is possible that similar variability exists for social behaviors.

We identified a positive effect of neighbor familiarity on the probability of nest success (Figures 5B and 6B,D). It has been shown that pied flycatchers engage in reciprocal predator mobbing with neighboring conspecifics (Krams et al. 2008). Long-term familiarity may increase the likelihood of such reciprocity as stable neighbors are less likely to defect, perhaps because they join in the mob sooner, and are therefore more likely to successfully deter a predator. Further in-depth, ideally experimental, study is needed to verify whether such mechanisms operate in the great tit.

Future investigation should focus on further aspects of familiarity in populations of territorial animals. Exploring the time scales on which individuals become familiar can bring insight into different social relationships. Juvenile birds do not have the scope for long-term familiarity and may form social bonds that are very dissimilar to those they would form as adult birds. Ultimately, we seek to identify the social contexts and relationships that affect individuals in different life stages and seasons.

CONCLUSIONS

Social context seems to be important for reproductive success in our study. Our results are in agreement with previous evidence that breeders respond to their social environment. Social factors are widely known to affect reproduction in group-living animals (Creel and Macdonald 1995). However, some solitary species (brown bears) have also been shown to be affected by social factors (Støen et al. 2006; Ordiz et al. 2008). Effects on breeders have also been recorded for territorial bank voles (Ylönen et al. 1990). The presence and direction of effects of social environment across taxa are likely to be a product of multiple factors, such as the species' ecology, mating system, levels of intraspecific competition, and behavior.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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Chapter 3

Long-term familiarity promotes joining in neighbour nest defence

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Long-term familiarity promotes joining in neighbour nest defence

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Familiarity plays an important role in the evolution of sociality and cooperation. Familiar individuals may gain a reputation for participating in, or defecting from, cooperative tasks. Previous research suggests that long-term familiarity with territorial neighbours benefits breeders. We tested the hypothesis that great tits (*Parus major*) are more likely to join in neighbours' nest defence if those neighbours are familiar from the previous year. We show that neighbours that shared a territory boundary the previous year are more likely to join their neighbours' nest defence than neighbours that did not share a boundary before. Closer neighbours did not differ from distant neighbours in their latency to join. For familiar neighbours that joined, there was no difference in call rate in relation to whether one or both members of the focal pair were familiar. First-time breeders (by definition unfamiliar) did not join each other's nest defence. This is the first evidence of a relationship between familiarity and joining in nest defence. Such direct benefits of familiarity may have important implications in the evolution of sociality.

Keywords: cooperation; nest defence; *Parus major*; familiarity; mobbing

1. INTRODUCTION

The social environment is important not only to group-living animals, but also to territorial species that are generally considered to have limited social interactions. Stable relationships with territorial neighbours are expected to lead to reduced aggression [1], and repeated interactions with the same individuals may aid the evolution of cooperation [2].

For many bird species, nest predation has a major impact on nesting success and hence, fitness [3,4]. Nest defence in passerine birds usually takes the form of predator mobbing. Mobbing involves an attack on a predator by prey individuals in order to drive it away. It is widespread among vertebrates, including fish, birds and mammals [5–7]. The more individuals participate in a mob, the higher the chance of deterring the predator [8,9]. Joint predator mobbing in territorial neighbours has been documented in passerine birds [10] including great tits [11].

Stable territorial relationships benefit breeders through reduced aggression between neighbours (known as the 'Dear Enemy Phenomenon' [12]). They may also benefit from undirected, mutually beneficial actions, such as alarm calls in response to predators [13]. There is some debate as to whether joint mobbing is driven by reciprocity [10,14], or by-product mutualism (*sensu* [15]). If it is driven by reciprocity, stable, long-term neighbours may benefit from reputations built up over repeated interactions. Great tits (*Parus major*) join group mobs in winter [16] and mob at nests of other pairs during breeding [11]. Recent findings suggest that long-term familiarity improves reproductive success in the great tit [17]. In this experiment, we tested the hypothesis that long-term familiarity between territorial neighbours is positively related to joining behaviour in predator mobbing. We then ask within the individuals that did join, how does distance affect latency to join and how does the degree of familiarity affect intensity of mobbing behaviour (call rate)?

2. MATERIAL AND METHODS

(a) *Field protocol*

The experiment took place in Wytham Woods, Oxfordshire between 12 and 27 May 2011. A population of great tits breeding in nest-boxes was monitored during the breeding season as in Perrins [18]. Breeder identities were determined when the young were 8–12-days old (hatching = day 1) from a previously fitted metal British Trust for Ornithology ring or electronic passive integrated transponder tag. Age was determined from plumage [19] as first year or older than 1 year. Trials were performed blind with respect to neighbour familiarity status to avoid researcher bias. This was achieved by assessing pairs of nests for familiarity of the breeders that were older than 1 year after the trials took place. Pairs of neighbouring nests consisted of three groups:

- *Familiar*. Adults were older than 1 year and at least one member from each nest had been neighbours in the previous year.
- *Unfamiliar*. Adults were older than 1 year, none of which had been neighbours in the previous year.
- *First year*. Adults were 1 year old and therefore were unfamiliar under our definition.

Trials were performed when nestlings were 17 days old (mean:16.5 days; s.e.: 0.245), or as close to 17 days as possible, if nest asynchrony posed a risk that one nest would fledge before the trial. First, the experimenter (A.M.G.-Z.) verified that nestlings were alive and had not fledged. The adults were then marked temporarily with non-toxic, acrylic paint in order to identify which nest-box they came from (adapted from Krams *et al.* [10]). The paint was applied to a piece of adhesive insulation foam placed inside the nest-box entrance, so that the birds would mark themselves when entering and leaving the nest-box. The birds exhibited little neophobia towards the marking foam, and feeding continued without interruption. Once marking on all birds was confirmed by observation, the trials took place. In the trials, the experimenter stood directly beneath the box, which hung from the tree 2–3 m above the ground. On approach, the experimenter noisily moved dead leaves on the ground with her feet, then scraped the bark of the tree with a wooden pole and, finally, scraped the pole against the woodcrete nest-box, a sound that often elicits alarm calls from parents during routine nest monitoring (A. M. Grabowska-Zhang, personal observation). The sequence of movements was designed to imitate the sounds of approach, interest in the nest and an attempt to enter the nest. Previous studies have shown a strong correlation between avian responses to humans and model predators [20]. Also, parent birds that respond strongly to humans suffer lower nest predation [21,22] and male great tits in our study population have a similar response to human observer together with chick distress call as they do to a model predator [23]. Great tits often mob humans when they ring chicks (A. M. Grabowska-Zhang, personal observation) or monitor the nest. The trial started when at least one of the parents at the focal nest started mobbing (this occurred in every trial), and lasted for 5 min. Mobbing in great tits involves emitting repeated alarm calls, pivoting on the perch, frequent hops between perches while approaching the predator and, sometimes, exaggerated flights. Mobbing by neighbours was recorded when the bird was heard (and subsequently seen) or seen and could be identified as belonging to the marked nest-box during observation.

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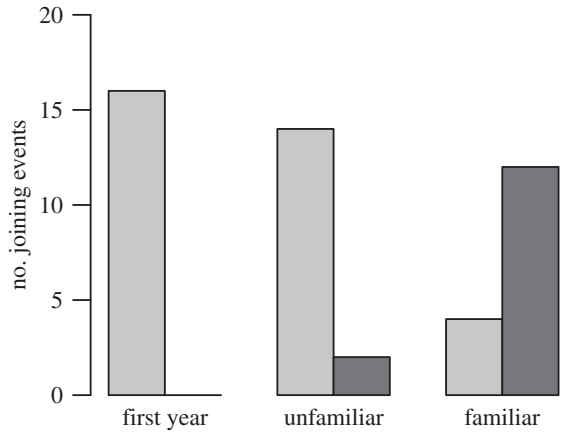


Figure 1. Outcomes of the trials. 'First year' refers to nests (eight pairs) where all adults were 1 year old breeders. 'Unfamiliar' nests (eight pairs) contained adults older than 1 year that had not been neighbours the year before. 'Familiar' nests (eight pairs) had adults older than 1 year and at least one member from each nest had been neighbours the year before. Light grey bars, did not join; dark grey bars, joined.

Latency to join and count of neighbour calls in the second minute after joining was recorded. The trial was repeated at the neighbouring nest after a period of about 1 h (mean: 63.8 min; s.e.: 2.3 min).

After the trials, distances between boxes were calculated from nest-box GPS coordinates using MapInfo v. 8.5 software. Breeding territories were estimated using Dirichlet tessellation, which has been shown to approximate measures obtained with mapped territories [24]. Territories of experimental birds were matched against their territories in 2010, to verify between-year familiarity through being neighbours.

(b) *Statistical methods*

We used R (v. 2.10.1) [25] for statistical analyses. We tested for differences between groups using parametric and non-parametric tests (detailed in §3). We modelled the latency to join using a Cox proportional hazards (PH) model. To avoid pseudoreplication, one observation from each nest pair was randomly removed, and the model was applied to the reduced dataset. We repeated the randomization and the model 1000 times to obtain mean parameter estimates and their confidence intervals. We tested for differences in call rate of neighbours that joined depending on the degree of familiarity. Responding birds were compared in two groups depending on whether they were familiar with one or both individuals in the focal nest. Unfamiliar birds that joined were excluded from the analysis, as that occurred only twice in the dataset.

3. RESULTS

(a) *The occurrence of joining*

For pairs of nests where each contained at least one familiar individual, in 12 out of 16 trials (seven out of eight nest pairs), at least one neighbour joined the mob. Individuals from the unfamiliar group joined the mob in just two out of 16 trials (one out of eight nest pairs). No neighbours joined the mob in first-years' nests (figure 1). Fisher's exact probability test [26] yielded $p < 0.001$. No unmarked great tits were observed to mob during the trials (see the electronic supplementary material). Mean distances between pairs of nests did not differ between groups (ANOVA: $F_{2,\ 21} = 1.04$, $p = 0.372$).

(b) *Latency to join*

We asked whether, among birds that joined ($n = 14$), distance affects time to joining. The Cox PH model yielded no evidence that neighbours from more distant nests joined nest defence later than closer neighbours (table 1).

Table 1. Average parameter estimates and their CI from 1000 iterations of Cox PH model for the effects of distance on the latency to join.

coefficient	parameter estimate	lower CI	upper CI
distance	−0.0139	−0.0552	0.0906

(c) *Neighbour call rate*

Neighbour alarm call rate was compared between birds familiar with one or both individuals from the focal nest. There was no difference in calls per minute between the two groups (Mann–Whitney test: $U = 4$, $n_1 = 8$, $n_2 = 4$, $p = 0.52$).

4. DISCUSSION

We demonstrate a significant influence of prior familiarity on joining behaviour during mobbing. Birds from familiar nests were more likely to join than neighbours from unfamiliar nests. Within the familiar nest pairs that joined, call rate did not differ between individuals that joined one or two familiar individuals. Hence, we have no evidence that the intensity of mobbing behaviour is affected by the degree of familiarity, although a small sample size limits the power of this analysis. Overall, these results indicate clear differences in behaviour towards familiar individuals. Joining in nest defence may be one of the mechanisms underlying the higher reproductive success of great tits that have familiar neighbours [17].

Familiar neighbours may have had more interactions with each other over time, and therefore more opportunity to build up a good reputation, which theoretically [2] aids the evolution of cooperation. While we cannot state why first-year birds never joined mobbing, we show that mobs of first-time breeders do not elicit a joining response. Recent work suggests that social network structure affects the likelihood of reciprocity being stable in a population [27]. First-time breeders spent the winter dispersing from their natal area, unlike the more sedentary older birds, and as newcomers to the settlement area, their relationships with neighbours may be less stable. Further work could investigate the social interactions of adults during winter flocking, to see whether associations are more likely to give rise to joining behaviour.

Overall, distant and close joining neighbours did not differ in latency to join. This suggests that variation in neighbour distance does not affect the neighbour's travel time towards the mob or delay between arrival near the neighbours' nest and joining the mob. This effect suggests by-product mutualism may not be operating here. Mutualism stems from an ultimately selfish behaviour; birds join their neighbours because their own nest is close enough to be at risk. Under this scenario, distant neighbours would invest less in joining than close neighbours. It is possible that the variation in distance in our sample was not sufficient to detect

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a distance effect, as pairs of nests were on average 70.1 m apart (s.e.: 4.7 m), perhaps too close for distance to affect the result.

We found that familiar neighbours were more likely to join in mobbing an intruder on an adjacent territory, and conclude that familiarity is important in social interactions. While determining the mechanism responsible for joining was not the main aim of our study, we cannot exclude the possibility that an interplay between selfish mutualistic responses and reciprocity-based reactions is involved in the system. Future studies may be able to tease apart the underlying processes.

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3.0

Chapter 4

Social stability and reproductive success in the great tit

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Abstract

Is flux in the social environment beneficial or detrimental to individuals? A variable social environment may benefit individuals through access to social information or new prospective mates. However, social change may also entail costs, for example due to renegotiation of social hierarchies and the risk of displacement by dominant individuals. We used a social network approach to investigate the relationship between the stability of the winter social environment and measures of fitness in great tits (*Parus major*). Since stability in an individual's close winter associations removes the cost of renegotiating social hierarchies, we predicted that a more stable social environment would lead to fitness benefits. We used

an automated detection system to monitor feeding associations of 1,655 individual great tits over the course of three winters. We quantified turnover in the pool of an individual's strongest associates as a measure of social stability, and found that high social stability was associated with an increased probability of breeding within the population the following spring. For 704 great tits that were observed in the winter, and which subsequently bred in the study population in three different years, we measured five aspects of reproductive success during the breeding season. We found that birds with more stable winter relationships fledged heavier young, but there were no other effects on reproductive output. Our results suggest that the social environment prior to breeding can have direct fitness benefits even for a species with limited sociality.

4.1 Introduction

The social environment of an individual can affect its fitness in a wide variety of ways. Interactions with conspecifics are important because they modify the environment that an individual experiences and can have a knock-on effect on that individual's contribution to the next generation. The structure of social networks that individuals are members of has been shown to influence fitness in a range of contexts. Network positions that connect groups have been shown, in house finches, to benefit relative attractiveness which is immediately relevant to selection those individuals are exposed to (McDonald 2007; Oh and Badyaev 2010). More indirect benefits may include connections in the network facilitating infor-

mation flow and informing individuals on the state of their potential competitors (Oliveira et al. 1998). The effect of stability in the network on reproductive success remains unexplored. However, the impact of an individual's position in the social environment on direct fitness measures, that is, those of reproduction, is beginning to be investigated in the empirical literature (Cameron et al. 2009; Frere et al. 2010). Longevity, which is correlated with fitness, has been shown to correlate with higher order network structure (variance in centrality) in female rock hyrax (*Procavia capensis*) (Barocas et al. 2011) and social bond strength in female chachma baboons (*Papio hamadryas ursinus*) (Silk et al. 2010). The latter species also showed increased infant survival for females with strong social bonds (Silk et al. 2003), showing direct fitness consequences of network position. Direct measures of male mating success have also been tied to network position in the wire-tailed manakin (*Pipra filicauda*) (Ryder et al. 2009), and forked fungus beetle (*Bolitotherus cornutus*) (Formica et al. 2012).

The number of social partners an individual is exposed to, and the frequency of interactions with those partners, are part of what shapes the position of the individual within the network. Many networks change over time due to, for example, preferences in social partner choice like homophily (preferential interactions between similar individuals) (McPherson et al. 2001). Individuals may be able to modify their social environment to their benefit by preferentially interacting with some individuals and avoiding others. However, most studies take a snapshot of social network structure and base their conclusions on the assumption that the

network is static (Sih et al. 2009) (although see Gross et al. 2006; Kossinets and Watts 2006). As a result, a position of an individual that is a result of a dynamic process of an individual moving from one group to another may appear as a static state, for example, the individual acting as a bridge between two groups by regularly interacting with members of both groups (Lusseau and Newman 2004). While information obtained from a static network can provide worthwhile information on individual social environments, incorporating measures of change can provide new insights into the importance of social interactions for individuals.

In this study we explore the importance of stability in strong connections for individual fitness in the great tit (*Parus major*). The question we address is whether change in the immediate social environment has an effect on the subsequent breeding success of an individual. Potential consequences of change in the social environment are not clear-cut. Change can bring benefits through optimal partner choice or the possibility of promotion in dominance hierarchy, but bears the cost of establishing new social ties and the risk of aggression towards newcomers (Eason and Hannon 1994). Variability in social experience has mostly been studied in social species that create stable, identifiable groups (White et al. 2010), but is less well understood in less social species which nevertheless interact in more fluid aggregations. It is likely that different pressures shape social effects in species with different ecologies; individuals of more social species living in permanent groups might benefit from change that leads to improved social skills, while for species that aggregate temporarily, stability might be more important

than change, due to larger costs of frequent changes in dominance structure. Our study species, the great tit, is strongly territorial during breeding, but aggregates in transient foraging flocks during winter, when food abundance is low and patchy. Foraging flocks have a dominance hierarchy, with older individuals generally dominating first-year birds, and males being more dominant than females (Drent 1983). The fission-fusion social environment and limited food supply may tend to favour stability in social relationships, due to the cost of renegotiating hierarchies that can perhaps lead to lower food intake in times when food is limiting.

