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Sex-based differences in social trade-offs in a wild bird society

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ABSTRACT

Social relationships of different types come with varied costs and benefits. Individuals in natural populations may experience selective pressure to trade off one social relationship with others optimally. Specifically, individuals associate with conspecifics to varying extents; if there is a limitation on social time then individuals will have to trade off how much to invest in one social relationship versus another. The factors affecting how individuals manage social trade-off dynamics, however, remain largely untested in wild populations. Here, we use a wild population of great tits (*Parus major*) as a model system for examining social trade-offs within social networks: specifically, how an individual's sex affects how they trade off associating with their future breeding partner versus with other conspecifics. We show that during the non-breeding season (winter), both males and females increasingly associate with their future breeding partner, but that there are sex-based differences in trade-off patterns. In existing breeding pairs, we find that males associate more with their partner than females do, as a proportion of their total social associations. In new pairs, juvenile males increase their proportional association with their partner more than juvenile females do as winter progresses. Additionally, we find that juvenile males undergo lower social group membership change whilst accommodating pair bonding. These findings demonstrate how demographic characteristics shape fine-scale social behaviour, contributing to the biological processes that emerge from social structure.

Keywords: fission-fusion society, pair bonding, social networks, social trade-off, wild populations

HIGHLIGHTS

- Social trade-offs occur in winter social networks of a wild great tit study system
- Sex differences shape trade-offs of affiliating with breeding partners versus non-partners
- Individuals vary by sex and age in how they reshape their social networks during pair bonding
- Stability of social associations is dependent on demographic factors and pair-bonding

INTRODUCTION

Diverse social relationships exist across animal societies. Previous research has reported a variety of benefits of sociality, including non-breeding social relationships increasing reproductive success for greater anis (*Crotophaga major*) and chimpanzees (*Pan troglodytes*) (Feldblum *et al*., 2021; Riehl & Strong, 2018). Contrastingly, there can be sociality costs, including competition (Ekanayake-Weber *et al*., 2024). Strong social relationships reduce lifespan and reproductive success in yellow-bellied marmots (*Marmota flaviventris*) and grooming adult conspecifics comes with aggression costs for juvenile Japanese macaques (*Macaca fuscata*) despite potential long-term benefits of this relationship

(Blumstein *et al.*, 2018; Schino & Alessandrini, 2015; Wey & Blumstein, 2012). Therefore, it is expected that individuals trade off costs and benefits of social relationships.

Social relationship trade-offs implicitly include opportunity costs if maintaining one relationship limits investment in another due to time or ecological constraints. Social relationships are often considered in terms of affiliative behaviour, or successive interactions, between two individuals associating in time and space (Hinde, 1976; Massen *et al.*, 2010). As such, social trade-offs may manifest as variation in how much an individual associates with different conspecifics. There are examples of individuals managing social trade-offs across vertebrates, including Japanese macaques (Schino & Alessandrini, 2015) and jackdaws (*Corvus monedula*) (Kings *et al.*, 2023). Experimental work shows jackdaws reshape social relationships to gain short-term benefits whilst maintaining strong bonds of longer-term value, highlighting how costs and benefits can occur on different timescales (Kings *et al.*, 2023). How social trade-offs occur and why individuals manage social trade-offs differently, however, remain largely untested in wild systems, despite trade-offs contributing to social structure and emergent biological processes (Cantor *et al.*, 2021).

One social relationship where trade-offs can apply is the mating pair bond: a strong, selective association between a male and female which breed together (although diversely defined) (Bales *et al.*, 2021). In socially monogamous animals, increased pair bond investment can bring individuals benefits. In birds, longer pair bonds within and between years can lead to increased reproductive success and survival (Culina *et al.*, 2020; D'Amelio *et al.*, 2024; Griggio & Hoi, 2011; Sánchez-Macouzet *et al.*, 2014), and stronger pair bonds can lead to faster breeding initiation (Maldonado-Chaparro *et al.*, 2021). Nevertheless, individuals may trade off associating with a future breeding partner versus with other conspecifics. Pair bonds are expected to return benefits at a future time (breeding), which imposes a strong temporal aspect to the social trade-off if pair bonding occurs well ahead of breeding (Culina *et al.*, 2020; Teitelbaum *et al.*, 2017). Additionally, to trade off against future benefits (e.g. reproductive success), there may be immediate pair bonding costs, including stress or energetic demands (Campbell *et al.*, 2009; Griffith *et al.*, 2011).

Opportunity costs arise if investing in a pair bond limits investment in other social relationships, characterised by how much an individual associates with its partner compared to others. Furthermore, pair bonding can reshape the identity of non-pair associates. For example, wild great tits (*P*arus major) may reshape their social connections in order to associate with their partner, despite enduring a potentially suboptimal social environment (Firth *et al.*, 2015). Opportunity costs occur given that associating with others can bring benefits not satisfied by the pair bond. An individual's social relationships beyond its partner can affect its ability to acquire information, gain territory, avoid predation, modulate competition, and sample potential mates, in a variety of mammals and birds (Aplin

et al., 2012; Beck *et al*., 2021; Farine & Sheldon, 2015; Micheletta *et al*., 2012; Oh & Badyaev, 2010; Schakner *et al*., 2017).

Pair members may have different optimal outcomes for pair bonding social trade-offs, despite being mutually invested in reproductive outcomes. Indeed, males and females frequently have different life history requirements, which may be supplied by social relationships (Tarka *et al*., 2018). If benefits of social position vary with sex, then we can predict sex-determined social patterns (e.g., Farine *et al*., 2015; Gokcekus *et al*., 2023; Weiss *et al*., 2021). For example, in a longitudinal study of immature baboons (*Papio ursinus*), during male baboons' development, they became less integrated than females in grooming social networks, perhaps owing to sex-based differences in the benefits of grooming and other social behaviours (Roatti *et al*., 2023). Additionally, in blue tits (*Cyanistes caeruleus*), males that move between social groups and associate with more females are more likely to find a partner and also sire extrapair young, showing a potential opportunity cost of not associating with more female conspecifics; no such equivalent pattern was found for females, demonstrating sex-based differences in optimal social behaviour (Beck *et al*., 2021).

Therefore, in societies with sex differences, males and females can have differing "social optima" (i.e. patterns of investment in social relationships that return the greatest benefits for a given cost). However, how individuals' phenotypes shape social trade-offs remains largely unknown. Specifically, we lack understanding of how an individual's sex affects how it manages pair bonding social trade-offs. Here, we examine this using a wild model great tit population. During winter (non-breeding season), great tits form fission-fusion feeding flocks, with these dynamic, loose aggregations creating opportunities for individuals to adjust their social position and respond to trade-offs (Farine *et al*., 2015; Voelkl *et al*., 2016). Pair bonds usually form between birds associating in these loose aggregations (Culina *et al*., 2020; Firth *et al*., 2018). Social proximity develops markedly between a pair during winter, with pair bonds defined by the two birds then going on to breed together the following spring (Abraham *et al*., 2025; Culina *et al*, 2020).

In this study, our aim was to assess how an individual's phenotype influences its management of social trade-offs. Specifically, we analysed an observational data set of fission-fusion flocking behaviour in a model great tit system to test the role of sex in social trade-offs during pair bonding. We used social network analysis to quantify social trade-offs and tested the effect of sex on social trade-offs using Generalised Linear Mixed Models (GLMMs). We considered two potential social trade-off scenarios faced by pair bonding great tits (Figure 1). First, we predicted that during winter an individual's sex affects how much it associates with its future partner compared to other conspecifics. Additionally, social trade-offs may also occur if spending more social time with a partner causes broader changes in an individual's social network; we predicted that an individual's sex affects how much it reshapes its social associations while associating with its partner during winter.

