



# Different types of social links contrastingly shape reproductive traits in a multi-level society of wild songbirds

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## Abstract

Social environments can influence individuals' health, reproductive success, welfare, and survival. These environments consist of diverse social connection types at multiple levels, which could influence different components of fitness in contrasting ways. Great tits (*Parus major*) exhibit a multilevel society with four major types of dyadic bonds: pair mates, breeding neighbours, flockmates, and spatial associates, all of which can influence fitness. Here, we show that these different types of dyadic bonds are differentially linked with reproductive success metrics in a wild great tit population, and that the consideration of spatial effects could provide further insights into these interrelationships. Specifically, more-social individuals had more fledglings, those that bonded more strongly with their pairmate laid earlier, and those with more spatial associates laid smaller clutches. These findings highlight the importance of considering multiple types of dyadic relationships when identifying the fitness consequences of sociality, and the need for work to experimentally test these relationships, particularly in spatially structured populations.

## Significance statement

Social connections are integral determinants of an individual's ability to survive and reproduce. Society is arranged according to a wide selection of different social bond types, all of which could influence these aspects of fitness in different directions, but these influences are rarely investigated and compared in the same population. To address this gap, we used a wild population of great tits with well-understood social and spatial lives to identify the socio-spatial drivers of reproductive fitness, finding a wide range of different sociality-reproduction links. These findings show broadly that different layers of societal organisation can have strong and contrasting effects for individuals' success in ecological systems. These divergent processes could generate and maintain diversity in social structure within and across systems.

**Keywords** Sociality · Spatial behaviour · Reproductive fitness · Social networks · Spatial analysis

## Introduction

Many animals live in complex societies (Ward and Webster 2016). The social behaviour of individuals within populations gives rise to structured social systems, and social interactions can influence individuals' decisions and behaviours, including foraging activity, mate choice, survival, and reproduction (Snyder-Mackler et al. 2020). Consequently, variation in sociality is an important determinant of overall fitness (Ellis et al. 2019; Menz et al. 2020; Bond et al. 2021; Siracusa et al. 2021; Turner et al. 2021). While social relationships come in many forms, sociality is often quantified using a single type of dyadic bond between individuals, for example by quantifying the strength of bonds between reproductive pairs, foraging partners, or group members. A

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key remaining question is how individual variation in different types of dyadic relationships simultaneously shape fitness outcomes in these complex societies.

Different kinds of dyadic relationships within populations can pave the way for hierarchically nested social relationships that form multilevel societies (Papageorgiou and Farine 2021). Indeed, all representations of social relationships are ultimately built upon dyadic units. Multi-tiered social structures often consist of breeding pairs or families that are nested within higher-order groups, allowing for flexibility in social interactions (Grueter et al. 2017). Small, stable units may come together to form larger fluctuating groups, such that individuals maintain and keep track of relationships at multiple levels (Papageorgiou et al. 2019). Assessing how these layers influence fitness is crucial to gaining a holistic understanding of how individual-level selection on behaviours build up to produce societal structure. However, quantifying these effects in wild populations can be difficult, as it requires fine-scale behavioural data from multiple social contexts across years alongside fitness outputs. Long-term, individual-based studies with high-resolution data are particularly useful in this regard (Clutton-Brock and Sheldon 2010; Sheldon et al. 2022).

The long-term study system of great tits (*Parus major*) at Wytham Woods provides an ideal opportunity to link different kinds of social relationships with fitness outcomes. Individuals are monitored during winter and spring over multiple years and in multiple social contexts, with associated data collected on reproductive success. Four broad types of associations exist within this population that are known to be biologically meaningful: pair mates (Culina et al. 2015a, b, 2020; Firth and Sheldon 2016; Firth et al. 2018), breeding neighbours (Grabowska-Zhang et al. 2012a, b; Gokcekus et al. 2023), winter flockmates (Firth et al. 2015, 2017, 2018b), and spatial associates (Farine et al. 2015; Firth and Sheldon 2016; Firth et al. 2018b).

In this monogamous species, **pair mates** bond and defend their territory during the breeding season, while also staying close during the non-breeding season (Firth et al. 2015). Pair bonds can be understood as the core unit of this multilevel society (Grueter et al. 2020). Spatial and social associations often have an influence on mate choice (Beck et al. 2020), and mate choice will in turn have an influence on fitness (Griffith et al. 2011; Ihle et al. 2015; Fayet et al. 2017). Stronger associations within the pair bond, often assessed in terms of familiarity over time, seem to convey fitness benefits in other species (van de Pol et al. 2006; Sánchez-Macouzet et al. 2014; Ausband 2019). In this population, pairs who meet earlier in the winter have higher reproductive success (Culina et al. 2020), pairs that stay together longer are more likely to survive (Culina et

al. 2015a), and unsuccessful individuals are more likely to divorce (Culina et al. 2015b; Gokcekus et al. 2023).

During the breeding season, territorial great tits have **breeding neighbours**, and these neighbours often also coexist in winter flocks (Firth and Sheldon 2016). Studies have shown that familiarity among neighbours can lead to mutual tolerance and decreases in aggression and energy required for territorial defence, potentially optimizing the timing of reproduction and facilitating coordination and cooperation – for example, in predator mobbing as defence (Beletsky and Orians 1989; Temeles 1994; Liebgold and Cabe 2008; Booksmythe et al. 2012; Grabowska-Zhang et al. 2012a; Bebbington et al. 2017; Riehl and Strong 2018; Siracusa et al. 2021; but see Müller and Manser 2007). Great tits in Wytham Woods benefit from having familiar neighbours (individuals that were neighbours in previous years), through increases in cooperation (Grabowska-Zhang et al. 2012a) and, presumably consequentially, higher reproductive success (Grabowska-Zhang et al. 2012b).