We measured the stability in the strongest associations of individual great tits throughout the winter to ask whether birds benefit from stable flock associations (flocking with the same, rather than different individuals) by increased reproductive success the following spring. We investigated the effect of the stability of strong associations on reproductive success asking two main questions: first, how does stability affect the probability that an individual will breed in the population the following spring; and second, among individuals that were identified breeding in the population, does social stability prior to breeding influence fitness related life-history traits?

4.2 Methods

The study was conducted in Wytham Woods, Oxfordshire, between August 2007 and June 2010. The resident population of great tits breeding in nest boxes was

monitored during the breeding season of 2008, 2009 and 2010 to assess reproductive success. Life-history traits (date of laying the first egg [laying date, where 1 = April 1], clutch size, fledging success, fledgling mass, and number of offspring recruited to the local breeding population) were recorded for all breeding attempts using a field protocol standardized throughout the study. Details of the methods have been described by Perrins (1965); the major sources of variation in these life-history traits are described by McCleery et al. (2004) and Browne et al. (2007). The identities of breeding individuals were established from British Trust for Ornithology rings by trapping adult birds in the nest-box, or a new ring was fitted in the case of previously unringed birds.

Environmental variables are known to affect breeding performance in our population (Wilkin et al. 2007), therefore we took into account those which have been shown to affect the measured traits. Local population density, measured in terms of territory size is known to affect reproductive performance (Wilkin et al. 2006). We included tesselated territory size in our analysis; tesselated territories are a measure of territory size where borders are equidistant between the focal nest and its first-order neighbours, and have been shown to approximate mapped territories in our population (Wilkin et al. 2006). The measure of spring temperature in each year was recorded as warmth sum (after McCleery and Perrins 1998), which is the sum of maximum day temperatures from 1 March to 25 April. This measure was included as it is known to influence the timing of breeding through changes in food abundance. Altitude within the study site has previously been

shown to affect reproductive traits (Wilkin et al. 2007), presumably through effects on plant phenology and the timing of food supply. Female age is known to affect the timing of breeding (Perrins and McCleery 1985) and was also included in the analyses of female life-history traits.

4.2.1 Winter data logging to determine social structure

We used passive integrated transponder (PIT) tags to record individuals outside of breeding season, when territoriality decreases and individuals can no longer be reliably traced to a nest. From 2007 onwards, the population monitoring protocol included fitting a PIT tag attached to plastic leg ring on almost every great tit captured in the population. Between 2007 and 2010, 96% of great tits captured breeding and 97% of those born in Wytham nest boxes were fitted with individual PIT tags. The PIT tags are detected when the magnetic field of the antenna induces voltage in the inert tag which sends its unique code to a data logger. The loggers were fitted onto column bird feeders and identities of tagged birds were recorded when a bird perched on the antenna to obtain a sunflower seed from the feeder. The feeders were placed on a metal pole, with the feeding perches circa 1.3 metres from ground level. We recorded the identities in the non-breeding season, between August and early March (details of dates can be found in the Supplementary Material). Fifteen loggers were rotated in a random sequence every 3 to 4 days between 61 fixed locations within the study site in the first two winters, and every 7 days in the third winter of the study. This

enabled a thorough coverage of the study site, while preventing the birds from gaining access to a consistently reliable food source. Every location received a logger twice every month for 3-4 days in the first two winters and once every month for 4-5 days in the third winter. Locations of logging points remained fixed throughout the study.

Associations were deduced from temporal proximity of individuals in the feeding detections. Individuals were associated if they were detected on the same feeder within 1 minute of each other. We used the simple ratio index (SRI) (Ginsberg and Young 1992) to quantify the strength of the association. The SRI measures the association as the number of sampling periods in which two individuals were associated divided by the number of sampling periods when at least one of them was detected. We considered detections on the same day at the same feeder as belonging to one sampling period. This relatively short association time was chosen as we wanted to capture the potential contribution of dominance interactions which occur at very short time scales. While a longer association time may capture interactions between birds in physical proximity to the feeder, it is unlikely to capture shorter scale events like restricting a subdominant's access to the feeder. Association strengths were analysed at monthly intervals by creating association matrices from each calendar month from September to February in 3 winters preceding breeding in 2008, 2009 and 2010. The strength of associations can be biased towards extreme values for individuals with few detections (due to low value of the denominator in the association index calculation); we there-

fore excluded individuals detected fewer than six times in any month from that month's association matrix.

To achieve a measure of stability, we ranked the associates of every individual each month by their association strength. The top 10 associates were assigned the status of that individual's strong associates. The list of strong associates was extended if lower-ranking individuals had the same association strength as the 10th ranking individual, and shortened if there were fewer than 10 individuals with association strengths greater than zero. The number of strong associates was chosen in favour of a threshold association strength to allow for individual differences in weighted degree, that is, the fact that some individuals have only weak connections. Ten neighbours is also the median number of first-order neighbours that breeding birds have in a territorial context (Grabowska-Zhang et al. 2012), which suggests that an individual is capable of maintaining this many socially meaningful relationships.

We explored three ways of constructing an index of stability, and chose the best performing index based on the number of strong associates consistent between months . We wanted to arrive at a measure that will capture information on the consistency of strong associations and not only their number. The first stability index was constructed with the number of strong associates that were consistent across multiple months divided by the number of strong associates that only appeared as strong associates in a single month times the number of months the individuals was observed in. The index was weighted so that the count of

associates consistent across more months was given more weight than the number of associates appearing in fewer months. This was done by multiplying the count of associates by the number of months they appeared in. Therefore, if n is the number of months an individual was detected in, and i is the number of months the associates appear in, the index is the expression of the count of the associates as follows:

$$\text{stability index 1} = \frac{\sum_{i=2}^{6} \text{count}_i \times i}{\text{count}_1 \times n} \tag{4.1}$$

Second measure was the ratio of stable associates (those present in two months or more) to total number of strong associates:

$$\text{stability index 2} = \frac{\sum_{i=2}^{6} \text{count}_i}{\sum_{i=1}^{6} \text{count}_i} \tag{4.2}$$

The third measure was a weighted index accounting only for strong associates in two or more months:

$$\text{stability index 3} = \sum_{i=2}^{6} (\text{count}_i \times n) + 1 \tag{4.3}$$

Our aim was for the variable to carry information about the stability of strong associations and be least influenced by the total number of strong associates an individual has over the winter – a measure carrying similar information to the individual's weighted degree. We therefore compared the amount of variance

shared between several candidate stability indices and the total number of strong associates.

4.2.2 Statistical approach

We used SocProg software to create association matrices and calculate association strengths. The stability index and statistical models and graphics were created using R statistical language and environment (version 2.14.0) (R Development Core Team 2005).

We used a Generalised Linear Mixed Model framework to analyse the effect of social stability on fitness. We analysed the impact on probability of breeding using a mixed model with binomial error structure and a logit link function and individual ID as a random factor. To correct for the potential selective disappearance of low quality individuals from the winter population, we incorporated the number of months in which an individual was detected as well as the month of final winter detection. We also included juvenile status (juvenile – under 1 year, adult – older than 1) to control for lower survival during the first year of life (Clobert et al. 1988). Some individuals in the analysis were observed in more than one winter (499 individuals out of 1655; 30%), it was therefore possible to split the variation in social stability into between individual and within individual components through subject centring. This allows us to separate the effects that are due to different responses within the same individual in different winters, or inherent differences between individuals that differ in their social stability.

For our analysis of breeding performance we used models with a normal error distribution to investigate effects on laying date, clutch size and fledgling mass. The nesting success model had a binomial error structure and a logit link; recruitment success was modelled using a mixed model with a Poisson error structure and a logarithm link function. All models included individual identity and year as random factors. Since preceding reproductive stages are known to affect later ones, we controlled for them in all models (for example, the fledgling mass model controlled for laying date and clutch size). Individual year warmth sum was excluded from the models. This was because it prevented the models from converging correctly, probably due to a large proportion of information shared with the year variable and small range of values in the variable itself (3 values shared across many data points). Between 27% and 30% of individuals in the analyses of reproductive performance appear in the data more than once; we therefore partitioned the stability variation into between and within individual components for these analyses.

4.3 Results

The best performing measure in terms of minimising variance shared with the total number of strong associates was index 1, as described in Equation 4.1. It shared the least amount of variance with total number of strong associates (17%). Index 2 (Equation 4.2) shared 23% of variance with total number of strong associates. Index 3 (Equation 4.3) shared 42% of variance with total

strong associates.

Social stability varied from 0 to 4 (median 0.0763, interquartile range: 0 - 0.203) for all individuals detected in the winter. Distribution of index values can be found in the Supplementary Material (Figure S1). Individuals that subsequently bred in the population varied in their stability from 0 to 2, with a median of 0.133 and IQR of 0 - 0.272. Juveniles had a lower median stability (0.11; range: 0 - 2) than adult individuals (0.39, range: 0 - 4) (Mann-Witney U = -128704, $p<0.001$), reflecting the fact that juveniles undergo natal dispersal in their first winter, whereas older individuals are more sedentary (Greenwood et al. 1979; Harvey et al. 1979).

4.3.1 Probability of breeding

Great tits that experienced a more stable social environment in winter had a greater probability of breeding in the study population the following spring; this effect was due to the within-individual component of the variation in social stability. The effect was independent of the month in which an individual was last detected, suggesting that the increase in the chance of breeding is not an artefact of death or emigration of individuals throughout the winter (Table 4.1). Juveniles were less likely to be seen breeding than older birds, but had the same response to social stability, since there was no significant interaction between juvenile status and stability of strong associations. The effect for juveniles and adults is shown in Figure 4.1A. The probability of breeding was not predicted by the number of

Coefficient	Estimate (z transformed)	SE	z	p
(Intercept)	-0.258	0.0721	-3.583	< 0.001
Social stability$_{(between\ individuals)}$	0.0708	0.0530	1.336	0.18
Social stability$_{(within\ individual)}$	0.1078	0.0525	2.051	0.04
Month of last detection	0.9466	0.0712	13.29	< 0.001
Number of months detected	-0.007	0.0554	-0.12	0.90
Juvenile status: juvenile	-0.518	0.1017	-5.097	< 0.001

Table 4.1: General Linear Mixed Model predicting the probability of breeding in great tits detected by feeding loggers in winter. The model includes 2,154 data points from 1,655 individuals. Individual ID and year of study was treated as random effects. Juvenile status effect has adult level set as 0

months an individual was detected in; that effect was the same for both juveniles and adults.

4.3.2 Breeding performance

We modelled the effect on the date of laying the first egg and the clutch size using a data set restricted to females only, as these are female life-history traits and have been shown to be predominantly controlled by the female of the breeding pair (Browne et al. 2007). The within-individual component of stability showed that females tended to lay earlier when their social stability in winter was high, as opposed to having a high turnover of strong associations (Table 4.2). This effect was smaller than the effect of other variables in the model (one standard deviation change in explanatory variable corresponds to 0.595 day decrease in laying date, Table 4.2) and was marginally non-significant. The between-individual component of stability did not predict variation in laying date. Neither component of

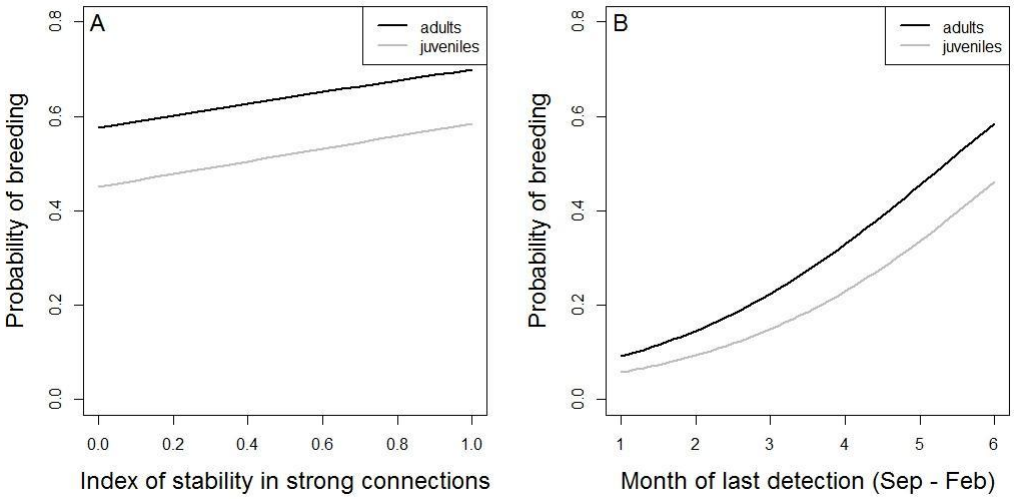


Figure 4.1: A) The probability of breeding depending on social stability in overwintering great tits, and B) the probability of breeding depending on the month of last detection (September to February). Both graphs are based on the predictions from a Generalised Linear Mixed Model. The untransformed effect is shown for birds older than 1 year in black and for juveniles in grey.

stability in winter associations predicted the females' clutch size (Table 4.3).

We performed the analysis of fledgling mass, fledging success and the number of recruits at the nest level by including nest identity as a random factor in addition to individual ID and year of study. The reason for it was that breeding performance measures at the same nest are not independent, as they are affected by both individuals' parental investment. We included attempts where only one parent was detected in the winter, but in 30.8% of nests in years 2008 and 2009 and in 39.2% of nests in 2010 both breeders were detected. These nests will have two measurements per breeding attempt, which was controlled for by including

Coefficient	Estimate (z transformed)	SE	z	p
(Intercept)	20.83591	1.89951	10.969	< 0.001
Stability$_{(between\ individuals)}$	-0.61769	0.32533	-0.262	0.80
Stability$_{(within\ individual)}$	-0.09063	0.34614	-1.899	0.055
Female age	-0.16553	0.70395	-0.235	<0.001
Territory size	-0.86981	0.36068	-2.412	<0.001
Elevation	1.61716	0.34207	4.728	<0.001

Table 4.2: General Linear Mixed Model predicting the date of laying the first egg in great tits detected by feeding loggers in the winter. The model includes 482 data points from 368 females. Individual ID and year of study was treated as random effects.

Coefficient	Estimate (z transformed)	SE	z	p
(Intercept)	8.655777	0.122544	70.63	<0.001
Stability$_{(between\ individuals)}$	-0.091663	0.076703	-1.20	0.20
Stability$_{(within\ individual)}$	-0.001567	0.049443	-0.03	0.99
Female age	0.453456	0.138076	3.28	<0.001
Territory size	0.186786	0.070320	2.66	<0.001
Lay date	-0.589511	0.062993	-9.36	<0.001

Table 4.3: General Linear Mixed Model predicting clutch size in great tits detected by loggers at feeders in the winter. The model includes 482 data points from 368 females. Individual ID and year of study was treated as random effects.

nest identity. We modelled the probability of fledging by using a binary nest success variable with value of 1 if at least one young successfully fledged the nest, and 0 if all young died before leaving the nest. Fledgling mass was taken as an arithmetic mean of the mass of all young present in the nest at 15 days old. The analysis was restricted only to nests that had live nestlings in them 15 days after hatching. The number of recruits from a nest was also restricted to nests that contained live young at 15 days old.

Stability of winter associations did not affect the probability that a breeder would successfully fledge at least one young (Table 4.4). However, among nests that were

Coefficient	Estimate (z transformed)	SE	z	p
(Intercept)	4.470	0.484	9.23	<0.001
Stability$_{(between\ individuals)}$	0.069	0.286	0.243	0.81
Stability$_{(within\ individual)}$	-0.270	0.240	-1.12	0.26
Age	0.479	0.52	0.923	0.36
Territory size	0.115	0.287	0.399	0.69
Lay date	-0.620	0.269	-2.31	0.02
Clutch size	-0.011	0.318	-0.036	0.97

Table 4.4: General Linear Mixed Model predicting the probability of fledging at least one young in great tits detected by feeding loggers in the winter. The model includes 899 data points from 500 nests. Nest ID, individual ID and year of study was treated as random effects.