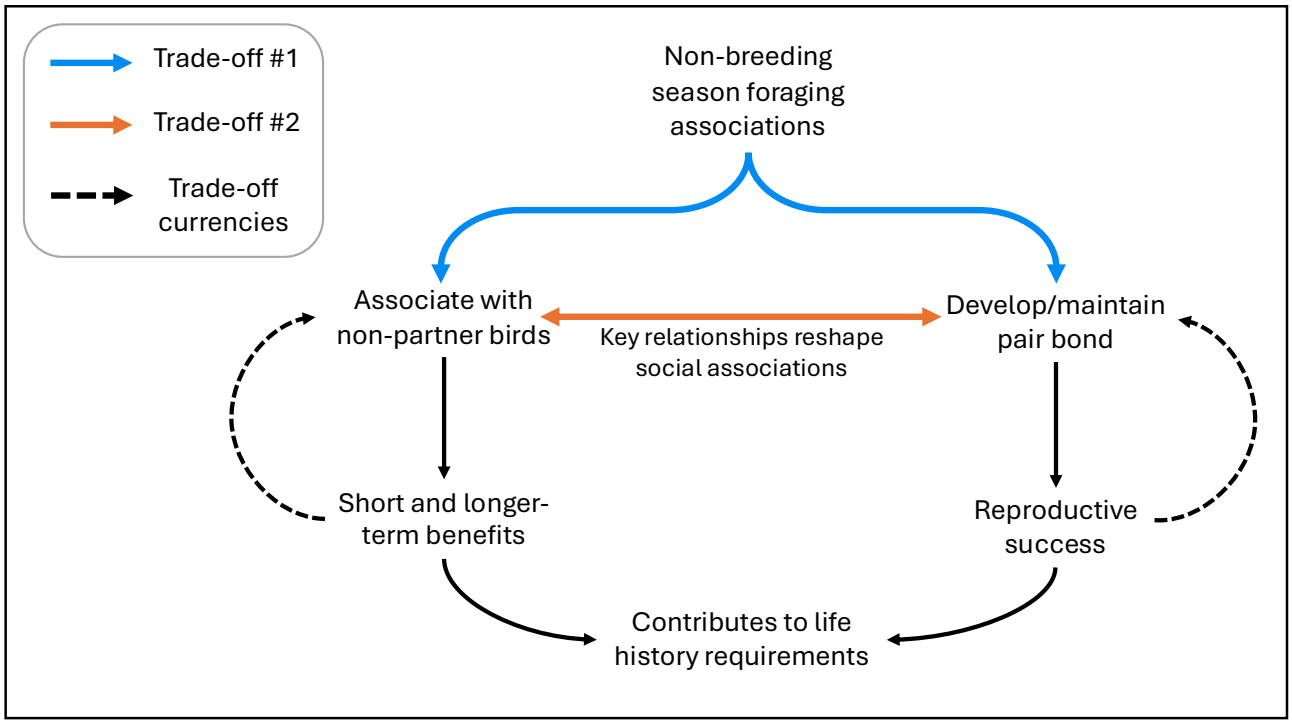

Figure 1: summary of potential social trade-offs faced by pair bonding great tits. Trade-off #1: associating with a future breeding partner versus associating with other conspecifics. Trade-off #2: extent to which existing social relationships are changed or lost during pair bonding. Males and females may receive different costs and benefits from different aspects of trade-offs.

METHODS

Study System

This research used the long-term study population of great tits at Wytham Woods (385-ha), Oxford, United Kingdom (51°46'N, 1°20'W). Like over 80% of bird species, great tits are socially monogamous, although extrapair paternity has been recorded in 49% of broods and 13% of offspring (Griffith, 2019; Patrick *et al.*, 2012). Biparental care is required and *c.*98% of pairs make a single annual breeding attempt (Firth *et al.*, 2018; Perrins & McCleery, 1985). Great tits breed in spring (April–July) and the Wytham Woods population nests almost solely in the woodland's 1020 nestboxes, facilitating long-term breeding monitoring. During breeding, 15-day-old pulli are fitted with a unique British Trust for Ornithology metal ring on one leg and a unique RFID microchip, contained within a plastic ring on the other leg. Additional winter mist-netting means *c.*90% of this population carry an RFID microchip, allowing high social behaviour coverage (Aplin *et al.*, 2013).

Ethical Note

All work (mist netting and ringing, and captivity), was carried out under BTO licences (BTO A5435) and reviewed and approved by the University of Oxford, Department of Zoology, Animal Welfare and Ethical Review Board (Approval number: APA/1/5/ZOO/NASPA/SHELDON/TitBreedingEcology), having considered any welfare or environmental implications of the procedures.

Social Association Data Collection

For three winters (December-March; 2011-2012, 2012-2013, 2013-2014), feeding stations were positioned throughout Wytham Woods at 65 fixed locations at *c.*250m intervals. For 13 consecutive weekends each winter, feeders were available for birds, and antennae scanned for RFID tags 16 times per second, pre-dawn to post-dusk. When individuals visited a feeder, they were identified by their RFID tag. During weekdays, the feeding ports were covered with opaque tubes, preventing carry-over effects (Crates *et al*., 2016). A machine learning algorithm was used to group visits into flocking events, capturing which individuals associated in flocks (Psorakis *et al*., 2012, 2015).

Social Network Analysis

To examine social associations, we used social network analysis in R (v.4.2.2) within RStudio (Posit team, 2023) (*igraph* (Csárdi *et al*., 2024) and *sna* (Butts, 2024)). To generate weighted social networks from flock memberships, we applied the "gambit of the group", assuming each bird in a flocking event was socially associated at that specific time (Franks *et al*., 2010). Flock membership is strongly preferential in this population, reducing this assumption's impact (Psorakis *et al*., 2012).

We quantified association strength between two individuals (a dyad) using the Simple Ratio Index (SRI) (Cairns and Schwager, 1987), which ranges between zero (dyad never co-occurred) and one (dyad always co-occurred in flocking events):

$$S_{AB} = \frac{x}{x + y_{AB} + y_a + y_b}$$

Where:

- S_{AB} = association (SRI) between birds A and B, within period when both present in system
- x = flocking events where A and B co-occurred
- y_{AB} = A and B detected at same time in system but at different feeders
- y_A = flocking events in which A occurred but B did not
- y_B = flocking events in which B occurred but A did not

We constructed social networks using dyads' SRI as the association strength between individuals (nodes). To capture temporal processes, we made networks for each weekend of data collection,

following the discrete snapshot approach (Pinter-Wollman *et al*., 2014). Additionally, we made networks for each full winter. Breeding pairs were identified using the following breeding season's data. We did not account for relatedness, as kin structure is relatively weak in this social system with <2% of social ties occurring between first-order relatives (Firth & Sheldon, 2016).

Relative partner affiliation

Association with future breeding partner relative to other conspecifics

To measure relative partner affiliation (i.e. the affiliation with partner compared to with all other conspecifics), we quantified the number of flocking events in which each individual was observed with and without its partner. Relative partner affiliation was modelled as binomial "successes" (flock with partner) and "failures" (flock without partner). We calculated this for each winter from the pair first being recorded together that season, limiting analysis to pair bonding, as well as for each weekend of data in the pair bonding window.