Outside of the breeding season, individuals also have **flock mates** that they forage with around the woodland in loose fission–fusion winter flocks (Farine et al. 2015). Studies in mammalian and avian species have demonstrated that having more (Cameron et al. 2009; McFarland et al. 2017; Ellis et al. 2019; Turner et al. 2021) or larger extent of (Silk et al. 2010; Cheney et al. 2016; Kohn 2017) social associations can come with fitness benefits (but see Menz et al. 2020; Sabol et al. 2020). It is possible that increased associations allow for more appropriate individual or group responses to social and environmental stressors (Micheletta et al. 2012; Young et al. 2014; Campbell et al. 2018), higher rates of cooperation (Berghänel et al. 2011; Samuni et al. 2018, 2021), and/or increases in dominance that lead to more successful reproduction (Schülke et al. 2010; Strauss and Holekamp 2019; Bray et al. 2021; Feldblum et al. 2021). In this system for instance, an individual's flock mates are known to influence patterns of social information acquisition during winter foraging (Firth et al. 2016).

During the winter, individuals are also **spatially associated** with others while foraging, which may indicate some form of association (or non-independence) but not necessarily direct social interactions. In this context, spatial associations refer to how often dyads were observed in the same place on the same day (regardless of whether they were seen in the same flock/group once there). The effects of such spatial overlap associations can vary based on factors such as predation risk and competition (Alberts 2019). The configuration and constraints of the external environment can also influence spatial proximity, and therefore associations, between individuals (He et al. 2019; Papageorgiou et al. 2019). Partitioning out these spatial associations can help to gain a clearer understanding of how different dyadic

relationships contribute to the formation of multi-level societies and their fitness consequences.

Finally, all of these links occur within the context of the **spatial environment**, which plays a role in “bottom-up” determination of the social network itself (Albery et al. 2021; Webber et al. 2023). Because the social network’s formation can be confounded with a variety of environmental (Fisher et al. 2021) and demographic drivers (Shizuka and Johnson 2019), many of which can also influence fitness, it is important to take the spatial environment – and particularly population density – into account when understanding sociality-fitness links.

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

## Methods

### Study system

Our study was conducted in Wytham Woods, Oxford, UK (51°46′N, 1°20′W) on the long-term study population of great tits (*Parus major*). These 385 ha of mixed deciduous woodland house ~1018 fixed nest boxes, with known GPS coordinates, that are monitored yearly to record breeding attempts and performance (Perrins 1965). Across the long-term data, ~300 boxes are occupied by great tits each year (range 110–495), with the remaining boxes either occupied by other species (primarily blue tits *Cyanistes caeruleus*, but occasionally coal tits *Periparus ater*, marsh tits *Poecile palustris*, or Eurasian nuthatches *Sitta europaea*). Either during the breeding season (at the nest) or throughout the year (through mist netting) individuals are caught, fitted with a unique BTO (British Trust for Ornithology) metal leg ring and a plastic leg ring with a passive integrated transponder (PIT) tag, aged and sexed, and measured to record standard morphometric information. It is estimated that 90% of the population is tagged (Aplin et al. 2013). It was not possible to record data blind because our study involved focal animals in the field.

## Data collection

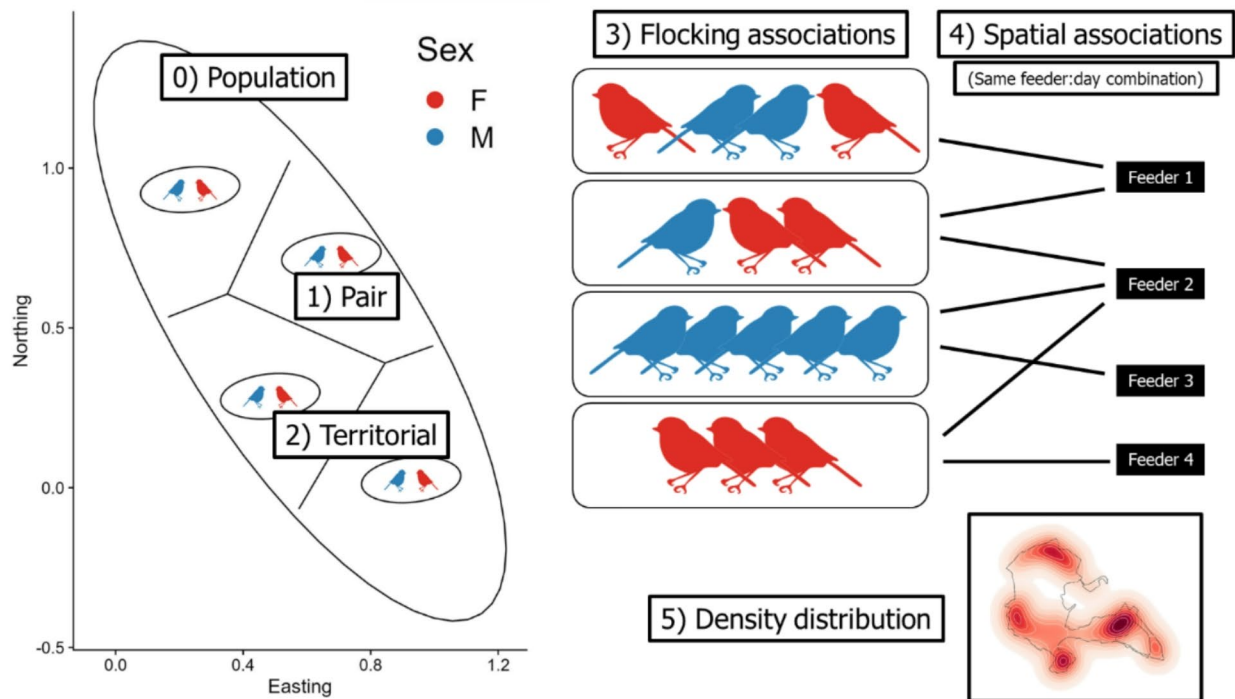
### Winter social network data collection