Coefficient	Estimate (z transformed)	SE	z	p
(Intercept)	18.16661	0.27458	66.16	<0.001
Stability$_{(between\ individuals)}$	0.09636	0.04347	2.22	0.028
Stability$_{(within\ individual)}$	0.05683	0.03776	1.51	0.13
Age	-0.03209	0.08770	-0.37	0.017
Territory size	0.12081	0.06135	1.97	0.048
Lay date	-0.24270	0.06239	-3.89	<0.001
Clutch size	-0.37141	0.05474	-6.79	<0.001

Table 4.5: General Linear Mixed Model predicting average fledgling mass in great tits detected by feeding loggers in the winter. The model includes 764 data points from 415 nests. Nest ID, individual ID and year of study was treated as random effects.

successful, breeders with more stable winter associations fledged heavier chicks (Table 4.5); the effect was significant at p = 0.028. Figure 4.2 illustrates the untransformed effect of stability on fledgling mass as predicted from the model. Stability of winter associations did not predict the number of young recruited to the breeding population the following year (Table 4.6).

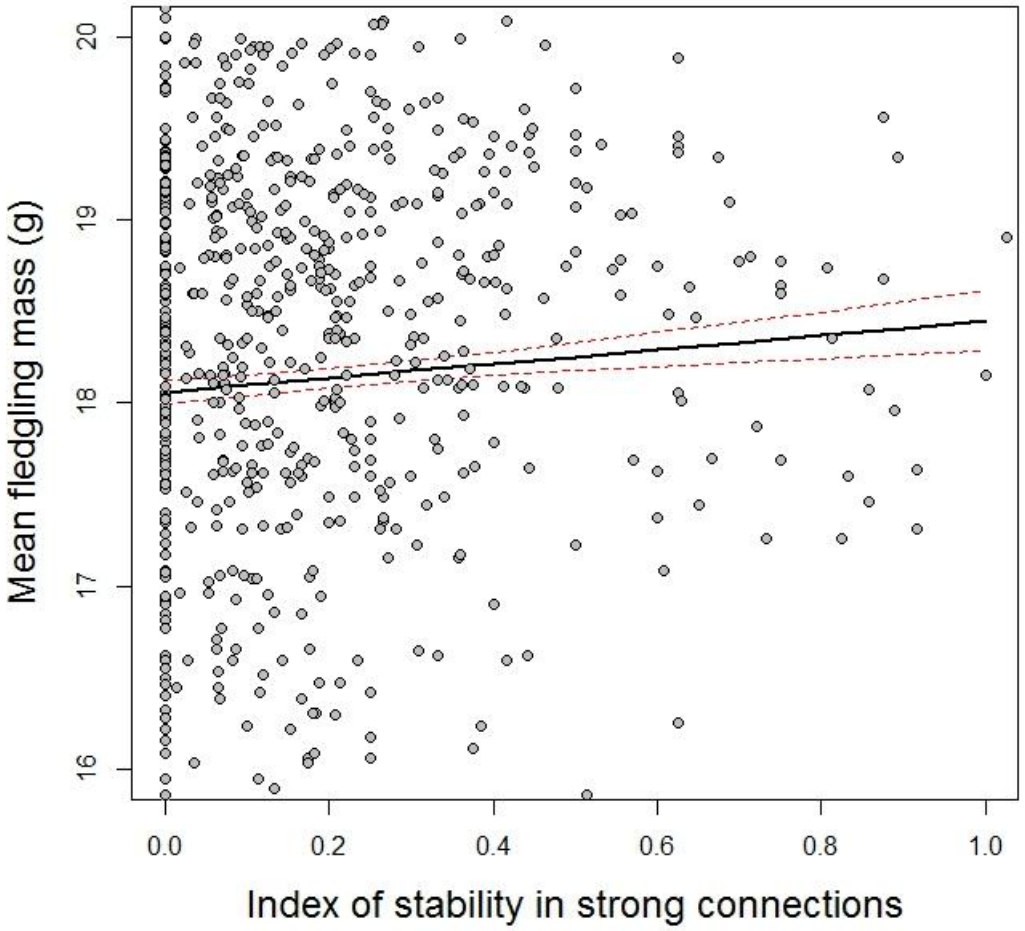


Figure 4.2: The untransformed effect of social stability measured as consistence in strong connections on the mean fledgling mass predicted from the General Linear Mixed Model (in black). Dashed red lines are 95% confidence intervals.

4.4 Discussion

Social interactions are known to affect individual fitness (Formica et al. 2012; Ryder et al. 2009). Here we investigate whether stability in social associations affects fitness in the great tit. Our results show that stability in strong associa-

Coefficient	Estimate (z transformed)	SE	z	p
(Intercept)	-1.543	0.154	-10.016	<0.001
Stability$_{(between\ individuals)}$	-0.034	0.090	-0.375	0.71
Stability$_{(within\ individual)}$	0.051	0.074	0.686	0.49
Age	-0.145	0.165	-0.876	0.38
Territory size	0.024	0.086	0.284	0.78
Lay date	-0.513	0.120	-4.273	<0.001
Clutch size	-0.036	0.095	-0.38	0.70
Fledgling mass	0.280	0.103	2.725	0.006

Table 4.6: General Linear Mixed model predicting the number of young recruited in the population the following year in great tits detected by feeding loggers in the winter. The model includes 746 data points from 415 nests. Nest ID, individual ID and year of study was treated as random effects.

tions during winter affects some aspects of reproductive success. We hypothesised that stability in an individual's strongest social relationships will be positively related to measures of reproductive success. We found that consistency within an individual's associations throughout the winter predicted a greater probability of breeding in the study population the following spring. We also found a relationship between stability in strongest associations and offspring mass. By using within- and between-subject centring (van de Pol and Wright 2009) we were able to separate the effects due to differences between individuals from those due to different responses within the same individuals measured multiple times.

We measured social stability by quantifying the consistency in those individuals with whom a focal individual associates most strongly over six winter months, and found that when individuals had stable associates they had a higher chance of breeding in the study population. This result is due to the within-individual component of the variation in social stability, suggesting that stability influences

the probability of breeding for the same individuals in different years, rather than showing differences in social stability in individuals with different chances of breeding. The result is independent of the individual's month of final winter detection, indicating that stable social relationships are associated with elevated probability of breeding independently of individuals disappearing from the population in the course of winter.

The absence of individuals from the breeding population might be caused by mortality before breeding begins, emigration to breed elsewhere, breeding in natural cavities or refraining from breeding in that year. The frequency of breeding in natural cavities is thought to be low (Harvey et al. 1979; Perrins 1979). It is possible that individuals that are not observed in the breeding population attempt to breed, but their attempt fails before they can be identified (6% of attempts in the case of females; Bouwhuis et al. 2010). It is also possible that their attempt is successful but the breeders could not be trapped. In our population, on average 80% of breeding females and 65% of breeding males are identified (Szulkin et al. 2009). It is important to acknowledge that breeders in the population could only be identified in this study when the young were a week old, due to increased risk of desertion from trapping early in reproduction. Our measure of probability to breed is therefore more accurately described as the probability to reach trapping stage in the breeding attempt.

Since our measure of social stability corrected for the number of months in which an individual was observed, it is unlikely that the effect is caused by low stability

score of individuals that were only detected in few months. Frequent changes in associations can reflect attempts to join different foraging flocks. Birds may be flexible in their decisions, for example if they are unsuccessful at gaining a stable position in a flock due to low dominance status and may therefore be less likely to secure a breeding territory, they may search for a less competitive, but perhaps suboptimal environment outside the woodland area. It is also possible that social instability reflects the social behaviour of individuals that are not resident in the area, and that change in social partners is connected to poor resource availability in their home range and foraging excursions to more distant patches. That pattern may then have a knock-on effect on breeding due to poor body condition or territory quality. A more in-depth spatial analysis is needed to determine a link between mobility in the habitat and social mobility.

Among the birds recorded breeding in the study population, birds with more stable winter associates fledged heavier chicks. Fledgling mass is generally a good predictor of survival and recruitment (Perrins and McCleery 2001; Tinbergen and Boerlijst 1990); heavier young survive better and are more likely to recruit. The effect was small in general terms (Schielzeth 2010) (one unit of standard deviation in stability index translated to increase if 0.09g in mass), but it suggests that fledgling mass is connected to intrinsic differences in social stability between individuals (between-individual effect), suggesting that breeders that tend to experience stable social bonds also tend to fledge heavy young. Individuals with a more stable social environment may simply be of better quality, and be able

to secure a stable position in the flock dominance hierarchy as well as provide better parental care to their young. Alternatively, there may be flexibility in the response to the social environment, but our analysis may not be powerful enough to detect within-individual effects due to a small proportion of individuals occurring in the dataset more than once. It is possible that better-quality individuals are able to secure and defend better quality habitat patches. Patterns of space use may affect the structure of social networks (Ramos-Fernandez et al. 2006) and if good-quality habitats are defended more, even at times when territoriality is low, this can lead to neighbourhoods where associations are very stable in areas where individuals are site-faithful. It has been shown that experienced breeders benefit from having the same territorial neighbours from one year to the next (Grabowska-Zhang et al. 2012). Further study of nesting site choice within groups of strong associates can help determine whether winter familiarity benefits territorial neighbours in this population. The non-significant trend towards earlier laying date within individuals with greater social stability suggests phenotypic plasticity in females when experiencing different levels of stability. The timing of egg-laying is known to mostly be influenced by environmental (McCleery and Perrins 1998; Wilkin et al. 2007) and individual female factors (Browne et al. 2007). Earlier egg-laying usually corresponds to better reproductive performance, as the females are able to time their breeding to the peak in food abundance. It is possible that stable relationships in the winter result in less stress and better body condition, such that females in better body

condition should be able to commence breeding sooner. However, females may be responding to finer cues in their environment and lay only at the optimal time, rather than as soon as they reach breeding condition. It is also possible that stability in social relationships is itself a consequence of an unknown effect that we have not controlled for in our analysis.

Further research is needed to determine whether stability of interactions is a property of an individual or perhaps it is governed externally, by factors like space use, resources or risk (Ramos-Fernandez et al. 2006). Increased effort into determining the fate of individuals that do not breed in the population may help to tease apart cases of emigration from mortality, and determine whether social behaviour is indicative of imminent emigration decision or death.

Here we show that the effects of the social environment can carry over across contexts. The stability in relationships in winter correlate with breeding decisions and performance. It is possible that the social environment shapes other aspects of individual life-histories by exposing individuals to differing levels of competition, stress or opportunities to gain access to resources. The importance of social interactions in a species with limited gregariousness suggests that variation in individual social experiences might be more important than previously anticipated, even in organisms that are not very high on the scale of sociality observed in some species.

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Chapter 5

Wherever I may roam: social viscosity and kin affiliation in a wild population despite natal dispersal

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Abstract

Social interactions have fitness consequences for many organisms. The process of dispersal redistributes individuals in space, and therefore affects the social context to which individuals are exposed. Kin structure can arise within populations in the absence of active kin-discrimination because of limits to dispersal. Because the degree of kin structure in populations is a key component of understanding kin selection and inbreeding, it is important to understand the relative contribution of proximate mechanisms that can lead to kin-structuring within

populations. During the vagrancy stage, social affiliation between individuals may be expected to be affected by the distance between their natal origin in space and time. We looked for kin structure in a population of juvenile great tits *(Parus major)* and asked whether it arises due to these limits to dispersal, or whether kin associate independently of these effects. Dyadic associations between 881 juvenile birds were quantified using an automated detection system over three consecutive winters. We show that the strength of association between non-siblings is affected predominantly by spatial proximity at fledging, and to a lesser extent, temporal proximity in birth dates. In addition, sibling pairs associate more often than expected by chance, independent of spatial and temporal effects. This latter effect is driven by pairs of brothers associating at a higher rate than other sex combinations of sibling pairs. Our results suggest that the structure of the winter population is affected firstly by limits to dispersal through incomplete population mixing brought about largely by spatial proximity with a minor temporal component. In addition, kin structure was revealed, and hence the scope for fitness-related interactions between kin. Both spatial and socially mediated population structuring can have implications for our understanding of evolution of sociality.

5.1 Introduction

The dispersal process consists of identifiable stages: prospecting, emigration, vagrancy, and settlement in the destination habitat (Ronce 2007). While emigration

and settlement decisions have received much attention in the literature (for example Michler et al. 2011; Parejo et al. 2007; Robinson et al. 2011), the vagrancy stage is generally less well understood (but see Jeanson et al. 2004; Selonen and Hanski 2011). This is largely due to the logistical difficulties associated with monitoring individuals during this life history stage. However, ecological factors occurring during vagrancy are very likely to have important effects on settlement and the subsequent fate of individuals. Vagrant individuals gather information about the quality of prospective sites by revisiting habitat patches (Selonen and Hanski 2011). Birds use public information such as sex ratio in different habitats to maximise their fitness (Steifetten and Dale 2012). Social interactions during this stage could also be a source of similar information that affects individual life-history decisions.

For social species social interactions during the vagrancy phase are likely to have particularly important consequences for aspects of subsequent settlement decisions. For example, previous work has shown that during this period male house finches *Carpodacus mexicanus* seem to choose a social environment that improves their attractiveness relative to rivals (Oh and Badyaev 2010). Dispersal can change the proximity of relatives in space and rearranges social structure as new individuals join new social groups. If establishing new social ties after moving to a new environment is costly (Eason and Hannon 1994), individuals may avoid changing social contexts and that can result in a socially mediated form of population viscosity during the vagrancy stage, where movement of individuals is

restricted due to social factors. Classically defined population viscosity (Hamilton 1964) can stem from the limited ability of an organism itself to move in its physical environment, as well as the restrictions that the environment poses on the final destination of the disperser, such as the availability and connectedness of suitable habitats (Wiens 2001). Social viscosity can potentially lead to similar patterns of population structure, if individuals are constrained in the movement between patches due to their social composition (Michler et al. 2011). This type of social restriction on movement of individuals is relevant in the context of kin selection and the evolution of cooperation, as it may have a similar effect on population structuring as conventionally defined viscosity.

Social interactions in animal populations are rarely random (Croft et al. 2004; Lusseau 2003), and have been shown to be influenced by a range of factors, including kinship (Wolf and Trillmich 2008), phenotype matching (Fowler et al. 2011) and population self-structuring (Lion and van Baalen 2008). Mechanisms that determine social structure of populations can broadly be divided into social interaction rules and movement rules (Sih et al. 2009). Interaction rules describe how social structure is influenced by interactions of certain classes of individuals, for example, the tendency for similar individuals to interact preferentially with each other (homophily) (McPherson et al. 2001). Movement rules, on the other hand, describe the ways in which space use affects social structure. Spatial and temporal proximity is essential for most types of social interaction, since encounters between individuals can only happen if both individuals are in the same place

at the same time. Social proximity (interaction rate) can reflect spatial proximity, especially in sedentary species (McDonald 2009). However, spatial factors can also be important for highly mobile individuals, such as those undergoing dispersal. The probability of a social encounter could thus be affected by how far the individuals can travel from their point of origin as well as the decision on when to disperse. Here we were interested in examining factors influencing the social structure of a wild population of great tits (*Parus major*) during the vagrancy stage of dispersal. Outside the breeding season great tits conform, at least superficially, to a classic fission-fusion social structure. Flocks of between four and 20 birds move through woodlands merging and splitting frequently (Hinde 1952; Morse 1978; Saitou 1978).

Our aim was to quantify the relative importance of indirect (i.e. spatial and temporal proximity of origin) and direct (kin-related) effects in determining social structure among interacting juveniles. Specifically we investigated: (1) whether associations between juvenile great tit during the vagrancy phase of dispersal can be predicted by their origin in space and time; (2) whether dispersing relatives associate at a different rate than non-relatives controlling for the influence of spatial and temporal proximity; (3) whether the sex composition of a dyad determines associations between siblings and whether the strength of this association could be explained in terms of inbreeding avoidance.

5.2 Methods

5.2.1 Study site and field methods

The study was conducted in Wytham Woods, Oxfordshire, UK, on a resident population of great tits that has been studied since the 1940s. The study site comprises of *circa* 380 ha of continuous woodland, surrounded by pasture and arable land, described in more detail by Wilkin et al. (2007). The study site includes 1,020 nest boxes, which have been kept at fixed locations throughout the study, save minor movements necessitated by tree falls. The boxes were digitally mapped using their GPS coordinates. All individuals used in this study originate from the Wytham population (i.e. were ringed as nestlings from nests boxes within Wytham Woods).

Between 2007 and 2009, 96% of great tits captured breeding and 97% of those born in Wytham nest boxes were fitted with individual passive integrated transponder (PIT) tags attached to plastic leg rings. A total of 1,815 adult and 6,702 nestling great tits were tagged during the study period. The tags allowed the bird identities to be recorded and logged when detected at bird feeders fitted with data loggers. A PIT tag detection occurred when the bird perched on an antenna to obtain a sunflower seed from the feeder, since the electro-magnetic field of the antenna induces voltage in the inert tag, which transmits its unique code. The data loggers fitted with two perching antennae were sourced from Francis Scientific Instruments Ltd, Cambridge. The feeders were placed on a metal pole,

with the feeding perches *circa* 1.3 metres from ground level. In order to prevent memory overload from multiple records of a tag on the same visit to the feeding perch, only the first transmission of tag ID in a visit was logged and logging was suppressed for 15 seconds; tag record times were rounded by the logger to the nearest 15 seconds. We recorded bird identities in the non-breeding season, from the end of summer until the end of winter, when shifts in behaviour connected to nesting start to occur (Dhondt et al. 1996). The recording seasons lasted from 8 August 2007 to 1 March 2008, 22 August 2008 to 10 March 2009, and from 27 August 2009 to 5 March 2010. A total of fifteen loggers were rotated in a random sequence every three to four days between 61 fixed locations within the study site in the first two winters, and every seven days in the third winter of the study. This enabled a thorough coverage of the study site, while preventing the birds from gaining a reliable food source. Locations of logging points remained fixed throughout the study. Every location received a logger twice every month for a period of 3-4 days in the first two winters and once every month for a period of 4-6 days in the third winter.