Additionally, how much a great tit associates with its future partner relative to other opposite-sex individuals may reflect a partner choice aspect of trade-offs (Culina *et al*., 2015). Therefore, we calculated individuals' sums of observations with its future partner and with all opposite-sex conspecifics: capturing the probability that if a bird is recorded with an opposite-sex bird, that bird is its partner (sex-based relative partner affiliation). Here, "successes" were the sum of flocks with partner, and "failures" the sum of total observations with non-partner opposite-sex individuals (i.e. summing every opposite-sex individual in a flock with the focal bird).

Social Association Stability

Correlation of an individual's social associations between time points

We predicted that an individual's sex would affect the social association stability it experienced, as the pair bond has the potential to reshape its social environment (Firth *et al*., 2015). We measured weekly social association stability for each individual as the correlation (ρ) of its association (SRI) with each individual from one weekend to the next, returning a single value for each individual for each weekend (Ilany *et al*., 2021) (Figures 2a & 2b). In addition, we calculated seasonal social association stability in the same fashion but measured between the weekends where it was first and last observed with its partner. We also measured how correlated its associations were with its partner's social associations when first recorded together (initial pair correlation), excluding the pair from the calculation, measuring how similar their social associations were initially, as a potential baseline for change.

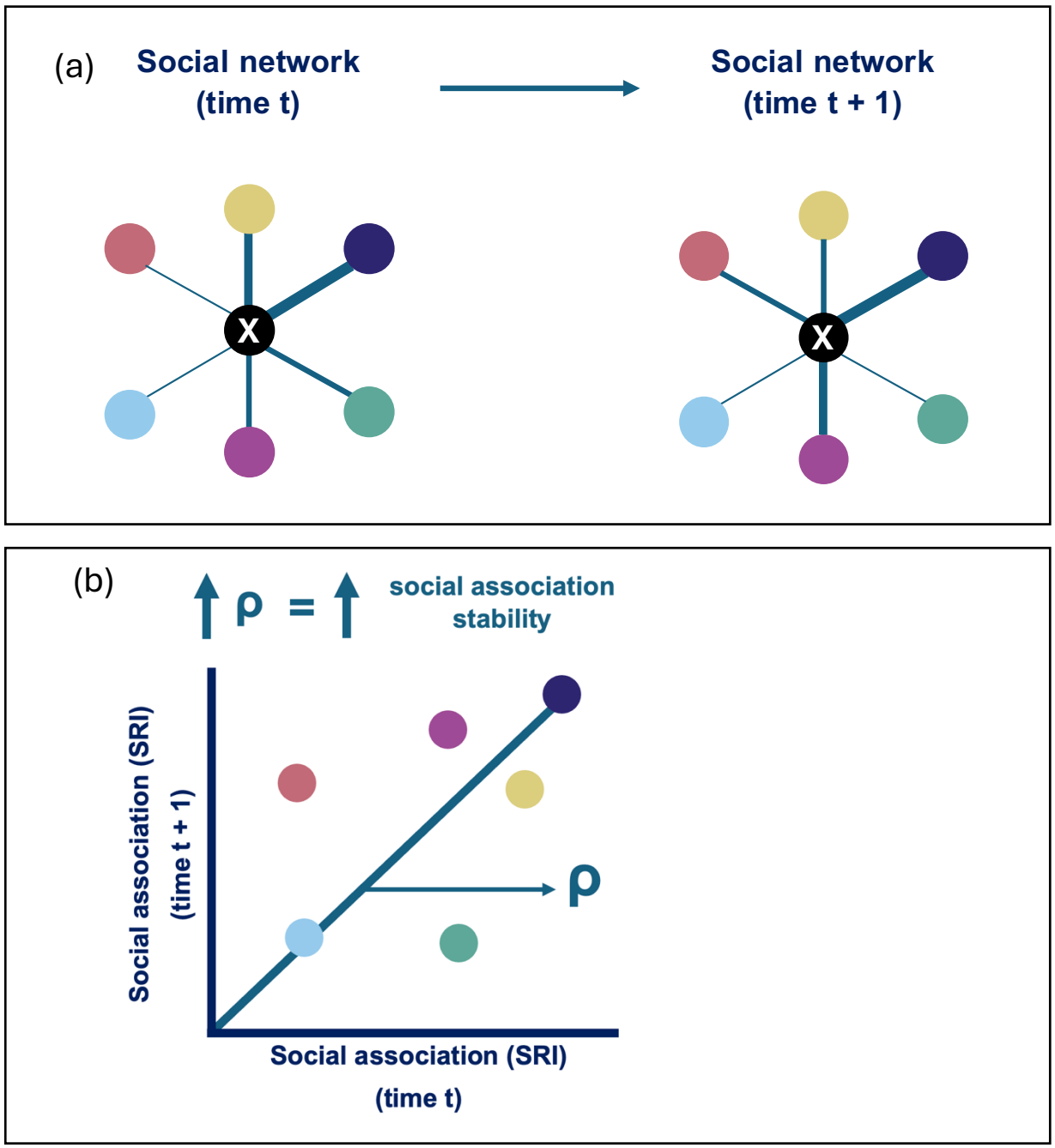

Figure 2: (a): individual *x* changes its associations between time *t* and *t+1*. Conceptual example. Colours denote different individuals, which are represented by nodes. Edge weights (thickness of lines connecting nodes) represent association (Simple Ratio Index). (b): resulting social association stability for individual *x* between time *t* and *t+1*. Coordinate: association of individual *x* with individual *y* at time *t*, association with individual *y* at time *t+1*.

Data Selection

All individuals detected in a flocking event during the study period, and all their associations with conspecifics during the relevant timeframe, were included in social networks and metric calculations. To focus analysis on birds where trade-offs could be quantified, models contained only entries for birds that:

i) had been confidently identified as either male or female (number of individuals that met these criteria for each winter: 2012: 1005; 2013: 831; 2014: 804);
ii) were observed breeding in Wytham Woods the following breeding season with an identified partner (2012: 379; 2013: 247; 2014: 328);
iii) were recorded in >1 weekend in a winter and had their partner recorded in >1 weekend in the winter before going on to breed together (2012: 311; 2013: 188; 2014: 219).

We classified breeding pairs according to whether they were existing pairs or new pairs, and within the latter, their ages (first-year or adult) in relation to their sex (Figure 3). We may expect behavioural differences between those forming and maintaining a pair bond, whilst age (including in relation to sex) is known to affect pair bonding dynamics in some birds and mammals (Firth *et al.*, 2018; Kelberman *et al.*, 2024, Sánchez-Macouzet *et al.*, 2014). Supplementary Results I contains social networks only including birds which fulfilled these model criteria, demonstrating variation in the strength and number of birds' social relationships and the emergence of pair bonds in networks (Supplementary Figure 1a-1c).

Statistical Analysis

We used GLMMs, summarised in Table 1, to test the effect of sex on: **1)** associating with a future breeding partner versus with other conspecifics and **2)** social association stability during pair bonding. See Supplementary Methods I for full variable definitions, and Supplementary Methods II and Supplementary Results II for further model details.

Table 1: summary of model groups and their variables. Fixed effects include all variables that were used in final models for each group; not all models used all fixed effects.