In this study, we use a shorter-term period of fine-scale high resolution behavioural sampling that nevertheless relies on the deeper and broader data available from the study system. This dataset allowed us to investigate a range of different levels of social structuring (Fig. 1). During the winter, great tits feed from patches of resources that are distributed throughout the woodland. Sunflower seed feeding stations with two opposing access holes equipped with RFID antennae (which automatically read and record the unique codes of the PIT tags on each bird - Dorset ID, Aalten, The Netherlands) were placed in a stratified grid at 65 fixed locations approximately 250 m apart. Feeders opened automatically every weekend over the winter (December–February, 2011–2014) from pre-dawn to after dusk. When birds used one of these feeders, tags allowed the detection of the time and date of their visit, creating a spatio-temporal data stream consisting of each individual visit to a feeder.

### Breeding season data collection

#### Fitness measures

During the breeding season (March–June), throughout Wytham Woods, Oxford, breeding adults and their chicks are marked with unique British Trust for Ornithology (BTO) rings following standard protocols since the 1960s (Perrins 1965) and also marked with the PIT tags since 2007 (as described above). Monitoring takes place through the stages of nest building, egg laying, incubation, and rearing offspring, and nests were checked weekly until eggs were found. Based on the assumption that one egg is laid each day, lay date was recorded (if one egg was found) or estimated (if more than one egg was found) as the date the first egg of the clutch was laid (Perrins 1965). In this population, earlier lay dates are known to be generally linked to increased reproductive success and output, and birds which breed late and miss the caterpillar peak generally experience lower reproductive success (Hinks et al. 2015; Cole et al. 2021; Gokcekus et al. 2023; Jones et al. 2025). After incubation began, clutch size was recorded as the maximum number of eggs within the nest. Parents were either identified on day 7 via RFID detection at their nest, or ringed (and tagged) at day 12 after eggs hatched, and all chicks were ringed, tagged and weighed at day 15. Subsequently, nests were checked to determine the number of chicks that had fledged in each breeding attempt.



**Fig. 1** Schematic detailing the levels of societal bond investigated in this study, moving up layers of social organisation through (1) pair bonds, (2) territorial neighbours, (3) flockmates, (4) spatial associations, and (5) density distributions. Silhouette taken from phylopic.org

### Labelling neighbours

In order to label territorial neighbours during the spring, we used the spatial arrangement of occupied nest boxes (of which all positions are known accurately to ~1 m) to estimate individual territories and their boundaries. For each occupied box, a Voronoi diagram (Thiessen polygon) was drawn to include all of the points that were closer to the focal box than any other occupied box (Adams 2001; Schlicht et al. 2014). This method of estimating territories and neighbours accurately accounts for population density and is highly correlated with territory sizes and boundaries that are manually determined (Wilkin et al. 2006; Grabowska-Zhang et al. 2012b; Schlicht et al. 2014) as well as with the winter social structure (Farine and Sheldon 2015; Firth and Sheldon 2016).

### Habitat quality

We calculated a habitat quality measure based on the number of oak trees within 75 m for each individual, using their nestbox location. We chose this metric based on earlier methodology (Gokcekus et al. 2023) and because we know from prior studies that oak trees are an important component of individuals' health and fitness. As such, we considered this an important factor to take into account when examining the drivers of reproductive success. Together with the

spatial autocorrelation effect detailed below, we hoped that this would allow us to extricate more purely socio-spatial drivers of reproductive success.

### Calculating socio-spatial measures

Each of the four measures of dyadic bonds (Fig. 4, Supplementary Fig. 4) was calculated based on the social associations of individuals during the winter following previously established protocols [76]. In the spatio-temporal data stream created by the feeder visits, intermittent bursts of clustered activity can be detected which denote flocks that are arriving to feed together (Psorakis et al. 2015). These flocks were detected using a Gaussian mixture model (GMM) that statistically assigns each focal individual visit to the group that it is most likely to belong to (Psorakis et al. 2012). In doing so, it identifies the bursts of foraging activity without subjective constraints (such as researcher specified time-windows) and flocking events found in this way are known to be biologically meaningful and carry over to various contexts (Farine et al. 2015; Firth and Sheldon 2015, 2016; Firth et al. 2016). We created a social network (association matrix) for each winter based on co-occurrences in flocks using the simple ratio index (SRI). The SRI values range from 0 to 1 and can be defined by the following equation:  $SRI = x / (x + yA + yB)$ , where:

- SRI is the strength of association between A and B.
- $x$  is the number of times A and B were in the same flock.
- $y_A$  is the number of times A was detected in a flock without B.
- $y_B$  is the number of times B was detected in a flock without A.

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

The relationship between **breeding neighbours** was quantified based on the territory and neighbour estimates described above and winter social networks. For every focal and each of their first-order neighbours (i.e. direct neighbours that they share a territory boundary with), we calculated the bond strength between them from the previous winter (following Firth and Sheldon 2016). For each individual, we calculated 3 metrics: the average bond strength to their male neighbours, female neighbours, and all neighbours (male and female combined). We made this distinction because we expected that different sexes might have divergent effects on each others' fitness and reproductive success, as found both in this system (Gokcekus et al. 2023) and others (Rudd et al. 2024).