5.2.2 Social Behaviour and dispersal in the great tit

The great tit is a small passerine bird common throughout Eurasian temperate forests. It breeds in secondary tree cavities but preferentially breeds in provided nest boxes. The place of birth of juveniles can therefore be easily mapped. Great tits fledge from the nest at 19-21 days of age, and later disperse from their

natal area as juveniles. After their first breeding season they remain relatively sedentary (Greenwood et al. 1979; Harvey et al. 1979). Natal dispersal in the great tit is thought to play a key role in inbreeding avoidance (Szulkin and Sheldon 2008b). The breeding population structure in not random with respect to relatedness in our study population, but it is not significantly different from a spatially structured null model where neighbouring individuals breed together (Szulkin et al. 2009). During the process of natal dispersal, individuals are exposed to changing physical and social environments. Great tits aggregate in large, mixed species, foraging flocks in the winter (Hinde 1952), within which they interact with con- and heterospecifics. Social interactions in the winter have rarely been studied in this species, since the birds are much more difficult to reliably identify and observe by eye when they are not bound to the nesting territory.

5.2.3 Individuals and associations

Associations between individuals could be deduced from temporal proximity in detections at a given logger location. Our study focused on the proximity between individuals, and our aim was to focus on individuals resident in the same area. We did not assume the individuals were directly interacting at a feeder if recorded there, but merely that they were associating, that is, present in the same area at the same time, and hence with the potential to interact. We chose 10 minutes as the time interval to define associations between juveniles. We chose this interval

in favour of a shorter one since a finer time-resolution might be disproportionately affected by dominance interactions, such as restricting subordinate individuals' access to the feeder, which happens in a matter of seconds. A period of 10 minutes permits birds present in the area to be detected at the feeder without the associations being confounded by differential access to the feeder.

As the association interval increases, so will the average strength of observed association defined by that interval. We tested the effect of different sampling periods on the mean association strength they produce; results are shown in Figure S1. The mean association rises with sampling period size and then levels off asymptotically, and a sampling period of 10 minutes is close to where the mean association strength starts to stabilise. We tested two contrasting time intervals (1 and 60 minutes) to assess their effect on the general conclusions from the analysis. Parameter estimates from those test models were similar to the parameters in the main analysis, and have been included in the Supplementary Material (Tables S1- S4).

Using associations defined as above, we created an association matrix for all juveniles detected in each calendar month (details in Supplementary Material, Table S5) during the study period. We performed the analysis on 881 juveniles from 495 families (natal nests) in three logging seasons (2007-8 to 2009-10; details in Table 5.1). Associations were quantified using the simple ratio index (SRI) (Ginsberg and Young 1992), which is an estimate of the proportion of times that birds were feeding together. We calculated the simple ratio index by using

		Sept	Oct	Nov	Dec	Jan	Feb	total for year
2007-08	individuals	97	106	153	164	172	178	252
	families	70	78	103	110	110	120	158
2008-09	individuals	176	139	81	87	137	149	242
	families	122	104	67	72	105	109	152
2009-10	individuals	112	193	186	188	145	254	387
	families	78	119	115	123	95	143	185

Table 5.1: Total numbers of individual juvenile great tits detected during the period of study and total numbers of natal nests (families) from which they originated.

our measure of association (two birds detected within 10 minutes of each other were considered associated), and considering all detections of those individuals at the same feeder on the same day; then the number of sampling periods (days) every month in which the individuals were associated was divided by the number of sampling periods in which at least one of them was identified (Ginsberg and Young 1992). Individuals with five or fewer detections in any single month (about 9% of individuals) were removed from that month's analysis in order to remove spurious extreme values of SRI produced by low detection rates.

Distances between natal nest boxes were calculated from box coordinates. Sibling status was assigned to individuals originating from the same nest box. A proportion of birds (c. 17%) would therefore be assigned sibling status when they are actually half-siblings, due to the occurrence of extra-pair paternity in this population (Patrick et al. 2012). However, they are still of relevance to the study because they originate from the same social cluster at fledging. It is possible, but less likely, that birds may associate with between-year siblings (born to the

same parents in different years), but since this study focuses on juvenile birds, these associations were not considered. We separated detections into one month sampling periods in order to allow for analysis of any variation in the strength of associations during the course of the winter.

As well as a measure of spatial similarity in natal origin (defined as the distance between natal nest boxes for a pair of individuals) we also defined a measure of temporal similarity in origin, expressed as the number of days between hatching of individuals from two different nests. Hatching date was recorded with 1 day accuracy by frequent nest checks around the expected date of hatching (calculated from clutch size + first egg date + 12 days), and will be a reasonably accurate estimate of fledging date, which was not recorded directly in our study. In addition we assigned sibling status (a dichotomous variable: yes/no) to each pair of individuals. To perform the models, we unfolded the matrices into a table where each row was a unique pair of individuals in a given month. Mean strength of association varied between years (Kruskal-Wallis test: $\chi^2 = 2906$, df = 2, $p < 0.001$), which was controlled for by including year as a fixed factor in our model.

We investigated the role of kin association by analysing the associations of siblings (and other individuals) of known sex in more detail. If kin are associating more than non-kin, this could be driven by cooperation between same sex siblings, as opposite sex siblings are at risk of inbreeding and strong associations may increase that risk. Juveniles cannot be reliably sexed on plumage until their first moult c. 2-3 months after fledging (Svensson 1992), and since juveniles in

the study were tagged as nestlings, we knew the sex of only those individuals that were subsequently captured breeding in the study site the following year, or during occasional mist-netting sessions in the winter. We restricted the dataset to the 41 females and 57 males that recruited into the breeding population and which also had a recruited sibling. The resulting sample comprised 8 sister-sister dyads, 29 brother-sister dyads, and 18 brother-brother dyads from 49 families (46 families with two recruits, 3 families with 3 recruits). Including information on the sex of 250 individuals that were trapped during the winter, but were not observed breeding, helped identify a further 68 sister-sister pairs, 117 brother-sister pairs and 76 brother-brother pairs. In all those additional pairs, either one or both of the siblings failed to recruit.

5.2.4 Statistical approach

We used an information theoretic approach (Burnham and Anderson 2002) to disentangle the importance of kinship, natal distance and asynchrony in predicting the strength of associations. Since the distance between natal sites and sibling status terms are confounded for some of the range of the data (all siblings, and only siblings, have a natal distance of 0), and sibling status and asynchrony were also related (siblings have, by definition, the same hatch dates, although in this case it is possible for non-siblings to have the same hatch dates), we could not include them in the same model. We included them in three separate models and compared the evidence ratios based on Akaike's Information Criterion (AIC)

for those models, to compare the relative importance of those three terms in explaining variation in the strength of associations. We built four *a priori* models comprising one of the three predictors (i.e. spatial distance, temporal distance, sibling status) hypothesised to affect associations and a base model including the effects of time in season in months and year, treating individual identity as a random factor. We built Generalized Linear Mixed Models (GLMM) with binomial error structure and logit link function.

The nature of both network and spatial data are such that the data will to some degree lack independence. Recent methodological developments suggest that although there is a downward bias in standard error estimates in spatially structured linear models, parameter estimates remain unbiased (Hawkins et al. 2007). Since we still could not exclude the possibility of bias in SE, we used a permutation approach to test whether parameter estimates were different to those expected if the data were distributed randomly. We performed 1,000 iterations of the permutation procedure. Variables were considered to have a significant effect if the parameter estimates lay outside of 95% of the permuted values. In all models, we z-transformed the predictor variables in order to standardise parameter estimates and make them directly comparable within the model.

We compared the associations of different sexes of sibling dyads using Kruskal-Wallis and Mann-Witney tests. All analyses were performed using R statistical environment (version 2.14.0) (R Development Core Team 2005).

5.3 Results

5.3.1 Structure of associations

The median number of detections per individual was 93 each month (range: 10 - 918, IQR = 52 - 166). The dyadic association matrix was sparse, as we observed 13,544 associations, only 9% of the total 144,870 possible associations, and the median strength for the observed associations was 0.04 (IQR = 0.015 - 0.085). We observed 170 associations between nestmate siblings, out of 770 possible sibling associations (hence 22% of possible associations).

5.3.2 Effects of kinship and origin in space and time

We constructed a base model incorporating the winter month and year as independent variables and individual identity as a random factor in order to control for these factors when investigating the effects of interest. The distance between natal nest boxes provided the most information compared to the base model (Table 5.2). Association strength decreased with increasing distance (β = -0.57, SE = 0.04, p <0.001) (Table 5.3; Figure 5.1). Substituting distance for either sibling status or asynchrony also lowered the AIC compared to the base model, albeit to a much smaller degree (Table 5.2).

Candidate model	Log Likelihood	AIC	Δ AIC	weight
dis + month + year	-2305	4622	0	1
sib + month + year	-2410	4831	209	4.1×10^{-46}
asy + month + year	-2414	4840	218	4.5×10^{-48}
month + year	-2416	4842	220	1.7×10^{-48}

Table 5.2: Ranked models explaining the strength of associations between juvenile great tits. The models are ranked according to the difference in AIC between that particular model and the top model. Akaike weights indicate the evidence for the model being the best within the set. Evidence ratios are calculated as the likelihood of the model compared to the next best model. All models contained individual identity (n=878) as a random factor.(dis - natal distance; sib - sibling status; asy - hatching asynchrony; month - month in the recording season, from September to February; year - year of study as categorical variable.)

Coefficient	Estimate (z transformed)	SE	p
natal distance	-0.57489	0.04107	<0.001
month	-0.01416	0.0355	<0.001
year 2007	reference level	NA	NA
year 2008	-0.12801	0.09666	<0.001
year 2009	0.12523	0.0787	<0.001

Table 5.3: Summary of the top model predicting strength of juvenile associations in the great tit. P values were obtained from permutation tests.

In order to explore whether sibling status or degree of temporal asynchrony explained residual variation beyond that captured by natal distance (Figure 5.1), we performed a GLMM analysis with Gaussian error structure on the residuals of the top model, first with sibling status and then with asynchrony as independent variables in two separate models. Both sibling status and asynchrony explained a small, but significant, amount of residual variation in association strength (Table 5.4), suggesting that both of those factors contribute to variation in association strength once the similarity in natal distance has been taken into account. There was an effect of sibling status controlling for asynchrony (slope=0.145, SE = 0.013, p<0.001), analysed by using sibling status to explain residual variance

Response = residuals of the strength of association controlling for distance, month and year	Estimate (z transformed)	SE	p
A) sibling status	0.0413	0.01275	0.003
B) asynchrony	-0.00243	0.00101	0.02

Table 5.4: Summary of two Generalized Linear Mixed Models exploring the effect of A) sibling status and B) asynchrony on the residuals of the top model (i.e. the strength of association controlling for distance, month and year). The response variable is the residuals of the top model; individual identity (n=878) was included as a random factor.

in the asynchrony model from Table 5.3, although it is important to note that sibling status also carries some information about distance.

5.3.3 Sibling associations

We compared the association rates of siblings depending on sex. Including all possible associations, sibling dyads of known sex composition associated at different rates (Figure 3; Kruskal-Wallis test: $\chi^2 = 17.4465$, df = 2, $p < 0.001$). Pairs of brothers associated more than pairs of sisters (Mann-Witney U = 1061.5, $p < 0.001$) and brother-sister pairs (Mann-Whitney U = 1461.5, p = 0.002). There was no significant difference between association rate of sister pairs and brother-sister pairs (Mann-Witney U = 471, p = 0.15). These results held when the data was restricted to the final winter month; it is therefore unlikely that the effect is caused by selective disappearance of non-recruits throughout the winter (see Supplementary Material Figure S3). The strength of nonzero associations did not differ between the groups (Kruskal-Wallis test: $\chi^2 = 3.05$, df = 2, p = 0.22), suggesting that pairs of brothers are more likely to associate than other sibling

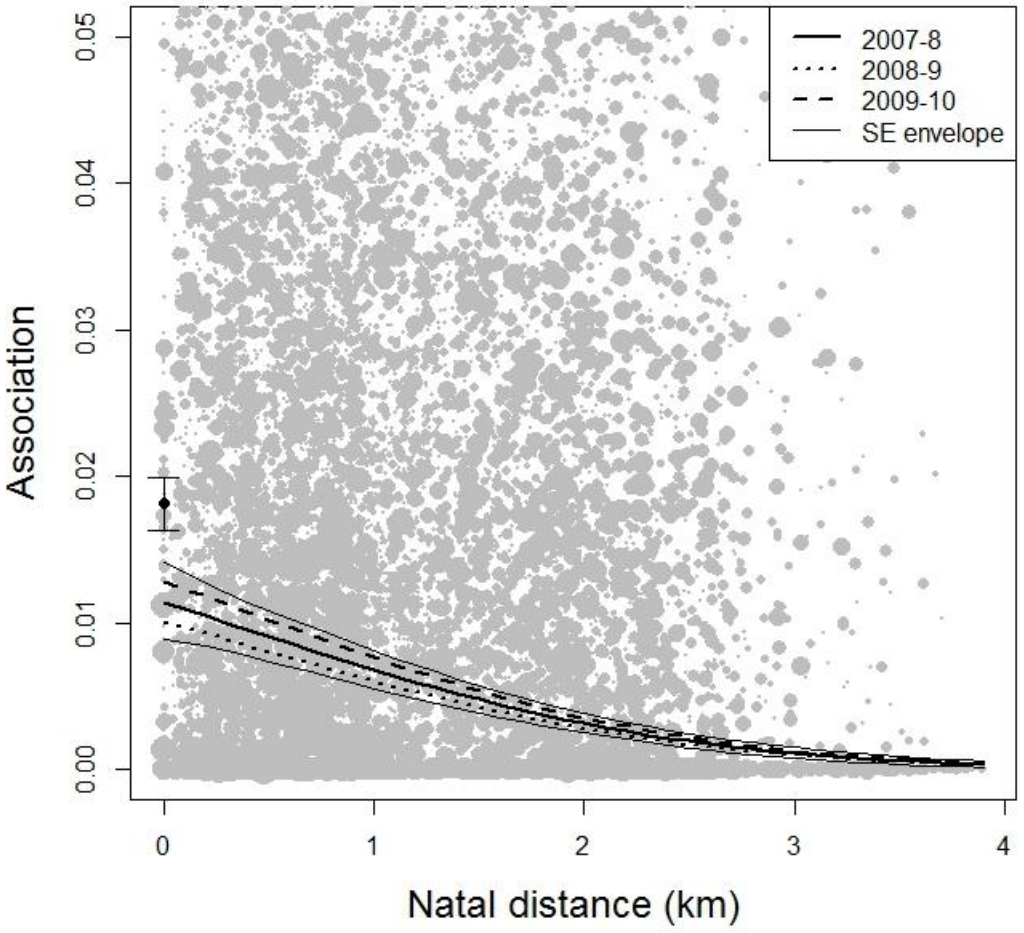


Figure 5.1: Effect of natal distance on juvenile great tit associations predicted from the top model (Δ AIC = 0), in three different seasons. X axis includes the full range of natal distances in the data. Average sibling association strength and its SE is shown for comparison with the model predicting associations based on natal distance alone. Thinner solid lines represent SE envelope for the slopes across the three seasons. Points are raw data of all possible associations ($n = 144,870$), including zero associations. The summary of observed association ranges for different distance classes can be found in Figure S2 in Supplementary Material).