Group	Response	Subset	Fixed effects included	Random effects
1	Seasonal relative partner affiliation	Single sex models	Pairing status, weekend count	Year, ID, location
		Combined sex models	Sex, age, weekend count, immigration status	
2	Weekly relative partner affiliation	Single sex models	Weeks since meeting (plus rescaled for quadratic models), pairing status, weekend count	Year, ID, weekend location
		Combined sex models	Weeks since meeting (plus rescaled for quadratic models), pairing status, weekend count	Year, Pair ID/ID, weekend location
3	Sex-based relative partner affiliation	Combined sex models	Weeks since meeting, sex, age	Year, Pair ID/ID
4	Seasonal Social Association Stability	Combined sex models	Initial pair correlation, sex, age, immigration status	Year, Pair ID/ID, location
5	Weekly Social Association Stability	Combined sex models	SRI, sex, weekend pair correlation, weeks since meeting, immigration, partner's age	Year, Pair ID/ID, weekend location

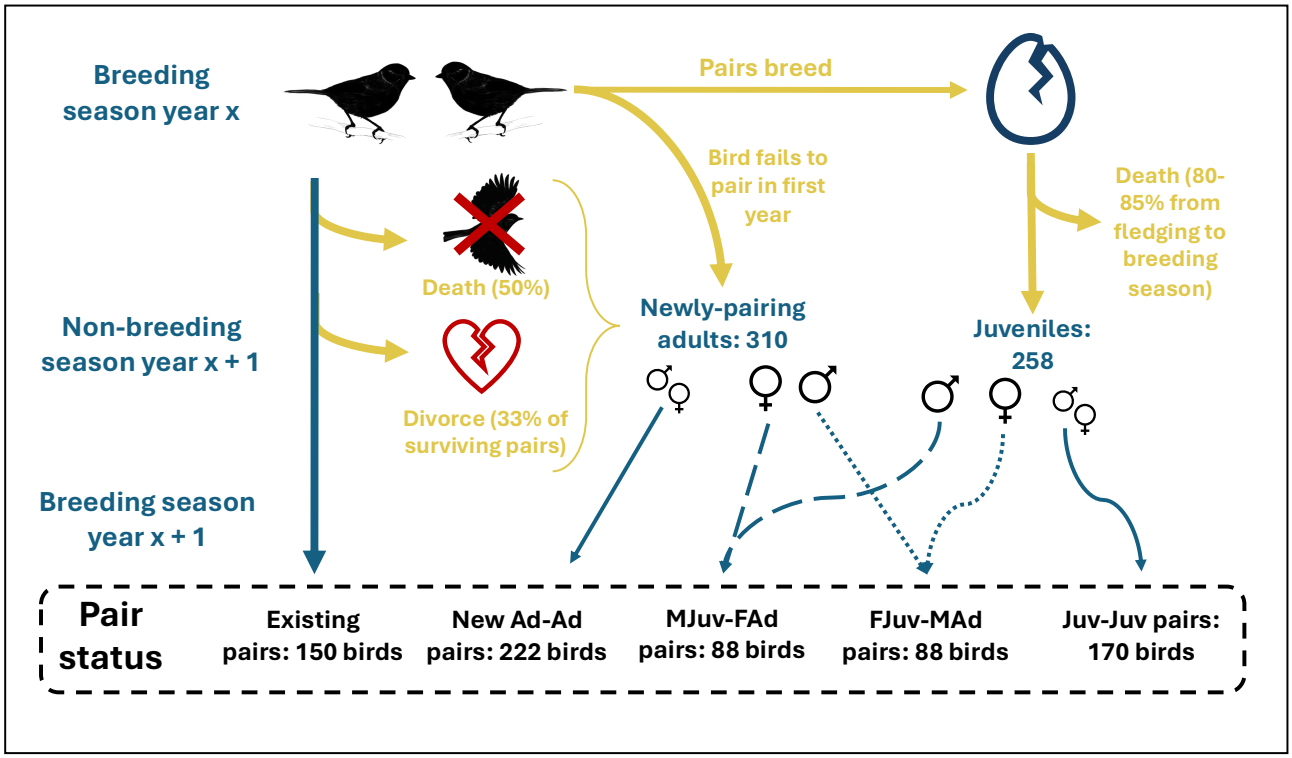

Figure 3: pair status classification. Yellow arrows denote demographic processes (Payevsky, 2006; Perrins & McCleery, 1985); blue arrows denote pairing processes. An individual can only appear in one of the pair types (black font) in one year but some individuals could appear across multiple groups over the course of the study given data come from several years (e.g. a MJuv-FAd pair in 2012 could be an Existing pair in 2013). Each group contains both pair members. Counts are number of individuals that fulfilled criteria for models, pooled across years. Existing: bred together in previous breeding season; Ad-Ad: newly-pairing adults (following partner death or divorce) which pair with adult; Juv-Juv: juveniles which pair with juvenile; MJuv-FAd: male juveniles paired with newly-pairing adult females; FJuv-MAd: female juveniles paired with newly-pairing adult males.

Prediction 1: Sex Affects Relative Partner Affiliation

Group 1

We constructed GLMMs with a binomial response variable of how many times a bird flocked with (successes) and without (failures) its partner over the winter, from when the pair first flocked together that season (seasonal relative partner affiliation). We initially constructed single-sex models, modelling affiliation as a function of pairing status and controlling for how many weekends a bird was recorded that season.

Single-sex models contained individual identity (ID) and year of data collection as random effects, and the individual's most visited feeding station (location) to control for spatial habitat variation indirectly affecting social structure (Supplementary Results IV) (Beck *et al*., 2023). For example, in this population, feeding stations nearer the woodland edge have larger local population sizes, which in turn affects social network structure, including increased clustering coefficients (Beck *et al*., 2023). To analyse flocking event data, we used a binomial error distribution and logit link function (MacKenzie *et al*., 2018). If models were over-dispersed (the model substantially under-predicting variance) we reran models with beta-binomial error distributions (Harrison, 2015). To quantify the effect of sex, we built models with both sexes but restricted by pairing type. We controlled for immigration status (born in Wytham or not), as immigrants in this population assort socially (Farine *et al*., 2015). When considering newly-pairing birds we included age (adult or juvenile – i.e. first-year) as a fixed effect, as age affects aspects of great tit social behaviour (e.g. Woodman *et al*., 2023).

All combined-sex models in all model groups included random effects of location and year, as well as individual ID nested within pair ID to account for pair dependency.

Group 2

To consider how trade-offs vary with time over the winter season, we modelled how many times a bird flocked with and without its partner in each weekend (weekly relative partner affiliation) as a function of how long ago the pair met that season. We excluded entries prior to the pair meeting and where a bird was not recorded in a weekend. Including a zero-inflation term considered entries where a pair were not observed together (Supplementary Results III). We initially constructed single-sex models. Here, the effect of pair status (Figure 3) interacted with how long ago the pair met that season, and we adapted the location random effect to be an individual's most-visited feeder that weekend (capturing 90.1% of visits) (Supplementary Results IV). Differing levels of feeder usage between individuals were captured by i) the number of datapoints per individual, which scales with the number of weekends that individual was recorded and ii) individual ID being a random effect, which models individual-level variation and down-weights sparsely observed birds.

To explore if birds non-linearly increase their relative partner affiliation as winter progresses, we fitted models with a quadratic effect of weeks since meeting (rescaled; mean = 0, standard deviation = 1), examining if "u" or "n"-shaped relationships existed (Salinas Ruíz *et al*., 2023).

We built combined-sex models restricted by pairing status, plus quadratic versions. Newly-pairing birds were additionally split by age. We constructed models for each pair type (Figure 3) for additional analysis.