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

To estimate winter **spatial associations**, we calculated the spatial temporal overlap for every possible dyad by accounting for the number of times individuals were observed at each feeder on the same day regardless of the specific foraging flocks they occurred in whilst at the feeder (following Firth et al. 2018a). So, for example, if two individuals spent equal proportions of time in the same location on the same day (not necessarily at the same time), they would be assigned a 1 even if they were never seen in the same flock together; if they were never at the same location on the same day, they would be assigned a 0. Proportions

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

To examine the role of socio-spatial demographic distributions, we additionally calculated local **density** following the protocol established for other social systems built from co-occurrence data such as badgers and deer (Albery et al. 2020, 2021). Using the 'adehabitathr' package in R, we created annual space use distribution kernels for the population based on their breeding locations and assigned each individual a local density measure based on the individual's location on that distribution (Albery et al. 2020, 2021). We calculated this on two timescales: annual (with a different density kernel for each year's breeding positions) and lifetime (with a single density kernel, summarised across the entire study period).

## Data analysis

We analysed three years (2011–2014) of data from 754 individuals. We ran separate models for males and females, for each of the five fitness variables derived from the breeding data (binary success, clutch size, lay date, mean chick weight, and number of fledglings), making ten models total. We consider the sexes separately here to avoid the non-independence between pair mates (their response variable values would be identical by definition), and also in line with previous research and findings that sociality can be considered separately between the sexes in this system (Firth et al. 2018a; Roth et al. 2019; Gokcekus et al. 2023). Click or tap here to enter text. and in others (Albery et al. 2022; Rudd et al. 2024). We fitted Generalized Linear Mixed Models (GLMMs) using the Integrated Nested Laplace Approximation (INLA) R package. This approach, which uses a deterministic Bayesian algorithm, allows us to fit a stochastic partial differentiation equation (SPDE) random effect based on breeding season locations. This effect models similarity emerging from the distance between points to account for spatial autocorrelation in the response variable (Rue et al. 2009; Albery et al. 2019); we used locations of nest boxes. Continuous variables were scaled to have a mean of 0 and a standard deviation of 1. The base model included year (as a categorical fixed effect), categorical age (juvenile vs. adult – which is known with certainty for all known individuals as this binary classification is meaningful and is designated on capture (Woodman et al. 2024), and habitat quality (the number of oak trees within a 75 m radius of the nest box). We also included individual identity as a random effect.

To investigate the effect of each of the dyadic relationship measures, we iteratively added the social effects (one measure of the social pair bond, three measures of breeding neighbour bonds, two measures of flockmate bonds, one measure of spatial associations, and two density measures (annual and lifetime); correlation matrix in Supplementary Fig. 1) the base model, and used Deviance Information Criterion (DIC) to identify the best fit. In each round, social effects were individually added until all had been included or their addition did not improve the model, using a cutoff of 2 DIC (following Albery et al. 2022; Gokcekus et al. 2023). We then added the SPDE random effect to investigate whether these findings were robust to us accounting for spatial autocorrelation, using the same DIC cutoff. We took this iterative approach because the socio-spatial variables were all somewhat correlated (Supplementary Fig. 1), such that fitting all at the same time would overfit and introduce problems with the model. Fitting all variables at once was therefore not possible, and nor are model averaging approaches viable. As such, this sequential fitting of a variety of socio-spatial metrics allowed us to compare the effects of each factor in isolation and together in a parsimonious way. Incorporating the spatial autocorrelation effect and comparing the model effects with and without allowed us to assess how much of our findings and estimates emerged from this confounding.

All response variables took a Gaussian family, except binary success, which was binomial. Fixed effect estimates were provided by the mean and 95% credibility intervals of the posterior estimate distribution. Significance was determined by examining each effect's overlap of the 95% credibility estimates with zero.

## Results

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

### Four levels of dyadic bonds

Individuals with stronger winter bonds to their pair mate had earlier lay dates, and this effect remained significant when controlling for breeding spatial autocorrelation (Fig. 2; Female: -0.13, CI: -0.19, -0.07; Male: -0.13, CI: -0.19, -0.07).

Individuals with stronger bonds to their male breeding neighbours had fewer fledglings. This effect was not significant after controlling for breeding spatial autocorrelation for males (-0.08, CI: -0.19, 0.04), but remained significant for females (-0.13, CI: -0.24, -0.02; Fig. 2).

Individuals with more bonds to flock mates (higher degree) had a higher number of fledglings (F: 0.19, CI: 0.07, 0.31; M: 0.18, CI: 0.06, 0.29), but this effect was not significant after controlling for spatial autocorrelation (F: 0.10, CI: -0.03, 0.23; M: 0.09, CI: -0.04, 0.22). Individuals with more bonds to flock mates had later lay dates, and this effect remained significant after controlling for breeding spatial autocorrelation (F: 0.10, CI: 0.03, 0.18; M: 0.10, CI: 0.03, 0.18; Fig. 2).

Individuals with more winter spatial associates had smaller clutches, but this effect was only significant after controlling for breeding spatial autocorrelation (F: -0.14, CI: -0.26, -0.03; M: -0.14, CI: -0.26, -0.03; Fig. 2). Although it was retained in the models, there were no significant effects of density on lay date (F: 0.06, CI: -0.01, 0.13; M: 0.05, CI: -0.02, 0.13).