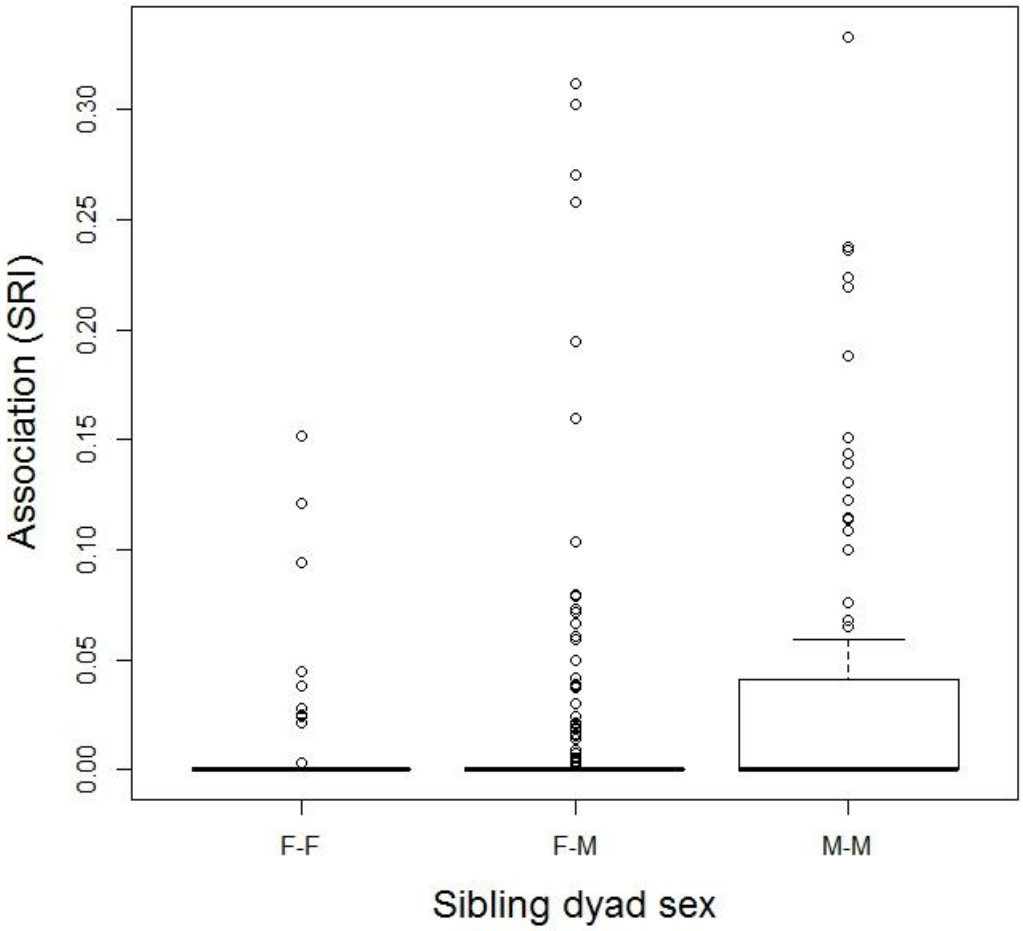


Figure 5.2: Median associations between siblings of known sex. "F-F" group are pairs of sisters, "F-M" are opposite sex sibling pairs, and"M-M" are pairs of brothers. Boxes represent interquartile range.

pairs, but when they do, their associations are of similar strength.

5.4 Discussion

This study shows that the location of fledging, and to a much lesser extent, time of fledging, have implications for the composition of the social environment that

juvenile great tits are exposed to. Both the spatial and the temporal distance had the expected, negative effect on association, as separation in space and time are both likely to reduce the probability of encounters, rather than facilitate them. The finding that birds that were born closer together in space associate more closely is most likely a result of the constraints put on feeding associations by the natal dispersal distance distribution. Most birds disperse a much shorter distance than those covered by the continuous habitat of the study site (median distance 788 m for females, 528 m for males) (Szulkin and Sheldon 2008b), therefore birds born relatively closer together will have a greater chance of temporarily residing in the same area than birds born further apart. These constraints may point to a spatial self-structuring process operating in the population (Lion and van Baalen 2008). Asynchrony in hatching dates had a significant, albeit small (Table 5.4), negative effect on associations. It is possible that such a small effect has little biological relevance in the population, but one potential process causing this effect is that families that are synchronous in breeding will also be more likely to break apart closer in time, increasing the chances of encounters between synchronous juveniles as they leave family groups. These results point to the importance of natal social context for interactions during dispersal. Recent work suggests that public and social information play a role in dispersal in other taxa (Cote and Clobert 2007) as well as among birds (Doligez et al. 2002; Parejo et al. 2007), including great tits (Michler et al. 2011). Conspecifics hatching at a similar time might thus play a role in the social environment of an individual. Exposure to

migrants from different areas also may provide social information for dispersing individuals.

Contrary to our prediction, pairs of siblings associated more than pairs of unrelated birds (Table 5.4). Higher association values between siblings may partly be explained by the fact that they originate from the same natal nest box, and fledge synchronously. However, the significant residual effect of kinship after these spatial and temporal factors have been taken into account suggests that siblings associate more even when accounting for their origin, and suggests that kin competition may not be very important during winter vagrancy (Lambin et al. 2001). In fact, the higher association of relatives once similarity in spatial and temporal origin had been accounted for suggests the possibility of cooperative alliances. The kinship effect is maintained when accounting for time of year, suggesting that the effect is not caused by the association of siblings that have not moved from the natal area early in the season.

Partitioning sibling associations between sex for individuals for which sex was known revealed that higher sibling association is largely driven by increased frequency of association between brothers (Figure 5.2), though we acknowledge that the effect can only be interpreted for the subset of individuals for which sex is known (birds that successfully recruited to the breeding population or were trapped independently). The lower association rate for brother-sister pairs than in brother pairs is in the direction expected for inbreeding avoidance operating in the population. The spatial proximity of brothers is initially surprising, since

it could increase the incidence of related males competing for territory vacancies before breeding. Budding dispersal (dispersal with kin) (Goodnight 1992) usually occurs in cooperative organisms such as social insects (Peeters and Ito 2001), cooperatively breeding birds and mammals (Clutton-Brock 2002; Sharp et al. 2008), and primates (Bradley et al. 2007). Kin discrimination in the great tit has mostly been studied in the context of mate choice (Kawano et al. 2009) and inbreeding avoidance (Van Tienderen and Van Noordwijk 1988). Great tits do not actively discriminate against related mates by divorcing or increasing promiscuity (Szulkin and Sheldon 2008a); very little is still known about kin recognition prior to mating (Szulkin et al. 2009) and intrasexual kin recognition.

Nevertheless, we demonstrate for the first time a social association between kin independent of spatial proximity. It is possible that in the absence of active kin recognition, brothers associate as a result of some other ecological or behavioural process. For example, brothers might associate more thanks to a well-established dominance relationship which leads to less conflict over access to food. Familiarity with nearby conspecifics has been shown to have fitness benefits in juveniles of other taxa (Liebgold and Cabe 2008; Seppa et al. 2001) and in experienced territorial great tits (Grabowska-Zhang et al. 2012). If brothers establish hierarchy before dispersing, they might reap benefits from each other's proximity due to reduced aggressive interactions (Fisher 1954). Great tit siblings have been shown to have correlated dispersal directions (Matthysen et al. 2005), which is likely to be linked to higher rates of association. However, the direction of causality

in this instance is a matter of speculation. Siblings may be associating because they are dispersing in a generally similar direction, or they settle closer to each other as a result of social viscosity in winter. Alternatively, both can result from behaviours occurring before dispersal, such as post-fledging family movements (van Overveld et al. 2011).

This study shows the importance of extrinsic factors on the social environment that juvenile great tits are exposed to. The spatial and temporal limitations to winter associations can affect the number and the quality of individuals a juvenile bird meets, which may in turn affect fitness-related decisions such as mate choice and the choice of settlement habitat. The spatial structure of the winter population may have consequences in the form of the non-random structure of the Wytham population observed during breeding (Szulkin et al. 2009), although a causal link between the two is yet to be established.

The presence of kin associations and social viscosity can have implications for the evolutionary role of population structuring. Firstly, dispersal may not necessarily lead to dissolution of kin structure, as is frequently assumed. Here we show sibling associations after accounting for spatial factors, which is reflective of kin structure in dispersing juveniles. Secondly, kin structure in associations can enable kin selection to operate within the population. While usually studied in the context of social species such as cooperative breeders, kin structure is widespread also in solitary and territorial animals (Foerster et al. 2006; Sera and Gaines 1994; Støen et al. 2005) and may give rise to kin-biased behaviours under

kin selection (Hatchwell 2010). Thirdly, the evolution of cooperation, whether by the means of kin selection or not, may depend on socially mediated population structuring. Given that many models for the evolution of cooperation require a form of population viscosity (Grafen and Archetti 2008; Hamilton 1964; Lion and van Baalen 2008; Taylor 1992), social viscosity maintained despite dispersal may be important for our understanding of evolution of cooperation and sociality in different systems.

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Chapter 6

Discussion

This thesis explored different aspects of sociality in the great tit and its links to individual fitness. I investigated social behaviour in decreasing order of the time-scale between social behaviour and its fitness consequences. In the first two chapters I focused on between-year familiarity in a territorial context to which which only experienced breeders are exposed. In the following two chapters I investigated social behaviour in the winter and its consequences for fitness on a finer time-scale, between winter and the subsequent spring. I also explore the within-season patterns of social associations in the pool of juveniles during the vagrancy stage of dispersal and identified kin structure in the pattern of associations in winter.

6.1 Summary of principal findings

The first two chapters of my thesis explored familiarity in a territorial context. In Chapter 2, using 41 years of breeding data from Wytham great tit popula-

tion, I quantified between-year familiarity between territorial neighbours and its relationship with five measures of reproductive success. Females with more familiar neighbours laid larger clutches, and both sexes benefitted from familiarity with neighbours by having an increased chance of fledging at least one young. The effect was predominantly caused by the between-individual variation in the response, suggesting that individuals respond differently to their social environment during the breeding season. Controlling for spatial structure in the analysis disentangled social effects from the effect of autocorrelation in reproduction measures within close neighbourhoods, suggesting true familiarity effect independent of spatial clusters of individuals with higher survival and thus familiarity. The increased nesting success of individuals surrounded by familiar neighbours led to new hypotheses about the mechanisms behind this pattern.

One of these hypotheses was tested experimentally in Chapter 3. Nest predation has a major impact on nesting success (McCleery and Perrins 1991; Ricklefs 1969), and nest defence behaviour by familiar neighbours could be involved in increasing the chance of nesting success. I hypothesised that familiar neighbours will be more likely to join each other in nest defence. Indeed, neighbours that shared a territory boundary the year before joined mobs more often than neighbours that did not, and neighbours that were first-time breeders. While the experiment did not explicitly test for whether such coalitions are a result of by-product mutualism (*sensu* Russell and Wright 2009) or reciprocity, it demonstrated a different response to stimuli from familiar versus unfamiliar individuals. Given the

importance of numbers for the effectiveness of mobbing behaviour (Krams et al. 2009) and the demonstrated preference for joining depending on familiarity, it is plausible that nest defence coalitions are one of the mechanisms through which individuals benefit from familiarity with neighbours.

In Chapter 4, I investigated the foraging associations of individuals in winter. I used winter logger detections to identify individuals' strongest associates for each month and quantified the turnover in the pool of those associates as a measure of stability in an individual's social environment. I then used stability as a predictor of the probability that an individual is recorded breeding in the study population, as well as a predictor of five measures of reproductive success. My results show that stability is a useful predictor of the probability of breeding, with chances of breeding being higher when social stability is high. This effect was due to the within-individual component of variance in stability, that is, individuals measured more than once varied in their probability of breeding depending on their social stability. This suggested that the response to social stability is plastic within individuals and that my measure of social stability reflects social behaviour changes prior to breeding in the study population. The lack of between-individual effect argues against the presence of intrinsic differences between individuals that make birds with less stable relationships more likely to emigrate or die. I also identified a between-individual effect of stability on fledgling mass, where individuals that had, on average, more stable social environments also tended to fledge heavier offspring. The between-individual effect suggested that there are inherent differ-

ences between individuals that cause some individuals to maintain social stability in winter as well as have heavier fledglings in breeding.

Finally, in Chapter 5, I looked at the structure of winter associations in juvenile great tits. I used spatial (nest of origin) and temporal (time of fledging) factors to predict the strength of associations between juveniles in the vagrant stage of the natal dispersal. I also asked whether the association between siblings is stronger than that predicted predominantly by sharing the same nest of origin and to a lesser extent, time of fledging. I found that sibling associations are stronger than expected from spatial and temporal factors alone. I also identified that the increased rate of association between siblings is driven by higher rates of associations between brothers. By identifying kin structure in the winter population I uncovered scope for kin-biased behaviours that could be kin-selected. It is uncertain whether cooperative tendencies exist among kin in the great tit, and stronger associations between brothers may be a result of another process that operates among juveniles. For example stable relationships originating from family groups pre-dispersal can be beneficial due to reduced aggression between familiar individuals in a novel group. The presence of kin structure in a population is important for the possibility of kin selection, and understanding how this structure arises has implications for our understanding of the evolution of sociality.

6.2 Perspectives

6.2.1 Familiarity and cooperation

The benefits of familiarity for reproduction, as well as the demonstrated different behavioural response towards familiar individuals, supports the importance of stable relationships in cooperation. In his seminal paper, Trivers (1971) pointed out that reciprocity-based cooperation will evolve in species that have the potential for repeated interactions with the same individuals, allowing cooperators to build a reputation that will facilitate further exchanges. Since mechanisms behind cooperative nest defence in great tits are still unclear, it is important to note that reciprocity is not unique in that respect and that cooperation maintained by other mechanisms, such as mutual benefits to cooperators, have also demonstrated reputational effects (reviewed by Clutton-Brock 2009).

Simple conceptual frameworks for cooperation such as the Prisoner's Dilemma ignore social structure and assume equal probability of contact between cooperators and defectors. However, recent models for the evolution and maintenance of cooperation show that social substructure favours cooperation, because it allows cooperators to choose partners for interaction (Ohtsuki et al. 2006; Santos et al. 2006). Following simple rules-of-thumb may provide individuals with a way of choosing partners for interactions that minimise their risk of being exploited by defectors. Familiarity may be considered as one of such mechanisms in that it provides a simple way of assessing individuals based on their interaction history.

Individuals may prefer to interact with those partners they previously interacted with, as newcomers may have bad, or unknown, reputation for participating in cooperative tasks (El Mouden and Gardner 2008).

In studies of cooperative behaviours, ideally one would be able to measure all the parameters that are required to pinpoint the mechanism behind the pattern of cooperation. To truly show reciprocity, for instance, an empirical study would have to show temporary fitness costs to the actor, which are often difficult to assess or quantify. Furthermore, different mechanisms may be operating simultaneously, and may be impossible to disentangle. It is possible, however, to identify conditions and behaviours that aid cooperation independent of the underlying mechanism. Different responses to former neighbours demonstrated in Chapter 3 suggests that reputation effects operate in Wytham great tits, at least in cooperative nest defence. This differentiation between relatively old, and new relationships is likely to be contributing to the positive fitness consequences of familiarity identified in Chapter 2. Further investigation into this question can tell whether such differentiation is adaptive, or perhaps a by-product of a different behavioural mechanism.

6.2.2 Fitness and social networks

In this thesis I used social network analysis to investigate the link between sociality in winter and spring reproduction. The notable result in Chapter 4 was that probability of breeding was predicted by the within-individual effect of so-

cial stability. The lack of between-individual effect argues against the existence of different types of individuals, perhaps inherent emigrants and inherent local recruits, and suggests a plastic response to the social environment within individuals. What remains to be answered is whether stability is causal in its effect and, for example, individuals with stable bonds benefit from reduced stress and starvation risk and are more able to survive and settle to breed. Alternatively the factors that cause local settlement as opposed to emigration or death could also affects patterns of social behaviour. Social experiences and their consequences vary between species. For the great tit, a relatively unsocial bird species, social stability proves to be more beneficial than change. Some studies, in contrast, have shown a positive effect of social lability (Oh and Badyaev 2010; White et al. 2010) on fitness. Social networks studies are still predominantly performed on species that form separate, identifiable groups that can be recorded by visual observation. The automated detection system employed in this study allowed observation of a comparatively much more volatile social structure (Krause et al. 2011). The species' different ecologies and levels of sociality determine what selective pressures are acting on individuals' social environment. Other population or species-specific factors are likely to be at play in determining the consequences of social behaviour.

As great tits are subject to many environmental effects in other stages of their lives, environmental stochasticity may also play an important part in how individuals respond to their social environment. The three winters when logging

data was collected, for instance, were relatively harsh (personal observation), and without large beech mast crops, which is a strong predictor of great tit winter survival (Perdeck et al. 2000). Increased starvation risk may turn selective pressure towards favouring stable relationships and against dominance hierarchy disputes that would be connected with changing social environments. An assessment of impacts of different ecological factors, such as starvation versus predation risk on the social structure in different networks would aid in identifying crucial components affecting how social structure ties in with fitness in Wytham great tits.

6.2.3 Sociality and kin structure

My findings in Chapter 5 highlight the importance of natal context even during the winter vagrant phase in juvenile great tits. This result is in agreement with recent studies of the importance of natal context for information gathering, dispersal and settlement decisions (Doligez et al. 2002; Michler et al. 2011; Parejo et al. 2007). Further in-depth analysis of social contacts in the winter may aid interpretation of the role played by intraspecific sociality for subsequent decisions in vagrant individuals.