Group 3

To consider partner choice aspects of non-breeding season social trade-offs, we modelled how much an individual associated with its partner versus with other opposite-sex birds as observations with partner (successes) and observations with opposite-sex conspecifics (failures) (sex-based relative partner affiliation). This was calculated for each weekend. To handle non-convergence, models excluded the weekend location random effect (Bolker *et al.*, 2009). We fitted combined-sex models, including fixed effects of weeks since meeting and sex, and a zero-inflation term.

Prediction 2: Sex Affects Social Association Stability During Pair Bonding

To assess changes in social associations during pair bonding, we built models with the response variable of individuals' social association stability: the correlation (ρ) of its association (SRI) with each other individual between time *t* and time *t+1*. This was measured from **i)** initially meeting its partner compared to its last recorded flocking with its partner that winter (seasonal social association stability) and **ii)** one weekend to the previous one (weekly seasonal consistency). We transformed all correlations from [-1, 1] to [0, 1] using $\frac{y+1}{2}$ and adjusted all correlations from [0, 1] to (0, 1) by subtracting *epsilon* (1*e*-10) from all values; no values were ≤0. This allowed use of GLMMs with a beta error distribution and logit link function for Model Groups 4 & 5. Transformed values are used throughout.

Group 4

Modelling seasonal social association stability, we allowed the effect of sex to depend on age and controlled for initial pair correlation: how correlated an individual's associations were with its partner's social associations when first recorded flocking together. For newly-pairing birds, a three-way interaction allowed the sex*age interaction to vary according to initial pair social correlation. We fitted combined-sex models for each pair status.

Group 5

To link changes in associations to pair bonding, we modelled an individual's weekly social association stability as a function of its pair's association strength in weekend *t+1* (SRI) and tested for an effect of sex. For existing pairs, we controlled for time since meeting that winter and weekend pair correlation: how correlated an individual's associations were with its partner's social associations in weekend *t*. Pair correlation could not be calculated for weekends where one pair member was absent in the previous weekend, so these entries were excluded. We modelled newly-pairing birds split by age, plus additional models testing if the effect of sex varied with time.

RESULTS

Winter social networks contained 1079 (2011-2012), 720 (2012-2013) and 773 (2013-2014) great tits. These social networks were built from 242,041 flocking events across the three years, with average flock membership of 9.040±0.013 individuals (mean ± standard error). Across years, 557 individuals were used in models. Of these, birds spent 10.8±0.117 weekends in Wytham Woods each winter and encountered 70.5±1.41 individuals (network degree). 26 individuals appeared in three years and 100 in two years. Supplementary Results II contains model outputs. Models were carried out as described in the Methods and values are reported throughout as: logit-transformed coefficient estimate±standard error, model p-value.

Prediction 1: An Individual's Sex Affects Relative Partner Affiliation

Group 1: seasonal relative partner affiliation

In combined-sex models, there was no significant effect of a bird's sex on its relative partner affiliation (association with partner relative to other conspecifics) over the whole winter (Model 1.3; new pairs; sex: estimate = -0.017±0.134, P = 0.773. Model 1.4; existing pairs; sex: estimate = 0.042±0.076, P = 0.579). Single-sex models predict similar values for pairing types between males and females (Models 1.1 & 1.2; Supplementary Results II).

Group 2: weekly relative partner affiliation relative to affiliation with other conspecifics

With time, birds increased affiliation to their future breeding partner (Figures 4-6). For new pairs, the effect of sex depends on age and time since meeting partner (Model 2.5; weeks since meeting*sex*age: estimate = 0.043±0.007, $P < 0.0001$). Additionally, we split newly-pairing birds by age, to consider if the effect of sex on relative affiliation through time to a new partner differs between juveniles and adults.

New pairs: effect of sex changes with time for juveniles

Male juveniles increased relative partner affiliation (shared flocking events with their partner, relative to their total flocking events) significantly more than female juveniles during winter (Figure 4b) (Model 2.6; weeks since meeting*sex: estimate = 0.031±0.005, $P < 0.0001$). This is despite male juveniles initially flocking proportionally less with their partner (sex: estimate = -0.190±0.052, $P < 0.001$).

Contrastingly, newly-pairing adult females initially flocked proportionally less with their partner (Model 2.7; sex: estimate = 0.127±0.052, P = 0.014) and also increased relative partner affiliation significantly more than adult males during winter (weeks since meeting*sex: estimate = -0.012±0.004, P = 0.002) (Figure 4a). Therefore, in newly pairing adults, the effect of sex is reversed relative to that observed in juveniles, although the magnitude of the effect is smaller.