### Spatial distributions

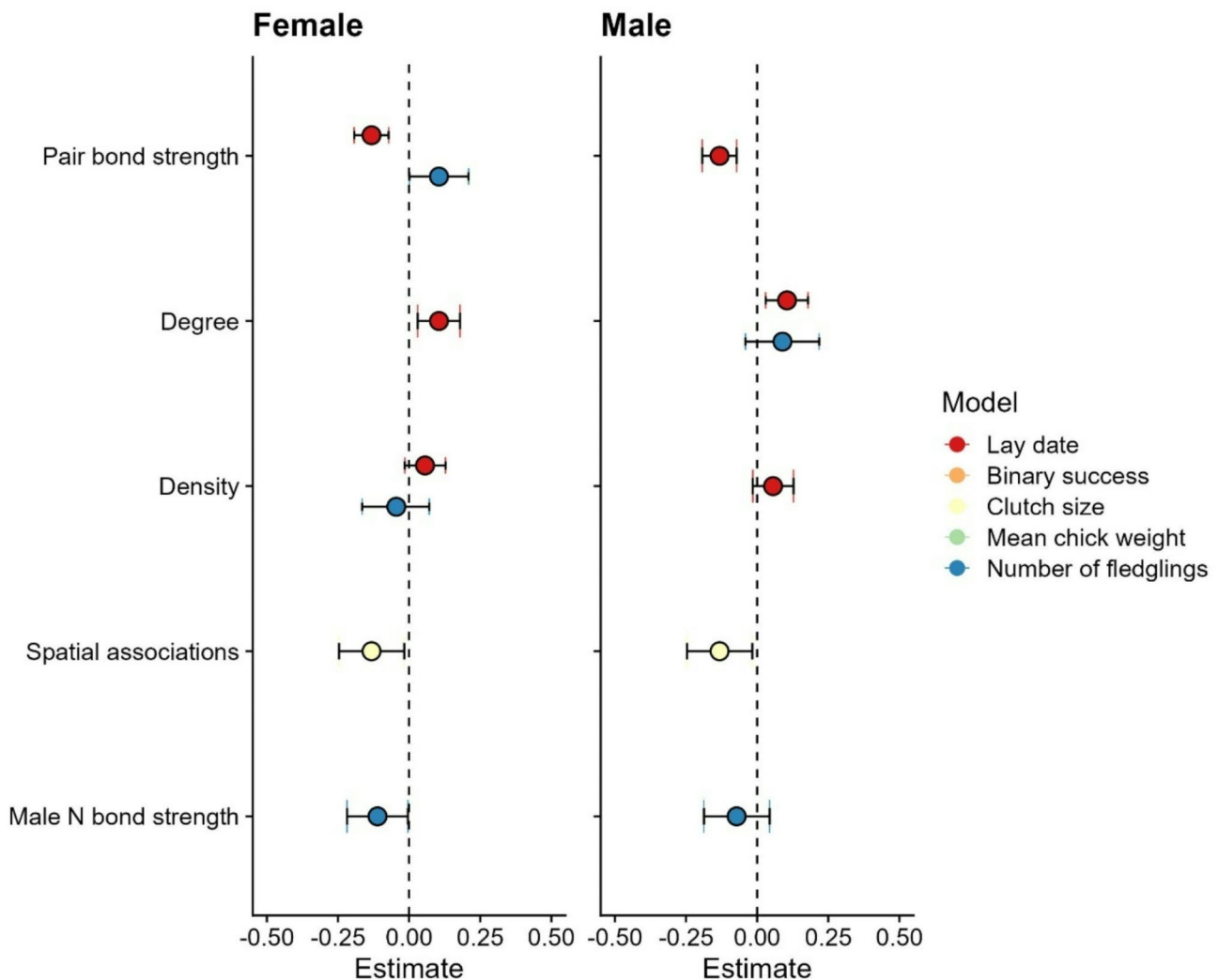
Adding the SPDE random effect (accounting for breeding spatial autocorrelation) improves all of the models substantially ( $\Delta\text{DIC} > 2$ ), with the exception of the binary success model (Table 1). The spatial distribution of each of the response (fitness) variables is graphically illustrated by projecting the SPDE random effect onto a two-dimensional plane (Fig. 3). Overall, the southern part of the woods tended to have lower reproductive success than the northern part, and lay dates are the latest in the central portion of the woods.

### Non-social spatial drivers

Individuals who bred in areas with better habitat quality had earlier lay dates (F: -0.09, CI: -0.16, -0.02; M: -0.09, CI: -0.16, -0.02) and larger clutches (F: 0.11, CI: 0.01, 0.21; M: 0.11, CI: 0.01, 0.21; Fig. 4), but this effect was no longer significant after controlling for breeding spatial autocorrelation.

### Other non-social drivers

Year had an influence on all of the variables except for mean chick weight (see Fig. 2). Juveniles had significantly later lay dates than adults (F: 0.35, CI: 0.21, 0.48; M: 0.35, CI: 0.17, 0.54). All social and non-social drivers were included in the same models (Table 2).



**Fig. 2** Summary of the social effects for all ten models, for females and males, with an SPDE effect to account for spatial autocorrelation. Points represent the estimate for each effect that was retained in the model selection process; error bars denote 95% credibility intervals