My work also showed a degree of kin structure in the social associations of vagrant juveniles. Further partitioning of sibling associations showed increased associations between brothers, which does not conflict with the current standing view that dispersal in the great tit plays an inbreeding avoidance function (Szulkin

and Sheldon 2008). While the result is surprising in light of the kin-competition avoidance role of dispersal, empirical evidence of kin competition is rather weak in many natural populations (Hatchwell 2010; Lambin et al. 2001).

My results show that dispersal may not always lead to the dissolution of kin structure, which has its implications for how population structure arises and is maintained in natural populations and the evolutionary role it plays. Kin structure makes kin selection possible in a population, and therefore the demonstration of socially-mediated population viscosity has its implications for the scope for kin-biased behaviours to be kin selected in a population. Kin selection is one of the most strongly supported mechanism explaining cooperation, both in empirical (e.g. Bradley et al. 2007; Clutton-Brock 2002; Sharp et al. 2008) and theoretical work (Hamilton 1964a, b; Lion and van Baalen 2008; Taylor 1992). The existance of socially-mediated kin structure in a population that otherwise exhibits very little kin clustering may widen our understanding of the evolutionary pathways leading to sociality.

6.3 More questions on sociality in the great tit

This thesis explored several different aspects of social behaviour in the great tit. Although it was able to identify several ways in which sociality affects the lives of individuals, it has also uncovered new questions we can ask about sociality in this species:

- This thesis proposed a potential mechanism behind improved probability of

nest success by individuals with familiar neighbours identified in Chapter 2, that I tested experimentally in Chapter 3. Further investigation should help elucidate why females with familiar neighbours lay larger clutches. A more detailed investigation into space use and neighbour interactions in the breeding season, perhaps using radio telemetry or the forthcoming RFID proximity tags (Krause et al. 2011), may help shed more light on more detailed effects of neighbour interactions. Perhaps reduced agonistic interactions and increased tolerance allow the female to improve her condition prior to egg-laying.

- Joining in neighbour nest defence can help minimise real or perceived predation risk in familiar neighbours. Chapter 3 showed great tits join mobs of familiar neighbours more often than unfamiliar ones, but the mechanism behind this response remains unresolved. Further experiments with the explicit aim of teasing apart signs of reciprocity from mutualism can shed more light on what best explains cooperative nest defence in great tits. Among other factors, measuring the fitness costs of joining would be essential for verifying reciprocity as an operating mechanism (Clutton-Brock 2009).

- The importance of social associations in winter can be further explored by investigating individual network metrics and their effects on fitness (Hinde et al. in preparation). Although Chapter 4 managed to tease apart some effects that are due to differences between individuals (and imply phenotypic

variation) and those that are due to different reactions within individuals (and imply phenotypic plasticity), more answers are needed. Does the lack of stability cause a lower probability of breeding the following spring, or is it a reflection of an external cause that also affects the social environment? Is the cause for not breeding emigration or mortality? Can we tentatively predict mortality or emigration from observing social behaviour? Further investigation into how social stability relates to territory and mate acquisition can help us to understand the impact of sociality on subsequent breeders.

- The investigation of structure in juvenile associations revealed social affiliation between brothers. A more detailed look at brother associations can answer how these affiliations arise and whether there are benefits to associating with kin in the winter. Measurement of any potential benefits of such affiliations can help identify whether kin selection operates on winter associations in Wytham population.

6.4 Overall conclusion

My thesis presented several aspects of social behaviour in the great tit and its consequences for individual fitness using long term breeding study data and automated logging of foraging association in the Wytham great tit population.

I have provided evidence for fitness benefits of long term familiarity between territorial neighbours, and experimentally shown that cooperation between familiar

neighbours is operating in the population. The clear effects of social interactions in a species that does not rank high on the sociality scale is noteworthy, as it suggests that even species that are not considered to lead very social lives can respond to very fine social cues that are sometimes hard to observe. I have also shown that the fine resolution foraging associations in winter also have an effect on the subsequent fitness of individuals, which also supports the assertion that individuals can respond to much finer stimuli than is sometimes assumed. I identified patterns of kin affiliation in vagrant juveniles despite natal dispersal, which suggests the potential for cryptic kin selection (Hatchwell 2010) on kin-directed behaviours that may be present during winter vagrancy.

The study of sociality in birds has been ongoing for many decades, and yet new patterns in the context of social behaviour continue to emerge. Novel technological approaches enabled the observation of social associations on a population scale. As the resolution and quantity of social behaviour data increases, so will the number of studies into their structure and significance. This will allow a better understanding into the patterns and evolutionary importance of sociality in species in which sociality is cryptic.

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Appendix A

Supplementary Material for Chapter 2

Supplementary material

	Female - both sexes	Female - Female	Female - Male	Male - Male
	ID:2 148, year: 40	ID: 1 183, year:40	ID: 1 936, year: 40	ID: 1 758, year:40
LD	ID: 3.06352 (1.75029)	ID: 4.738243 2.17675	ID: 2.442 (1.563)	ID: 4.48537 (2.11787)
	year:	year:	year:	year:
	(Intrc)38.93634 (6.2399)	(Intrc) 46.588 (6.826)	(Intrc)12.18155 (3.4902)	(Intrc)11.552 (3.399)
	FAMw 0.41450 (0.64382)	FAMw 1.473 (1.214)	FAMw 1.20324 (1.0969)	FAMw 0.079 (0.281)
	NNw 0.37495 (0.61233)	NNw 0.543 (0.737)	NNw 8.30668 (2.88213)	NNw 0.083 (0.2878)
	famb 0.17021 (0.41256)	FAMb 0.0737 (0.271)	FAMb 0.2291 (0.47869)	FAMb 0.0175 (0.132)
	NNb 0.26643 (0.51617)	NNb 0.901 (0.949)	NNb 0.64806 (0.80502)	NNb 0.007 (0.084)
CS	ID: 0.92339 (0.96093260)	ID: 1.061 (1.030)	ID: 0.958 (0.979)	ID: 0.862 (0.928)
	year:	year:	year:	year:
	(Intrc) 0.47470 (0.689)	(Intercept) 0.40103 (0.633)	(Intrc)0.394 (0.628)	(Intrc) 0.388 (0.623)
	FAMw 3.5585e-04 (0.0189)	FAMw 2.5623e-03 (0.0506)	FAMw 0.0077 (0.088)	FAMw 0.00215(0.0464)
	NNw 3.2588e-08 (0.000181)	NNw 3.3031e-04 (0.0182)	NNw 0.223 (0.472)	NNw 0.331 (0.576)
	FAMb 1.2719e-03 (0.0357)	FAMb 1.3751e-06 0.00117	FAMb 0.0091(0.0954)	FAMb 0.00494 (0.0703)
	NNb 4.1142e-02 (0.203)	NNb 2.1994e-03 (0.0469)	NNb 0.0181 (0.134)	NNb 0.000746 (0.0273)
FM	ID: 5.625 (2.372)	ID: 5.31366 2.30514	ID: 3.943 (1.986)	ID: 1.117 (1.0567)
	year:	year	year:	year:
	(Intrc) 12.390768 (3.52005)	(Intrc) 10.224 (3.197)	(Intrc)12.128 (3.483)	(Intrc) 6.912 (2.629)
	FAMw 0.0489 (0.221)	FAMw 0.102 (0.319)	famw 0.801 (0.895)	FAMw 0.487 (0.698)
	NNw 0.0781 (0.280)	NNw 0.129 (0.35869)	NNw 0.0509 (0.226)	NNw 1.298 (1.139)
	FAMb 0.0567 (0.238)	FAMb 0.583 (0.764)	famb 0.2195 (0.469)	FAMb 0.0854 (0.292)
	NNb 0.730439 0.85466	NNb 0.731 (0.855)	NNb 2.575 (1.605)	NNb 1.709 (1.307)

NS	ID: 0.51116 (0.715)	ID: 0.535 (0.731)	ID: 0.2733 (0.523)	ID: 5.662 (2.379)
	year:	year :	year:	year:
	(Intrc) 1.5223 (1.233818)	(Intrc) 1.253 (1.119)	(Intrc)1.418 (1.191)	(Intrc) 0.914 (0.956)
	FAMw 2.3483e-03 (0.0485)	FAMw 0.0213 (0.146)	FAMw 0.0888 (0.298)	FAMw 0.368 (0.607)
	NNw 1.013e-03 (0.0318)	NNw 0.00402 (0.0634)	NNw 0.00237 (0.0487)	NNw 0.139 (0.373)
	FAMb 5.82e-05 (0.00763)	FAMb 0.145 (0.381)	FAMb 0.00498 (0.0706)	FAMb 0.216 (0.464)
	NNb 6.1396e-02 (0.247783)	NNb 0.0464 (0.215)	NNb 0.372 (0.610)	NNb 0.546 (0.739)
RS	ID: 0.658 (0.811)	ID: 0.622 (0.789)	ID: 0.692 (0.832)	ID: 0.751 (0.866)
	year:	year:	year:	year:
	(Intrc) 0.557471 (0.74664)	(Intrc) 0.570 (0.755)	(Intrc)0.510 (0.714)	(Intrc) 0.414 (0.643)
	FAMw 0.0521 (0.228)	FAMw 0.0800 (0.283)	FAMw 0.233 (0.483)	FAMw 0.121 (0.348)
	NNw 0.105 (0.324)	NNw 0.363 (0.602)	NNw 0.381 (0.618)	NNw 0.744 (0.863)
	FAMb 0.0184 (0.136)	FAMb 0.0205 (0.143)	FAMb 0.0318 (0.178)	FAMb 0.0469 (0.217)
	NNb 0.0262 (0.162)	NNb 0.326 (0.571)	NNb 0.0761 (0.276)	NNb 0.510 (0.714)

Table S1. Summary of Random effects in each of the global models (Variable: Variance(SD)). Top column contains number of groups for each random factor.

Response: AVF				
Candidate model	Deviance	AICc	Delta	Weight
SRV+REC	0.05	-147.58	0	0.57
SRV+POP+REC	0.05	-145.33	2.24	0.19
SRV	0.05	-144.52	3.06	0.12
SRV+POP	0.05	-144.39	3.19	0.12

REC is the recruitment rate measured as the mean number of recruits per brood, SRV is the adult survival rate, POP is population size. The dependent variable is AVF - the mean familiarity in a year.

Table S2. Summary of model selection predicting mean annual familiarity. The top model has the lowest AIC_C value by 2.24.Given that support, we used the top model only for inference about the level of mean familiarity.

Parameter	Estimate†	SE	t value	Pr(>|t|)
(Intercept)	0.120451	0.005609	21.475	<2e-16
REC	-0.0292	0.012465	-2.343	0.0246
SRV	0.038624	0.012465	3.099	0.0037

REC is the recruitment rate measured as the mean number of recruits per brood, SRV is the adult survival rate. The dependent variable is AVF - the mean familiarity in a year.

Table S3.Top model predicting mean annual familiarity.

	Estimate†	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.308	0.3423	-12.583	<0.001
DIS	-0.00545	0.000263	-20.699	<0.001
TER	-3.8E-06	1.61E-06	-2.324	0.0201
EDG	0.000755	0.000165	4.58	<0.001
AC	24.45	3.307	7.391	<0.001

DIS - distance moved from previous year, EDG - distance from the edge of the forest, TER - territory size, AC - spatial autocovariate. Global model also contained AGE - the age of the focal breeder, and ALT - altitude.

Table S4. Top model predicting familiarity for neighbors of either sex of the female.

	Estimate†	Variance	SE	Unconditional SE	Lower CI	Upper CI	Relative importance
(Intercept)	-3.75	0.0413	0.451	0.451	-4.63	-2.86	
AC	17.2	166	3.59	3.59	10.1	24.2	1
DIS	-0.00447	1.25E-14	0.000335	0.000335	-0.00513	-0.00382	1
EDG	0.000553	2.31E-15	0.000219	0.000219	0.000123	0.000982	1
TER	-3.4E-06	2.03E-23	2.12E-06	2.12E-06	-7.6E-06	7.29E-07	0.58

DIS - distance moved from previous year, EDG - distance from the edge of the forest, TER - territory size, AC - spatial autocovariate. Global model also contained AGE - the age of the focal breeder, and ALT - altitude.

Table S5. Averaged model predicting familiarity for female neighbors of female.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.605	0.497	-7.253	<0.001
DIS	-0.00645	0.000419	-15.406	<0.001
TER	-5.9E-06	2.59E-06	-2.263	0.02365
EDG	0.001001	0.000253	3.952	<0.001
AC	18.19	4.683	3.883	<0.001

DIS - distance moved from previous year, EDG - distance from the edge of the forest, TER - territory size, AC - spatial autocovariate. Global model also contained AGE - the age of the focal breeder, and ALT - altitude.

Table S6. Top model predicting familiarity for male neighbors of the female

	Coefficient	Variance	SE	Unconditional SE	Lower CI	Upper CI	Relative importance
(Intercept)	-3.95	0.0231	0.39	0.39	-4.71	-3.18	
AC	14.4	30	2.34	2.34	9.84	19	1
DIS	0.0106	8.03E-06	0.0532	0.0533	-0.0938	0.115	0.25
EDG	0.000283	2.7E-15	0.000228	0.000228	-0.00016	0.00073	0.41
TER	-5.5E-06	3.01E-23	2.34E-06	2.34E-06	-1E-05	-9.1E-07	0.93

DIS - distance moved from previous year, EDG - distance from the edge of the forest, TER - territory size, AC - spatial autocovariate. Global model also contained AGE - the age of the focal breeder, and ALT - altitude.

Table S7. Averaged model predicting familiarity for male neighbors of the male.

Candidatate model	Deviance	AICc	Delta	Weight	Evidence ratio
Response: LD					
FS*+ALT+DIS	23022.71	23036.74	0	0.72	1
FS*+ALT+DIS+FAMw	23022.58	23038.62	1.88	0.28	0.388889
Response: CS					
AC+FAMb+LD	13124.36	13138.39	0	1	na
Response: FM					
ALT+CS+TER	22557.17	22571.2	0	0.28	1
ALT+CS+LD+TER	22555.61	22571.66	0.46	0.22	0.785714
ALT+CS+FAMb+TER	22555.74	22571.78	0.58	0.21	0.75
ALT+CS+FAMb+LD+TER	22554.29	22572.34	1.14	0.16	0.571429
ALT+CS+NNb**+TER	22556.85	22572.89	1.69	0.12	0.428571
Response: NS					
ALT+CS+FAMb+TER	2539.67	2553.7	0	0.15	1
ALT+CS+TER	2541.95	2553.97	0.27	0.13	0.866667
ALT+CS+NNb**+TER	2540.19	2554.23	0.52	0.12	0.8
AC+ALT+CS+FAMb+TER	2538.82	2554.86	1.16	0.08	0.533333
ALT+CS+FAMb+LD+TER	2539.09	2555.13	1.43	0.07	0.466667
ALT+CS+FAMb+NNb**+TER	2539.11	2555.15	1.44	0.07	0.466667
AC+ALT+CS+TER	2541.14	2555.17	1.47	0.07	0.466667
AC+ALT+CS+NNb**+TER	2539.31	2555.35	1.65	0.07	0.466667
ALT+CS+LD+TER	2541.34	2555.37	1.66	0.07	0.466667

ALT+CS+FAMb+FAMw+TER	2539.58	2555.62	1.91	0.06	0.4
ALT+CS+LD+NNb**+TER	2539.58	2555.62	1.92	0.06	0.4
ALT+CS+FAMb+NNw**+TER	2539.6	2555.65	1.94	0.06	0.4
Response: RS					
AC+FM+LD+NNb**+TER	5651.01	5667.05	0	0.45	1
AC+FAMb+FM+LD+NNb**+TER	5649.99	5668.04	0.99	0.28	0.622222
AC+FM+LD+NNb**+NNw**+TER	5650.02	5668.07	1.02	0.27	0.6

Table S8. Model selection summary for focal female's reproductive traits depending on her familiarity with neighbors of either sex. Models differing from the top model in their AIC value by less than 2 are displayed and used for model averaging.