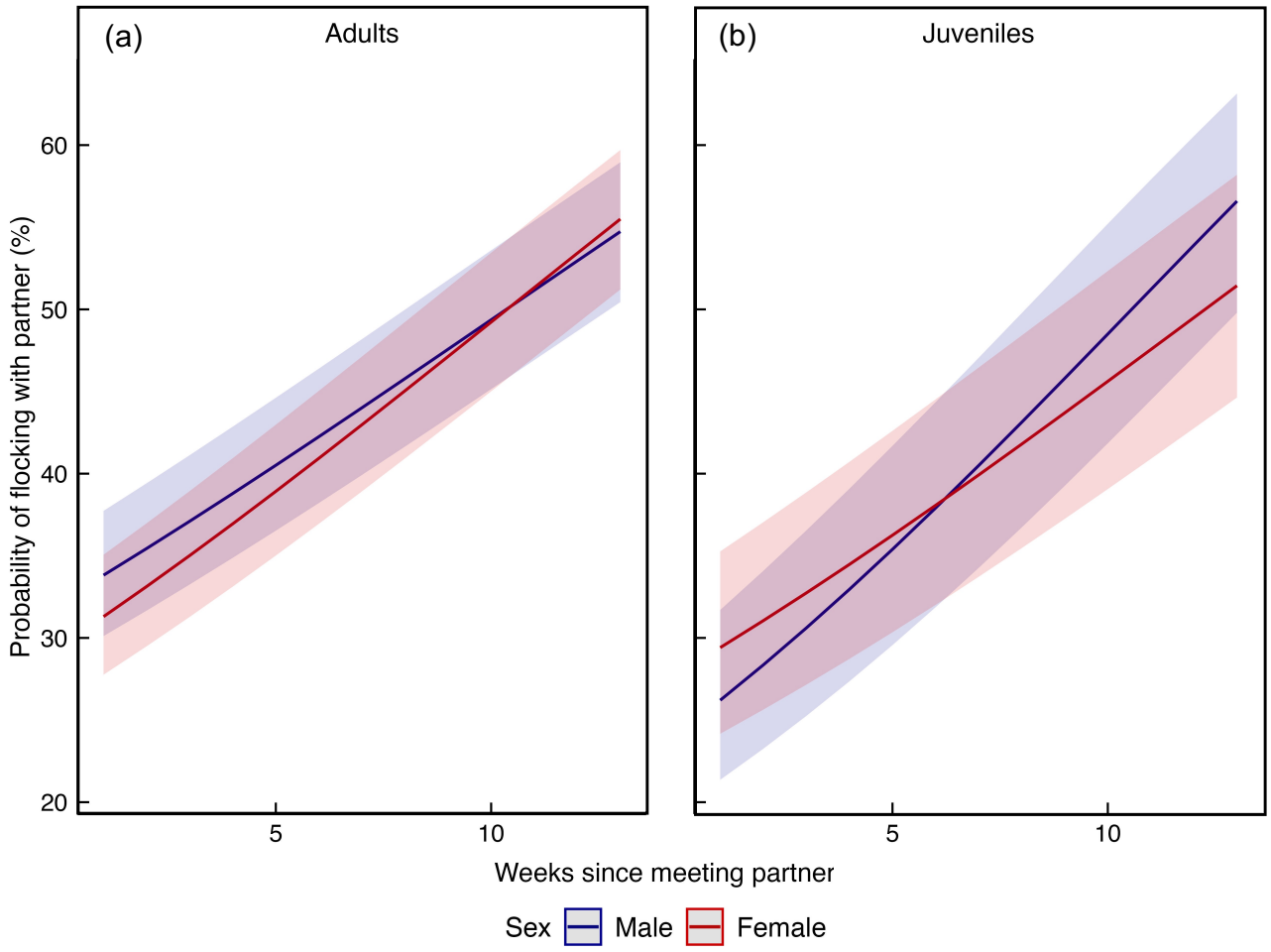

Figure 4: male juveniles increase relative partner affiliation more than female juveniles as time progresses. Lines show predicted values from zero-inflated binomial GLMMs; ribbons show 95% confidence intervals around model predictions. "Probability of flocking with partner" represents response variable of Group 2 GLMMs and reflects relative partner affiliation. (a): Model 2.7, newly-pairing adults, 3027 observations and (b): Model 2.6, juveniles, 2116 observations. Models 2.6 and 2.7: (successes, failures) ~ weeks since meeting*sex + partner's age + (1|year) + (1|pair ID/individual ID) + (1|weekend location).

Additionally, we fitted quadratic models to consider if great tits increase relative partner affiliation non-linearly. A quadratic effect is significant for juveniles, and male juveniles again increase relative partner affiliation significantly more per week than female juveniles (Figure S2, Supplementary Results III) (Model 2.8; (rescaled weeks since meeting)^2: estimate -0.059±0.009, $P < 0.0001$; rescaled weeks since meeting*sex: estimate: 0.105±0.018, $P < 0.0001$). Therefore, juvenile males increase their relative partner affiliation (potentially non-linearly) week-on-week more than juvenile females.

Existing pairs: males associate proportionally more with partner

In existing pairs, males consistently associate relatively more with their partner (relative partner affiliation) than females do (Model 2.14; sex: estimate = 0.089±0.047, $P = 0.057$) (Figure 5), but there is no support for a quadratic effect (Model 2.15; (rescaled weeks since meeting)^2: estimate -0.007±0.018, $P = 0.705$).

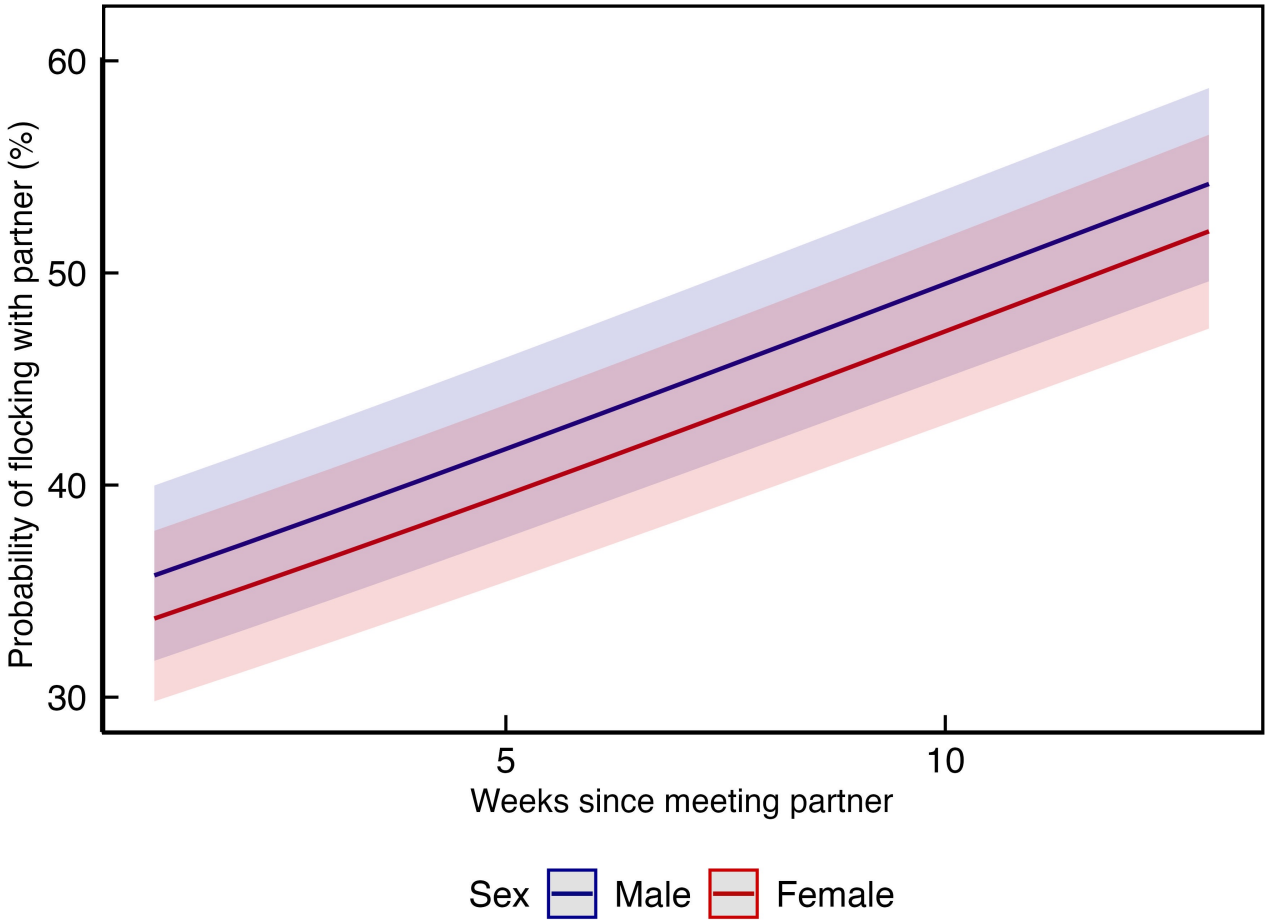

Figure 5: in existing pairs, males affiliate more with their partner than females do through time. Lines show predicted values from zero-inflated beta-binomial GLMM (1615 observations) (Model 2.14): (successes, failures) ~ weeks since meeting + sex + (1|year) + (1|pair ID/individual ID) + (1|weekend location). Ribbons show 95% confidence intervals around model predictions. "Probability of flocking with partner" represents response variable of Group 2 GLMMs and reflects relative partner affiliation. In an alternative model, weeks since meeting*sex had estimate 0.002±0.008; there's no evidence for the effect of sex changing as the non-breeding season progresses.

Group 3: Sex-Based Relative Partner Affiliation

New pairs: age, sex and time interact to shape sex-based relative partner affiliation

For new pairs, the proportion of opposite-sex associations with the partner was statistically significantly related to the three-way interaction of weeks since meeting*sex*age (Figure 6) (Model 3.2; estimate = 0.043±0.012, $P < 0.001$). That is to say, the effect of time on sex-based relative partner affiliation depends on both sex and age. The effect of sex is pronounced in newly-pairing adults, with a steeper increase in sex-based relative partner affiliation for females than males (Figure 6a) (weeks since met*sex (male): estimate = -0.034±0.003, $P < 0.0001$).