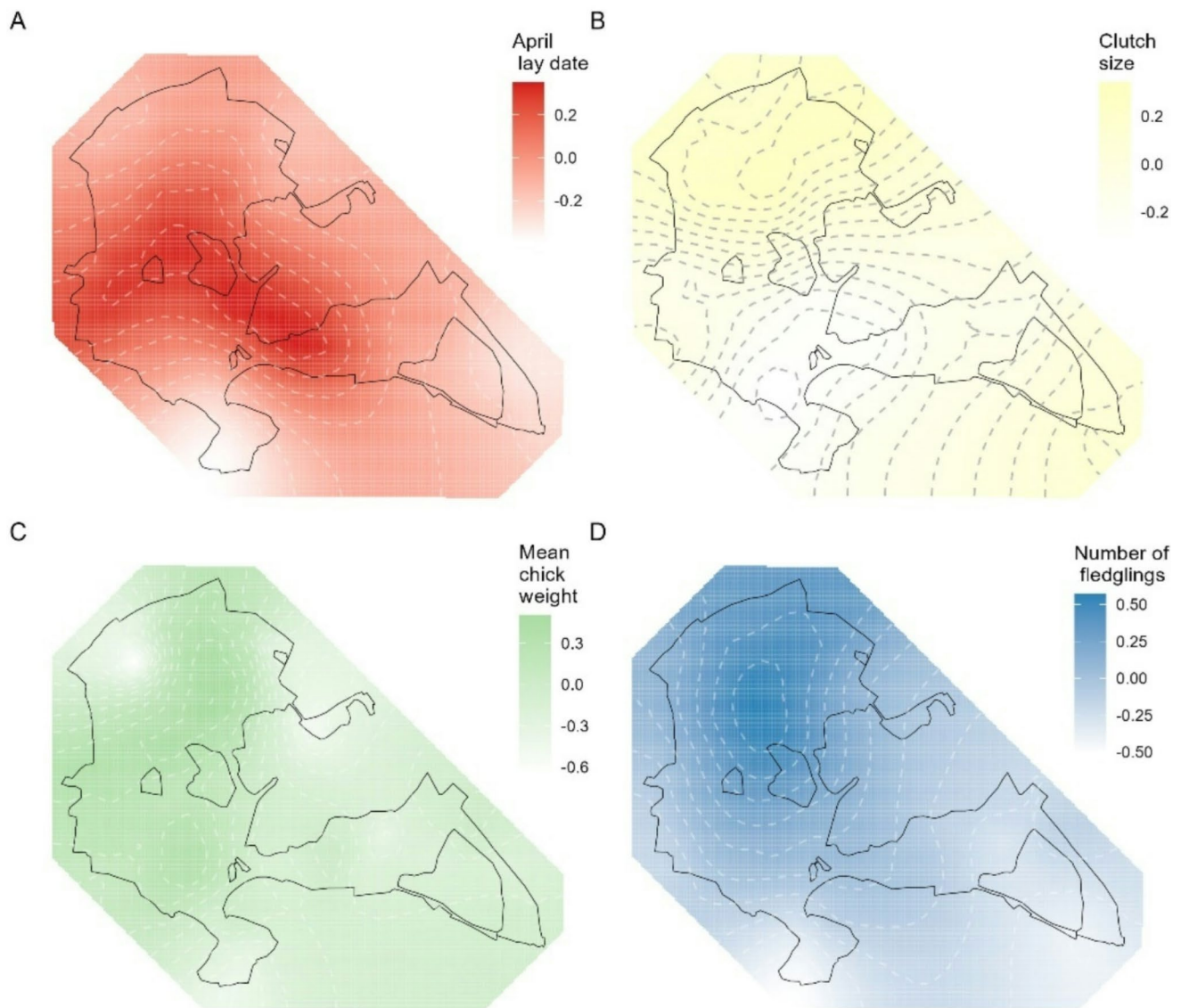
**Table 1** DIC for base and SPDE models

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

## Discussion

Individuals exist in complex multi-level societies, every layer of which might influence fitness, but much work linking sociality with fitness has focused on a single type of dyadic bond. Using three years of behavioural and reproductive data in wild songbirds, we demonstrate fitness

consequences of four types of social interrelationships that are found within multilevel societies (Culina et al. 2020). These findings broadly support findings in other systems (e.g. macaques (Schülke et al. 2010), killer whales (Ellis et al. 2017), and social cuckoos (Riehl and Strong 2018) that sociality is associated with increased fitness. However, a wide range of animal species inhabit complex multi-layered societies, including some primates (Schreier and Swedell 2009), birds (Camerlenghi et al. 2023), and elephants (de Silva and Wittemyer 2012), for example. Additionally, it is often acknowledged that aspects of sociality can be disadvantageous, through a variety of mechanisms (e.g. Loeb and Zink 2006; Rehan et al. 2014; Maestriperi and Georgiev 2016). Our study is notable in demonstrating that even in