Response: LD					
	Deviance	AICc	Delta	Weight	Evidence ratio
AC+FS*+ALT+NNb**	23600.55	23616.59	0	0.98	1
AC+ALT+FAMb+NNb**	23608.39	23624.43	7.84	0.02	0.020408
Response: CS					
AC+LD	12474.41	12486.43	0	0.58	1
AC+LD+TER	12473.09	12487.12	0.68	0.42	0.724138
Response: FM					
ALT+CS+NNb**+TER	21483.84	21499.88	0	0.15	1
ALT+CS+NNb**+NNw**+TER	21482.13	21500.18	0.3	0.13	0.866667
ALT+CS+LD+NNb**+TER	21482.37	21500.42	0.54	0.11	0.733333

AC+ALT+CS+NNb**+TER	21482.71	21500.76	0.88	0.1	0.666667
ALT+CS+LD+NNb**+NNw**+TER	21480.79	21500.86	0.98	0.09	0.6
AC+ALT+CS+NNb**+NNw**+TER	21480.91	21500.98	1.1	0.09	0.6
ALT+CS+TER	21487.18	21501.22	1.33	0.08	0.533333
AC+ALT+CS+LD+NNb**+TER	21481.37	21501.44	1.56	0.07	0.466667
ALT+CS+NNw**+TER	21485.52	21501.56	1.68	0.06	0.4
ALT+CS+LD+TER	21485.55	21501.6	1.71	0.06	0.4
AC+ALT+CS+LD+NNb**+NNw**+TER	21479.72	21501.8	1.92	0.06	0.4
Response: NS					
AC+ALT+CS+NNb**+NNw**+TER	2377.72	2395.77	0	0.26	1
AC+ALT+CS+NNb**+TER	2380.36	2396.4	0.63	0.19	0.730769
AC+ALT+CS+FAMb+NNb**+NNw**+TER	2376.35	2396.41	0.64	0.19	0.730769
AC+ALT+CS+FAMb+NNb**+TER	2379.02	2397.08	1.3	0.14	0.538462
AC+ALT+CS+LD+NNb**+NNw**+TER	2377.23	2397.3	1.53	0.12	0.461538
AC+ALT+CS+FAMw+NNb**+NNw**+TER	2377.58	2397.65	1.87	0.1	0.384615
Response: RS					
CS+FAMb+FM+LD+NNw**+TER	5480.19	5498.25	0	0.29	1
CS+FAMb+FM+LD+NNb**+NNw**+TER	5478.76	5498.83	0.58	0.22	0.758621
CS+FAMb+FM+LD+TER	5483.52	5499.56	1.31	0.15	0.517241
CS+FAMb+FM+LD+NNb**+TER	5482.03	5500.09	1.84	0.12	0.413793
CS+FAMb+FAMw+FM+LD+NNw**+TER	5480.12	5500.19	1.94	0.11	0.37931
AC+CS+FAMb+FM+LD+NNw**+TER	5480.12	5500.19	1.94	0.11	0.37931

Table S9. Model selection summary for focal female's reproductive traits depending on her familiarity with female neighbors. Models differing from the top model in their AIC value by less than 2 are displayed and used for model averaging.

Candidate model	Deviance	AICc	Delta	Weight	Evidence ratio
Response: LD					
FS*+AC+ALT+DIS+FAMw+WRM	20318.17	20338.25	0	0.17	1
FS*+AC+ALT+DIS+FAMw+NNb**+WRM	20316.34	20338.43	0.18	0.15	0.882353
FS*+AC+ALT+DIS+WRM	20320.56	20338.63	0.38	0.14	0.823529
FS*+AC+ALT+DIS+NNb**+WRM	20318.74	20338.81	0.57	0.13	0.764706
FS*+AC+DIS+FAMw+WRM	20321.13	20339.2	0.95	0.1	0.588235
FS*+AC+ALT+DIS+FAMb+FAMw+WRM	20317.55	20339.64	1.39	0.08	0.470588
FS*+AC+DIS+WRM	20323.61	20339.66	1.41	0.08	0.470588
FS*+AC+ALT+DIS+FAMb+WRM	20319.81	20339.88	1.64	0.07	0.411765
FS*+AC+ALT+DIS+FAMb+FAMw+NNb**+WRM	20316.04	20340.15	1.9	0.07	0.411765
Response: CS					
AC+FAMb+LD	10899.16	10913.2	0	0.64	1
AC+FAMb+LD+NNw**	10898.26	10914.32	1.11	0.36	0.5625
Response: FM					
AC+ALT+CS+FAMb+TER	18529.28	18547.35	0	0.32	1
ALT+CS+FAMb+TER	18532.08	18548.13	0.78	0.22	0.6875
AC+ALT+CS+FAMb+NNw**+TER	18528.22	18548.29	0.95	0.2	0.625
ALT+CS+FAMb+NNw**+TER	18530.91	18548.98	1.63	0.14	0.4375
AC+ALT+CS+FAMb+NNb**+TER	18529.21	18549.29	1.94	0.12	0.375
Response: NS					
ALT+CS+FAMb+TER	2043.33	2057.37	0	0.26	1

ALT+CS+FAMb+NNb**+TER	2042.2	2058.25	0.88	0.17	0.653846
ALT+CS+FAMb+NNw**+TER	2042.35	2058.4	1.03	0.15	0.576923
AC+ALT+CS+FAMb+TER	2042.87	2058.93	1.56	0.12	0.461538
ALT+CS+FAMb+FAMw+TER	2043.11	2059.16	1.79	0.11	0.423077
ALT+CS+FAMb+NNb**+NNw**+TER	2041.14	2059.2	1.83	0.1	0.384615
ALT+CS+FAMb+LD+TER	2043.31	2059.36	1.99	0.1	0.384615
Response: RS					
AC+CS+FAMb+FM+LD+NNw**+TER	4547.79	4567.87	0	0.34	1
AC+CS+FM+LD+NNw**+TER	4550.87	4568.93	1.06	0.2	0.588235
AC+CS+FAMb+FM+LD+TER	4551	4569.07	1.2	0.19	0.558824
CS+FAMb+FM+LD+NNw**+TER	4551.72	4569.79	1.92	0.13	0.382353
AC+CS+FAMb+FAMw+FM+LD+NNw**+TER	4547.71	4569.8	1.93	0.13	0.382353

Table S10. Model selection summary for focal female's reproductive traits depending on her familiarity with male neighbors. Models differing from the top model in their AIC value by less than 2 are displayed and used for model averaging.

Candidate model	Deviance	AICc	Delta	Weight	Evidence ratio
Response: LD					
FS*+AC+ALT+WRM	15807.02	15823.08	0	0.37	1
FS*+AC+ALT+FAMw+WRM	15806.34	15824.42	1.34	0.19	0.513514
FS*+AC+ALT+TER+WRM	15806.8	15824.88	1.8	0.15	0.405405
FS*+AC+ALT+FAMb+WRM	15806.92	15825	1.92	0.14	0.378378
FS*+AC+ALT+NNw**+WRM	15806.97	15825.05	1.97	0.14	0.378378
Response: CS					
AC+LD	8660.13	8672.17	0	0.69	1
AC+LD+TER	8659.68	8673.73	1.56	0.31	0.449275
Response: FM					
AC	14155.03	14165.06	0	0.46	1
AC+ALT	14154.84	14166.88	1.82	0.18	0.391304
AC+TER	14154.84	14166.88	1.82	0.18	0.391304
AC+ALT+TER	14152.97	14167.01	1.95	0.17	0.369565
Response: NS					
AC+CS	1171.32	1181.35	0	0.21	1
AC+ALT+CS	1169.88	1181.92	0.57	0.15	0.714286
AC+CS+LD	1170.44	1182.47	1.13	0.12	0.571429
AC+ALT+CS+LD	1168.75	1182.8	1.45	0.1	0.47619
AC+CS+NNw**	1171.06	1183.1	1.75	0.09	0.428571

AC	1175.09	1183.1	1.76	0.09	0.428571
AC+CS+NNb**	1171.1	1183.13	1.78	0.08	0.380952
AC+CS+FAMb	1171.1	1183.14	1.79	0.08	0.380952
AC+CS+FAMw	1171.17	1183.2	1.86	0.08	0.380952
Response: RS					
CS+FAMb+FM+LD+TER	4138.89	4154.95	0	0.16	1
CS+FM+LD+TER	4140.92	4154.96	0.01	0.16	1
CS+FM+LD+NNw**+TER	4139.46	4155.52	0.56	0.12	0.75
CS+FAMb+FM+LD+NNw**+TER	4137.49	4155.56	0.61	0.12	0.75
CS+FAMb+FAMw+FM+LD+NNw**+TER	4135.7	4155.8	0.84	0.11	0.6875
CS+FAMw+FM+LD+NNw**+TER	4137.77	4155.85	0.9	0.1	0.625
CS+FAMb+FAMw+FM+LD+TER	4138.42	4156.5	1.55	0.08	0.5
CS+FAMw+FM+LD+TER	4140.51	4156.57	1.61	0.07	0.4375
CS+FAMb+FM+LD+NNb**+TER	4138.58	4156.65	1.7	0.07	0.4375

Table S11. Model selection summary for focal male depending on his familiarity with male neighbors. Models differing from the top model in their AIC value by less than 2 are displayed and used for model averaging.

Variable abbreviations:

Variable abbreviations in all tables:

LD - laying date

CS - clutch size

FM - mean fledgling mass

RS - number of recruits

FS - female status, resident or immigrant

AC - spatial autocorrelation covariate

ALT - altitude

DIS - distance moved from previous year

FAMb - between-individual component of the number of familiar neighbors

FAMw - within individual component of the number of familiar neighbors

NNb - between-individual component of familiarity with the nearest neighbor

NNw - within-individual component of familiarity with the nearest neighbor

EDG - distance from the edge of the forest

TER - territory size

RS - number of recruits

WRM - warmth sum, the sum of maximum daily temperatures from 1st to 25th April

* - Immigrant as the reference category

** - Unfamiliar as the reference category

Global models used in model selection in all datasets were as follows:

global.LD<- lmer (LD ~ NNb + NNw + FAMb + FAMw + TER + ALT + FST + DIS + AC + (1|ID) + (NNb + NNw + FAMb + FAMw |year), data, family = "gaussian")

global.CS<- lmer (CS ~ NNb + NNw + FAMb + FAMw + TER + LD + EDG + AC + (1|ID) + (NNb + NNw + FAMb + FAMw |year), data, family = "gaussian")

global.FM<- lmer (FM NNb + NNw + FAMb + FAMw + TER + LD + CS + ALT + AC + (1|ID) + (NNb + NNw + FAMb + FAMw |year), data, family = "gaussian")

global.NS<- lmer (NS NNb + NNw + FAMb + FAMw + TER + LD + CS + ALT + AC + (1|ID) + (NNb + NNw + FAMb + FAMw |year), data, family = "binomial")

global.RS<- lmer (RS NNb + NNw + FAMb + FAMw + TER + LD + CS + FM + AC + (1|ID) + (NNb + NNw + FAMb + FAMw |year), data, family = "poisson")

Appendix B

Supplementary Material for Chapter 3

Supplementary Material

1. Supplementary information about the study system

The great tit (*Parus major*) is a small (ca.18 g) European passerine common in temperate forests of Eurasia. Great tits nest in secondary tree cavities, but preferentially choose nest boxes for breeding. Juvenile great tits disperse from their natal area after fledging [1]. Previous work has shown that once first time breeders settle on a breeding territory, very little dispersal occurs in subsequent years [2]. Details of the standard nest-monitoring protocol for the study population can be found in [3].

When the young were between 8 and 12 days of age, the adults were trapped inside the nest box with a spring-loaded trap. Trapping began on day 8 of the nestling period to minimise the risk of nest desertion. The breeders were identified from their British Trust for Ornithology (BTO) ring, or ringed if it was their first capture. All birds in this population are fitted with a passive integrated transponder (PIT) tag when they are caught with a nest box trap, mist net or ringed in the nest. Therefore trap-shy birds which had been caught before or ringed as nestlings could be identified from their PIT tag, detected by an antenna fitted around the nest box opening.

Under the standard protocol in the population, chicks were ringed in the nest on day 15. Great tits usually fledge between 19 and 21 days of age, so we chose 17 days as the trial day to ensure that the young would still be in the nest. We try not to disturb the birds more than once in a day, and day 17 is mid-way between ringing and expected fledging. We also wanted to ensure a sufficient response from the parents themselves, so we chose a day late in the nestling period, as nest defence is stronger when nestlings are older [4].

Breeding territories were estimated using Dirichlet tesselation, which has been shown to approximate measures obtained with mapped territories. Tesselation constructs a polygon representing the territory by drawing edges that are equidistant to the focal nest box and its first order neighbours. Territories of experimental birds were matched against their territories in 2010, to verify between-year familiarity through being neighbours.

2. Supplementary information about the field protocol

As soon as data on breeder identity were available, candidate experimental nests were determined. The nests had to be in adjacent territories and synchronous enough for the trials at both nests to take place on the same day (chicks old enough so that the parents were trapped, but young enough to still be in the nest). Both nests had to contain breeders older than one year. Conversely, breeders in the 1st time breeder group had to be confirmed to be 1 year old. Seventeen pairs of nests met the conditions for older breeders. Eight pairs of nests with first year breeders were chosen for the third group. One nest containing older breeders failed between the ringing of chicks (day 15) and the trial (day 17). The fact that 8 out of 16 older breeder nest pairs were familiar, and the resulting equal sample sizes of experimental groups, was coincidental.

On the day of the trial, the focal nest and the candidate neighbour nest breeders were marked with non-conspicuous colours (brown and dull purple). Males and females can be distinguished in the field by the width of the black breast stripe on the under parts, and the combination of knowing the nest of origin (from paint markings) and sex enabled individual identification in the field. The presence and calls of other species were recorded during the trial.

In order to elicit mobbing at the focal nest, the experimenter stood directly beneath the focal nest box, which was suspended on a metal bracket on the main tree trunk between 2 and 3 metres above ground. On approach , the experimenter noisily moved dead leaves on the ground with her feet, then scraped the bark of the tree with a wooden pole, and finally, scraped the pole against the woodcrete © nest box, a sound that often elicits alarm calls from parents during routine nest monitoring (personal observation). The sequence of the movements was designed to imitate the sounds of approach, interest in the nest, and an attempt to enter the nest.

In several instances, the marked bird was heard before it could be seen from close enough to identify it from markings and sexual dimorphic traits. In these instances the time when the bird was first heard

was included as the joining time. Alarm calls were counted when they could be positively ascribed to a marked individual, which always happened within 2 minutes of first hearing them. Once mobbing began, it lasted until the end of the trial in every case, but continuous visual account of all calling birds proved difficult for longer periods, so we limited the call count period to one minute. Alarm calls comprised of a series of short "tink" calls, interspersed with longer, broad frequency "churring" calls.

No unmarked great tits were observed to mob during the trials. The natural variation in the population means that some of the other, unmarked neighbours would have fledged their brood by the time of the trial, or indeed, their brood would have failed before the trials. First years' nests surrounding older breeders nests might have also contributed to lack of response from other neighbours.

3. Supplementary information about the analysis

Arrival latency data were analysed using Cox proportional hazards model. Cox PH models were developed for survival data, as they represent a time-dependent data series. Latencies to mob can be viewed in the same way, with latency treated as survival time and joining event treated as a "death" event. All instances in which neighbours did not join were excluded from the analysis, as our question focused on the effect on latency for birds that did join the mob.

References:

1. Greenwood P.J., Harvey P.H., Perrins C.M. 1979 Role of dispersal in the Great Tit (*Parus-Major*) - causes, consequences and heritability of natal dispersal. *J Anim Ecol* **48**(1), 123-142.
2. Harvey P.H., Greenwood P.J., Perrins C.M. 1979 Breeding area fidelity of Great Tits (*Parus major*). *J Anim Ecol* **48**(1), 305-313.
3. Perrins C.M. 1965 Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J Anim Ecol* **34**(3), 601-647. (doi:10.2307/2453).
4. Regelmann K., Curio E. 1983 Determinants of Brood Defense in the Great Tit Parus-Major L. *Behav Ecol Sociobiol* **13**(2), 131-145.

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Appendix C

Supplementary Material for Chapter 4

Supplementary Material

	2007-08	2008-09	2009-10
month 1	20 Aug-30 Sep	22 Aug-30 Sep	27 Aug-30 Sep
month 2	1 Oct-31 Oct	1 Oct-31 Oct	1 Oct-31 Oct
month 3	1 Nov-30 Nov	1 Nov-30 Nov	1 Nov-30 Nov
month 4	1 Dec-31 Dec	1 Dec-31 Dec	1 Dec-31 Dec
month 5	1 Jan-31 Jan	1 Jan-31 Jan	1 Jan-31 Jan
month 6	1 Feb-1 Mar	1 Feb-10 Mar	1 Feb-5 Mar

Table S1. Details of dates used for monthly association matrices of juvenile great tits.