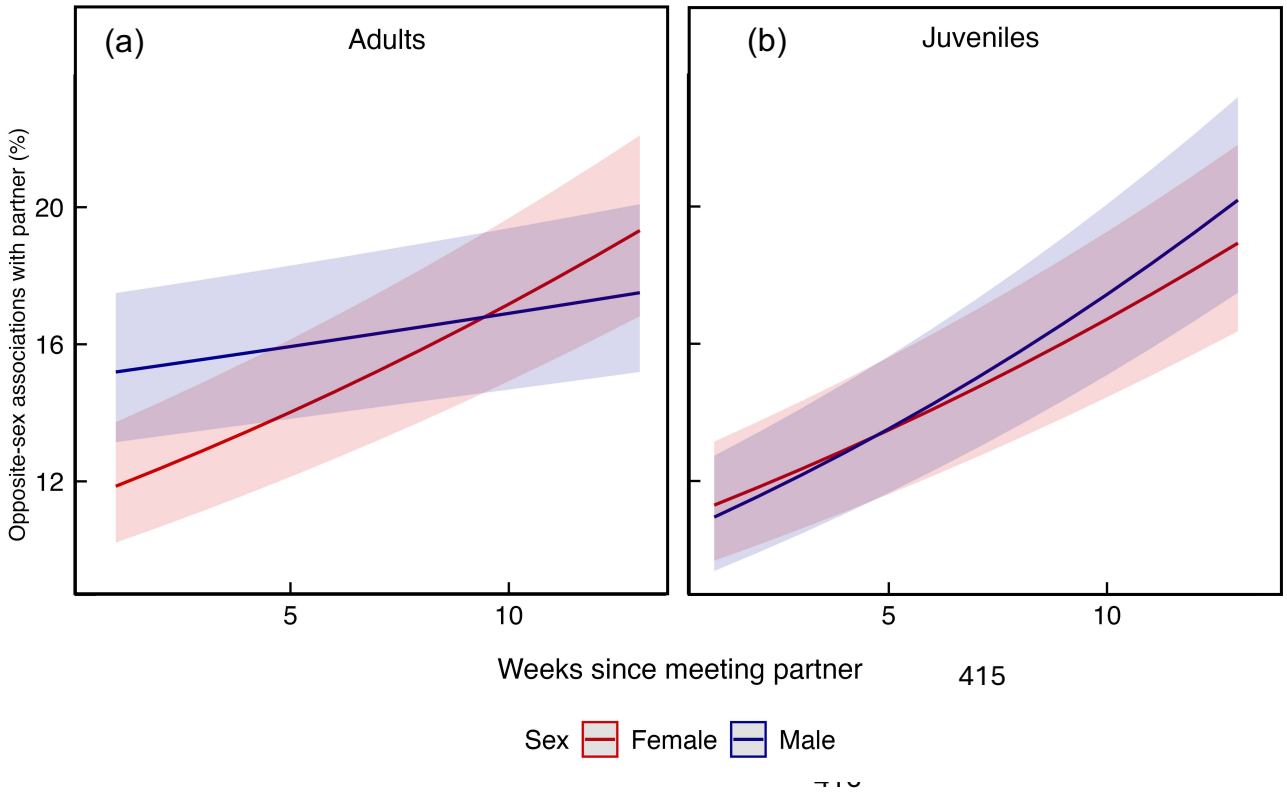

Figure 6: for new pairs, a three-way interaction of age, time and sex shape sex-based relative partner affiliation. Lines show predicted values from zero-inflated beta-binomial GLMM (observations 5143) (Model 3.2): (observations with partner in weekend, observations with non-partner opposite-sex birds in weekend) ~ weeks since meeting*sex*age + (1|year) + (1|pair ID/individual ID). Ribbons show 95% confidence intervals around model predictions. Weekend location was not included as a random effect to aid convergence.

Prediction 2: Sex Affects Social Association Stability During Pair Bonding

Group 4: seasonal social association stability

Effect of sex depends on age

The effect of sex on a great tit's seasonal social association stability - the correlation (ρ) of its association (SRI) with each other individual from first to last being recorded flocking with its partner in a winter - depends on age (Model 4.1; sex*age: estimate = 0.188±0.080, P = 0.018). Within juvenile-juvenile pairs, males have higher correlations (Model 4.4; sex: estimate = 0.173±0.086, P = 0.045).

To assess whether the effects of sex and age on seasonal social association stability depend on how correlated a pair's associations are when they meet (initial pair correlation), we tested a three-way interaction for new pairs (initial pair correlation*sex*age; Model 4.2) and a two-way interaction for existing pairs (initial pair correlation*sex; Model 4.3). This interaction was not significant for either group (existing: estimate = 0.654±0.538, P = 0.22; new: estimate = -1.05±0.567, P = 0.064) (Figure 7).

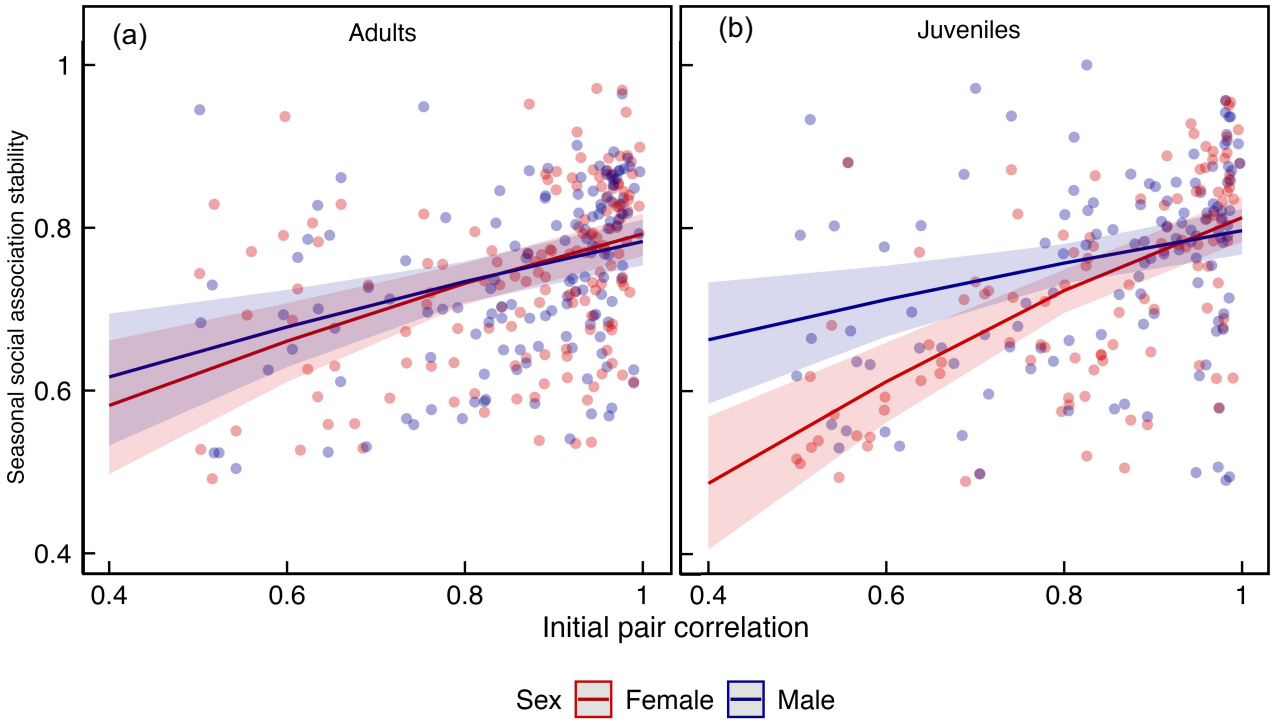

Figure 7: male juveniles have higher seasonal social association stability than female juveniles when initial pair correlation is lower. Beta GLMM (516 observations) (Model 4.2): seasonal social association stability ~ initial pair correlation*sex*age + (1|year) + (1|pair ID/individual ID) + (1|location). Lines show predicted values of seasonal social association stability for each group at each value of initial pair correlation and ribbons show 95% confidence intervals for predicted values. Points show raw data.