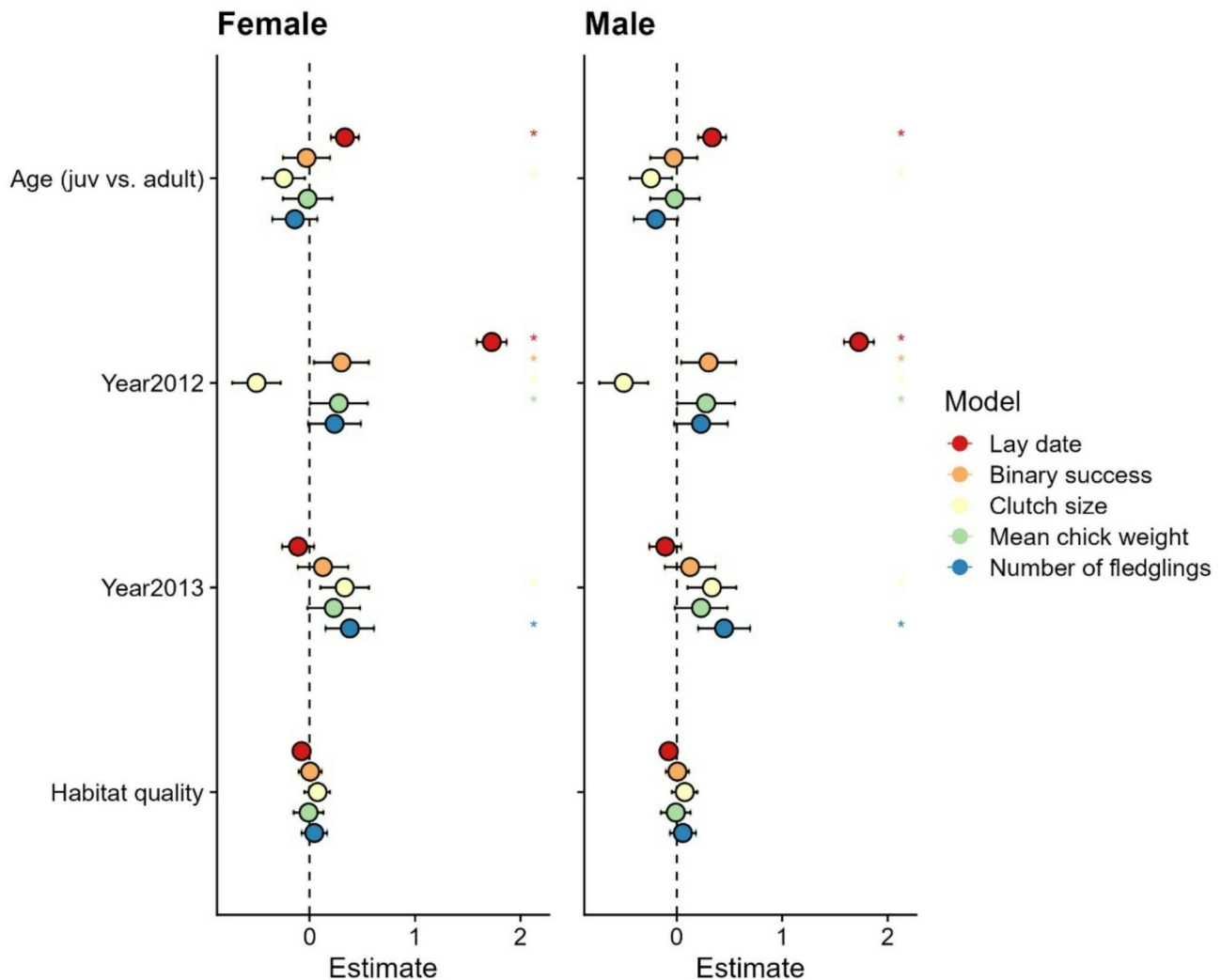


**Fig. 3** 2D projection of the spatial distribution of each fitness variable (for females), when accounting for both the fixed and random effects in each model, on the link scale. Includes **a**) lay date, **b**) clutch size,

**c**) mean chick weight, and **d**) number of fledglings. Darker shading denotes higher success (B-D), or later lay dates (A); contours have been added to guide the eye regarding the spatial distribution

this relatively simple society of songbirds, connectedness in different social layers contributes to different reproductive traits, and in divergent directions. Additionally, accounting for breeding-position-associated spatial autocorrelation in fitness outcomes improved 4/5 models, matching with previous results surrounding the importance of accounting for spatial effects in this (Gokcekus et al. 2023) and other social systems such as red deer (Albery et al. 2021) and African lions (Rudd et al. 2024). Due to all these divergent correlations and their spatiotemporal heterogeneity, the emergent nonrandom clustering among social and reproductive phenotypes could have complex consequences for the social ecology and evolution of this and other populations. For

example, great tits exhibiting certain social phenotypes may experience stronger selection on different fitness components than others; nonrandom spatiotemporal patterns of fitness traits may emerge as a result of patterns of social connectedness; and changes in social network structure may have strong ramifications for individuals' relative investment in specific reproductive traits, which could influence resilience to environmental change – for example, in the face of advancing Spring phenology (Visser and Holleman 2001). As such, analyses that examine multiple layers of social functioning could be invaluable in understanding animal populations' ecology and fitness (Silk et al. 2018; Finn et al. 2019; Fisher et al. 2021; Hasenjager et al. 2021).



**Fig. 4** Summary of the non-social effects with the SPDE effect to control for spatial autocorrelation. Points represent the estimate for each effect that was retained in the model selection process and error bars

denote 95% credibility intervals. Asterisks on the far right denote significant effects (credibility intervals not overlapping zero)

Our results demonstrate support for a consistent finding in this population: the importance of the pair bond in determining lay dates, with individuals that met earlier in the winter (Culina et al. 2020) or who had bred together in the past (Gokcekus et al. 2023) having earlier lay dates. Our findings show this relationship still holds even when simultaneously considering other kinds of social links. Historically, many external factors have been used to predict lay dates (Perrins and McCleery 1989), including temperature (van Noordwijk et al. 1995; Visser et al. 1998), habitat quality (Wilkin et al. 2007), caterpillar growth (Visser et al. 2006), and presence of parasites (Oppliger et al. 1994) among others. Yet the strength of the pair bond seems to consistently be an important predictor of lay date, and these results follow previous findings in suggesting that lay date

indeed depends on others in the social system (Evans et al. 2020).

Previous studies in this population have shown that individuals breed close to their highly associated former flock mates (Firth and Sheldon 2016) and that neighbours who are socially familiar (due to year-to-year territory sharing) have higher fitness (Gokcekus et al. 2023). However, when controlling for other types of dyadic bonds, having strong winter bonds to subsequent breeding neighbours was not actually beneficial in this sample: in fact, females with stronger bonds to neighbouring males had fewer fledglings. It is possible that tolerating males may actually come at a cost if it leads to having fewer resources. Additionally, if females with stronger bonds to male neighbours are more likely to have extra-pair copulations, males may subsequently

**Table 2** Model statistics for female main models (same information for males can be found in supplementary table 1); bold variables are significant in both models, italic variables are only significant before controlling for breeding Spatial autocorrelation; \*variables are only significant after controlling for breeding Spatial autocorrelation