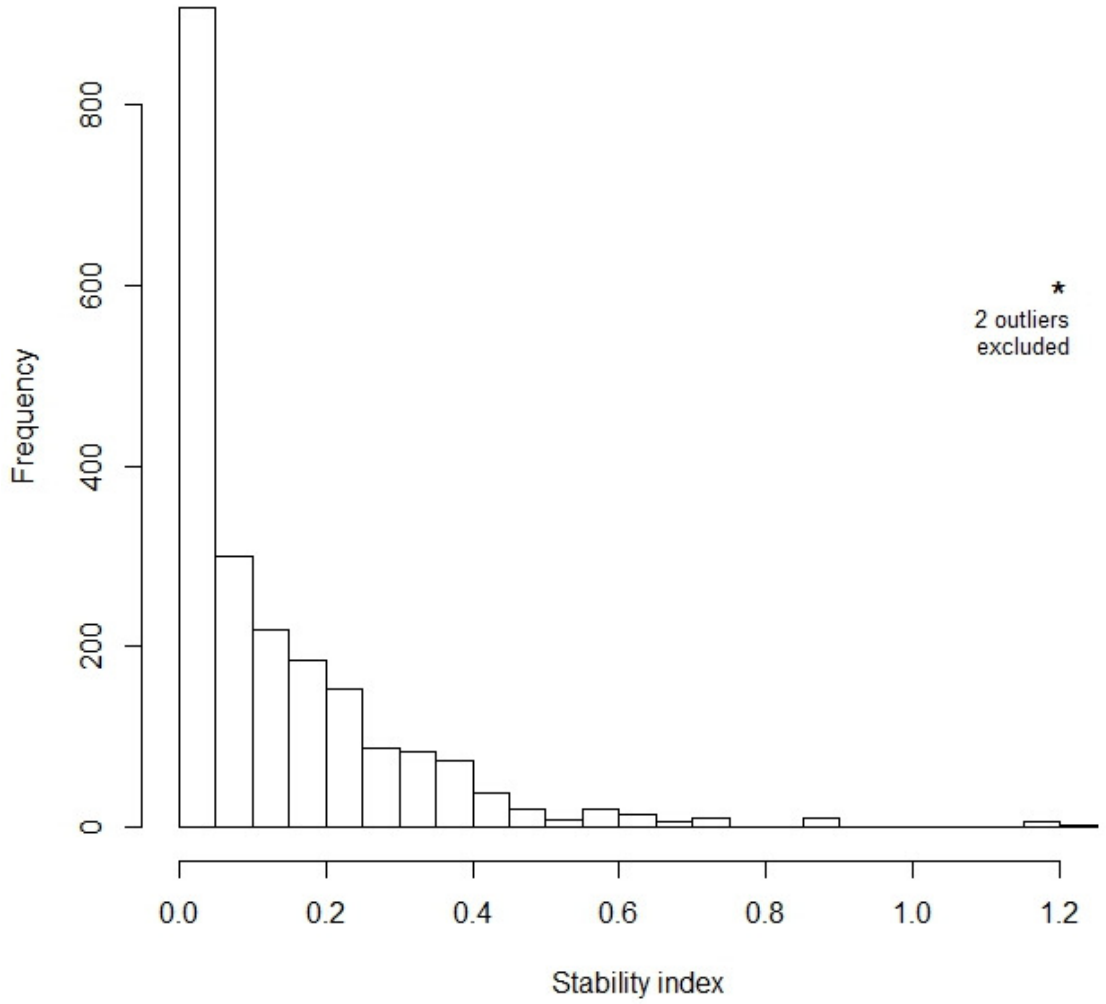


Figure S1. The distribution of the stability index values. Two outlier values of 2 and 4 have been excluded from the graph.

Appendix D

Supplementary Material for Chapter 5

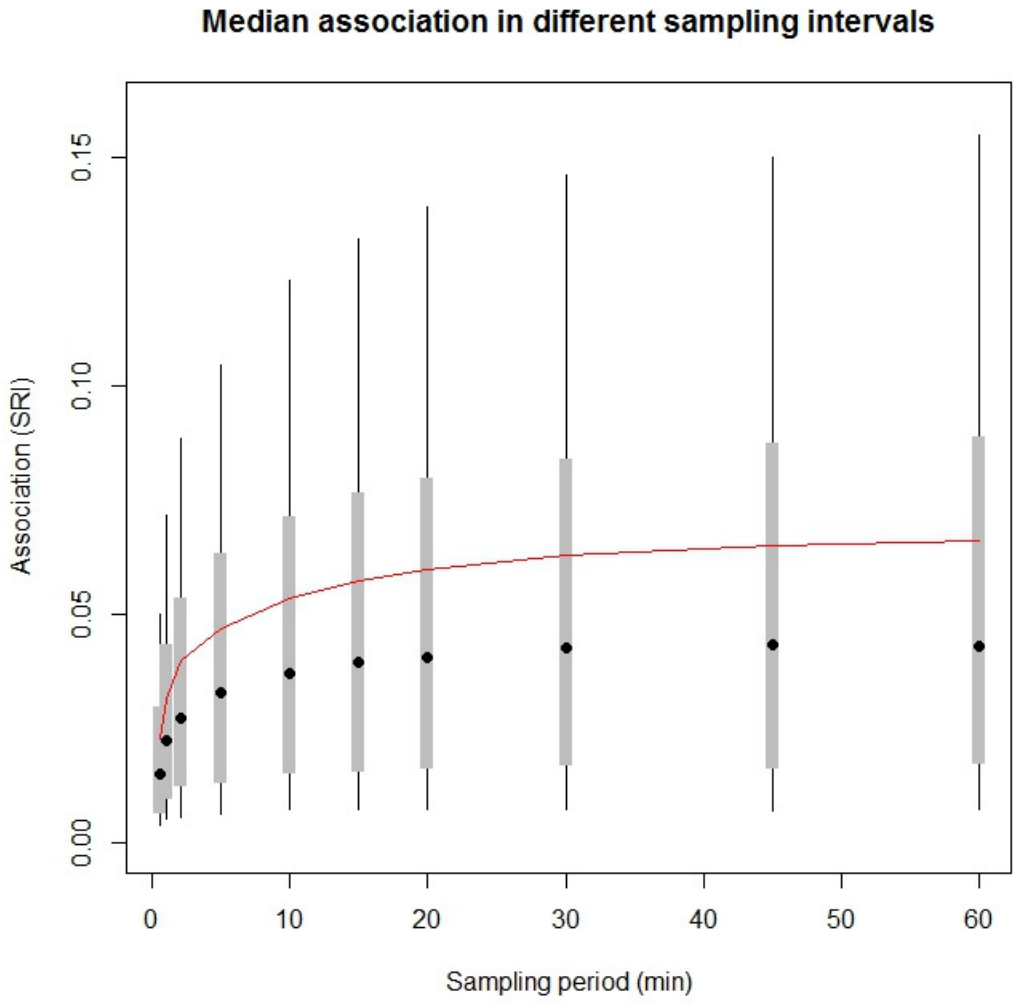


Figure S1 The effect of varying sampling periods on the foraging associations of juvenile great tits. Only observed (nonzero) associations were taken into account. The points represent the median with interquartile range shaded in grey. Whiskers extend from 10th to 90th percentile. The curve is a smoothing spline fitted to the means.

Testing models based on different time intervals to define association:

Candidate model	Log Likelihood	AIC	ΔAIC	weight
dis +month + year	-1189	2391	0	1
sib +month + year	-1242	2496	105	1.58×10^{-23}
asy +month + year	-1244	2500	109	2.14×10^{-24}
month + year	-1245	2501	110	1.30×10^{-24}

Table S1. Model selection summary for associations defined as detections within 1 minute.

Coefficient	Estimate (z transformed)	SE	p

natal distance	-0.57954	0.05843	<0.001
month	-0.05573	0.05026	0.31
year 2007	reference level	NA	NA
year 2008	-0.20173	0.13898	<0.001
year 2009	0.12362	0.11093	0.003

Table S2. Summary of the top model predicting strength of juvenile great tit associations defined as detections within 1 minute. P values were obtained from permutation tests.

Candidate model	Log Likelihood	AIC	ΔAIC	weight
dis +month + year	-3151	6314	0	1
sib +month + year	-3295	6602	288	2.90×10^{-63}
asy +month + year	-3301	6615	301	4.35×10^{-66}
month + year	-3305	6619	305	5.89×10^{-67}

Table S3. Model selection summary for associations defined as detections within 60 minutes.

Coefficient	Estimate (z transformed)	SE	p
natal distance	-0.575207	0.034913	<0.001
month	-0.007643	0.030154	0.32
year 2007	reference level	NA	NA
year 2008	-0.061238	0.081266	<0.001
year 2009	0.129851	0.067442	<0.001

Table S4. Summary of the top model predicting strength of juvenile great tit associations defined as detections within 60 minutes. P values were obtained from permutation tests.

season	**month 1**	**month 2**	**month 3**	**month 4**	**month 5**	**month 6**
2007-08	20 Aug-30 Sep	1 Oct-31 Oct	1 Nov-30 Nov	1 Dec-31 Dec	1 Jan-31 Jan	1 Feb-1 Mar
2008-09	22 Aug-30 Sep	1 Oct-31 Oct	1 Nov-30 Nov	1 Dec-31 Dec	1 Jan-31 Jan	1 Feb-10 Mar
2009-10	27 Aug-30 Sep	1 Oct-31 Oct	1 Nov-30 Nov	1 Dec-31 Dec	1 Jan-31 Jan	1 Feb-5 Mar

Table S5. Details of dates used for monthly association matrices of juvenile great tits.

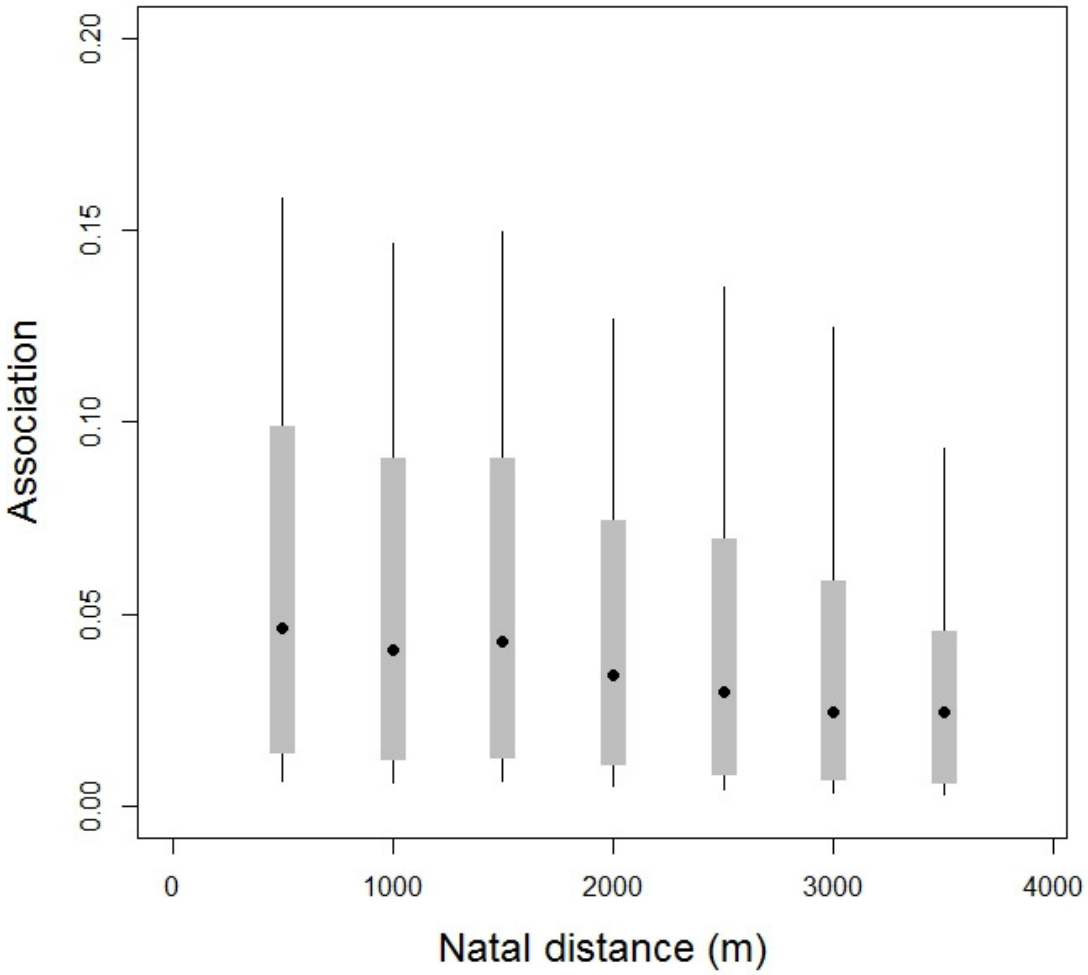


Figure S2. Observed juvenile associations (n=13,544) plotted against natal distance classes binned by 500m. Points designate medians; grey boxes are the interquartile range; whiskers extend from 10th to 90th percentile.

Sibling associations

We restricted the sibling association test to verify that the difference in associations between sexes were not caused by increased associations at the start of the season due to individuals that have not finished dispersing, or other processes that might have changed the pattern over the course of the season. Associations restricted to the final recording month differed significantly between different dyads of different sex composition (Kruskal-Wallis chi-squared = 8.0717, df = 2, p-value = 0.017). Brother dyads differed significantly from brother-sister dyads (Mann-Witney U = 202.5 , p = 0.017) and from sister dyads (Mann-Witney U = 142 , p = 0.018). there was no significant difference between sister dyads and brother-sister dyads (Mann-Witney U = 28.5 , p = 0.71)

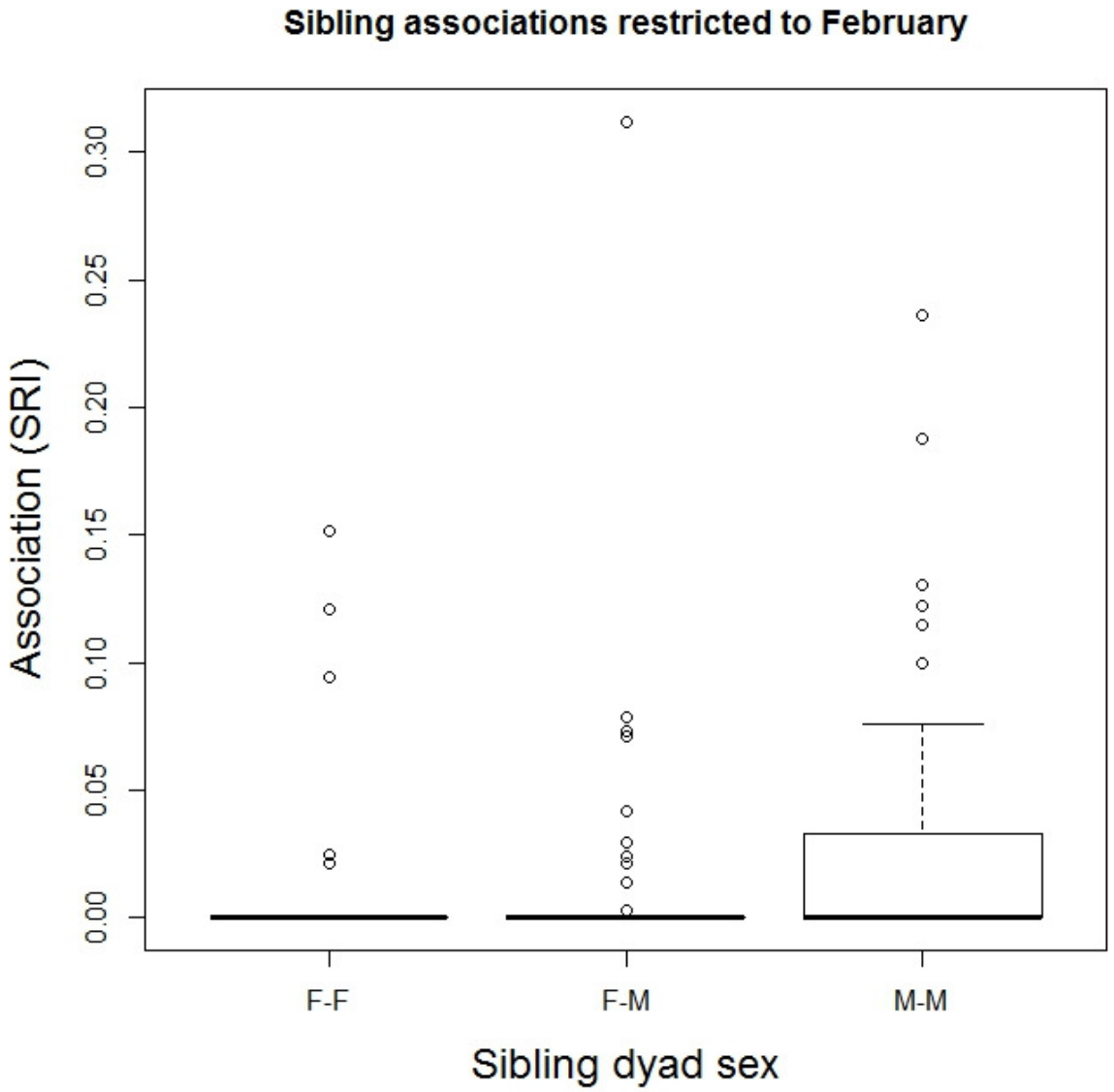


Figure S3. Sibling associations in the last recording month of all recording seasons. Results suggest that the pattern is stable over time and is not caused by disappearance or emigration of individuals over the course of winter.