Response	Variable	Estimate	Lower	Upper	SPDE Mean	SPDE Lower	SPDE Upper
Lay date	(Intercept)	-0.52	-0.64	-0.40	-0.52	-1.17	0.13
	<b>Age (juv. vs. adult)</b>	0.35	0.21	0.48	0.34	0.20	0.47
	<b>Year 2012</b>	1.72	1.58	1.87	1.73	1.59	1.87
	Year 2013	-0.12	-0.27	0.03	-0.11	-0.26	0.04
	<i>Habitat quality</i>	-0.09	-0.16	-0.02	-0.08	-0.16	0.01
	<b>Pair bond strength</b>	-0.13	-0.19	-0.07	-0.13	-0.19	-0.07
	<b>Degree</b>	0.12	0.05	0.19	0.10	0.03	0.18
	Density	0.04	-0.02	0.11	0.06	-0.01	0.13
Binary success	(Intercept)	-0.12	-0.30	0.06	-0.12	-3.58	3.34
	Age (juv. vs. adult)	0.01	-0.21	0.23	-0.03	-0.25	0.20
	<b>Year 2012</b>	0.30	0.04	0.56	0.30	0.04	0.56
	Year 2013	0.12	-0.12	0.36	0.13	-0.11	0.37
	Habitat quality	0.01	-0.09	0.11	0.01	-0.10	0.12
Clutch size	(Intercept)	0.09	-0.09	0.27	0.12	-1.03	1.26
	Age (juv. vs. adult)	-0.21	-0.41	-0.01	-0.25	-0.45	-0.04
	<b>Year 2012</b>	-0.46	-0.69	-0.23	-0.52	-0.75	-0.29
	<b>Year 2013</b>	0.39	0.16	0.62	0.34	0.10	0.57
	<i>Habitat quality</i>	0.11	0.01	0.21	0.08	-0.04	0.20
	Spatial associations*	-0.08	-0.19	0.03	-0.14	-0.26	-0.03
Mean chick weight	(Intercept)	-0.14	-0.34	0.06	-0.18	-0.60	0.21
	Age (juv. vs. adult)	0.03	-0.21	0.27	-0.02	-0.25	0.21
	Year 2012	0.25	-0.04	0.53	0.28	0.00	0.55
	Year 2013	0.19	-0.07	0.45	0.23	-0.02	0.48
	Habitat quality	0.02	-0.09	0.13	-0.01	-0.15	0.13
Number of fledglings	(Intercept)	-0.19	-0.38	-0.01	-0.17	-1.20	0.85
	Age (juv. vs. adult)	-0.09	-0.31	0.12	-0.16	-0.37	0.05
	<i>Year 2012</i>	0.28	0.01	0.54	0.25	-0.01	0.50
	<b>Year 2013</b>	0.47	0.22	0.73	0.45	0.20	0.70
	Habitat quality	0.05	-0.05	0.15	0.04	-0.08	0.16
	<i>Degree</i>	0.19	0.07	0.31	0.10	-0.03	0.23
	<b>Male neighbour bond strength</b>	-0.20	-0.31	-0.09	-0.13	-0.24	-0.02

provide less parental care in the nest or spend more time investing in other females (Magrath and Komdeur 2003; Eliassen and Jørgensen 2014).

This finding on breeding neighbours raises the possibility that the previously observed positive effect of neighbour familiarity (Grabowska-Zhang et al. 2012b; Gokcekus et al. 2023) is actually due to general sociality and/or early establishing of territories and not the result of cooperation that arises due to specific bonds with particular individuals. However, it is also possible that breeding neighbour familiarity is most important for an aspect of fitness that we cannot measure: whether individuals are able to establish a territory at all. In support of this possibility, a previous study on this population showed that immigrants are more likely to fail in establishing a territory (and therefore establishing a breeding attempt) than integrated members (Kidd et al. 2015). Furthermore, it is possible that individuals that are familiar over multiple years are easier to identify because they become associated with territory boundaries. If there

is a limit on the number of individuals that great tits can identify, having stronger bonds with neighbours may not be as beneficial as having neighbours that are familiar over the years simply because birds are more likely to be aware of this between-year familiarity (Gokcekus et al. 2021). This study only used a few years of data because it required fine-resolution understanding of multiple behaviours, and it is possible that larger datasets of similarly fine-scale data might be able to inform on these questions more effectively.

Individuals with more connections (higher degree) during the winter have more fledglings, which is in line with the general idea that being more social comes with fitness benefits (Snyder-Mackler et al. 2020). However, this effect was weakened when accounting for spatial effects, raising the possibility that part of this relationship may be explained by higher-quality areas supporting stronger bonds. On the other hand, individuals with more connections also had later lay dates, possibly suggesting that dedicating social time to other flockmates trades off against the social bond with

their pair mate and thus potentially pushes back one's lay date. When considering winter spatial relations, we find that individuals with more winter spatial associates have smaller clutches. As resources are provided only on weekends at these feeding stations, it is unlikely that the reduced clutch sizes are the result of resource competition at the feeders themselves; instead, females who spend the winter in areas with more conspecifics might anticipate greater competition and lay smaller clutches accordingly to avoid overstressing the available resources. This result also highlights the importance of explicitly testing and controlling for spatial associations when investigating more apparent measures of sociality.

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

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**Author contributions** SG, JF, BCS, and GFA conceived of the study. SG conducted the analysis and wrote the first draft of the manuscript, supervised by all other authors. All authors offered their input and comments on the manuscript.

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**Data availability** The data and code are available on github (<https://github.com/gfalbery/pyramidscheme2>) and on zenodo (DOI: <https://doi.org/10.5281/zenodo.15209687>).

## Declarations

**Ethical approval** The study was conducted in accordance with the ASAB/ABS guidelines (Buchanan et al. 2012) and was subject to re-

view by the local ethical review committee of the Department of Biology, University of Oxford (Reference number: APA/1/5/ZOO/NAS-PA/Sheldon/BehaviouralContagion). Birds were caught, ringed and equipped with PIT-tags by experienced ringers under BTO licences.

**Conflict of interest** The authors declare no conflict of interest.

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