Group 5: weekly social association stability

Males have higher weekly social association stability for a given level of pair association

Seasonal social consistencies may however reflect broader patterns. Individuals with initially higher correlations with their partner's associations (initial pair correlation) are also those with higher seasonal social association stability, with pairs perhaps forming from relatively stable flocks. Therefore, we modelled social association stability between weekends (weekends *t* and *t+1*) as a function of the pair's association (SRI) in weekend *t+1* and tested for sex differences.

Being more associated with its partner is related to an individual having a higher individual weekly social association stability (Figure 8). For existing pairs and newly-pairing adults (Figure 8a), there was no significant effect of a bird's sex (Model 5.1; existing; sex: estimate = 0.029±0.030, P = 0.345. Model 5.2; newly-pairing adults; sex: estimate = 0.019±0.026, P = 0.579). For newly-pairing juveniles, males have higher weekly social association stability for a pair to have a given level of association (Figure 8b) (Model 5.3; sex: estimate = 0.114±0.035, P = 0.001). This effect may however diminish with time (Figure 9) (Model 5.6; sex*weeks since meeting: estimate = -0.024±0.010, P = 0.013).

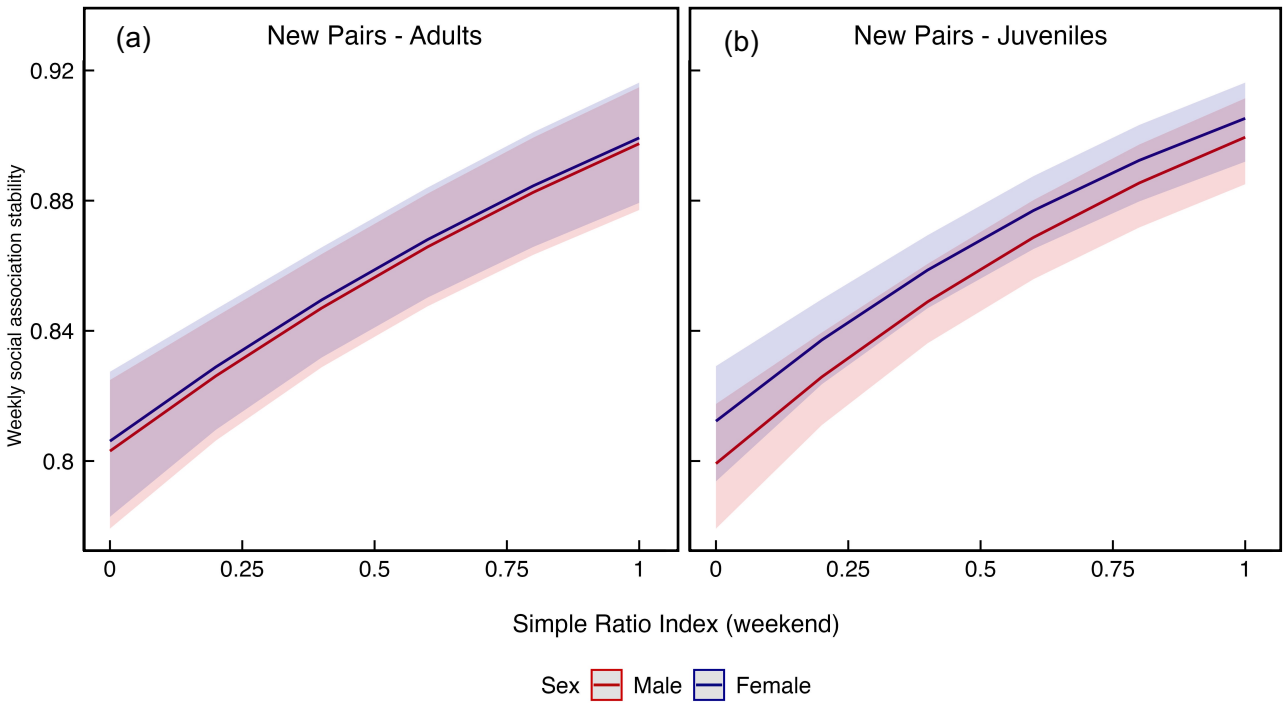

Figure 8: for newly-pairing juveniles, males changed their associations less (higher weekly social association stability) than females for a given level of association (Simple Ratio Index) (b). For newly-pairing adults, no sex difference is apparent (a). Beta (logit link) GLMMs: Models 5.2 (newly-pairing adults, 1929 observations) (a) & 5.3 (newly-pairing juveniles, 1239 observations) (b): weekly social association stability ~ simple ratio index + sex + weeks since meeting + pair correlation + immigration + partner's age + (1|year) + (1|pair ID/individual ID) + (1|weekend location).

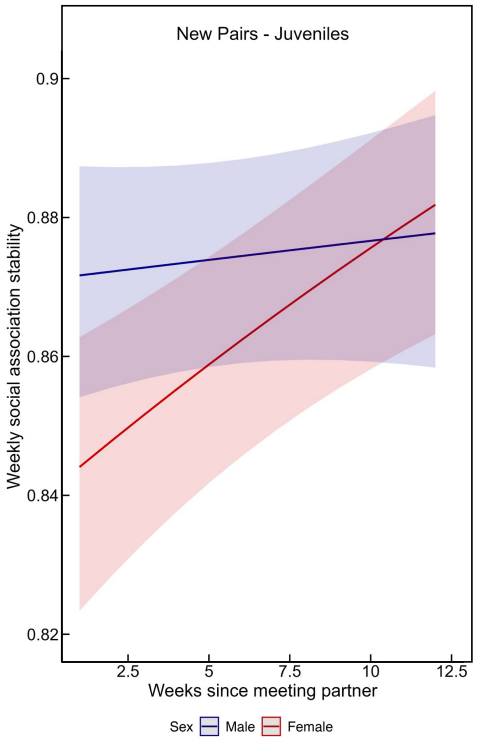

Figure 9: sex interacts with time to shape newly-pairing juveniles' social association stability. Beta (logit link) GLMM: (newly-pairing juveniles, 1239 observations) (Model 5.6): weekly social association stability ~ simple ratio index + sex*weeks since meeting + pair correlation + immigration + partner's age + (1|year) + (1|pair ID/individual ID) + (1|weekend location).

DISCUSSION

We use a large wild bird dataset and social network analyses to provide new insights into how sex affects social trade-offs in a socially monogamous passerine. During the non-breeding season (winter), great tits associating with conspecifics at foraging sites face a social trade-off: developing pair bonds of long-term value (a pair bond with a future breeding partner) at the potential expense of losing short-term benefits from other social relationships (Figure 1: trade-off #1). We find sex-specific patterns in social associations, including that juvenile male birds increase how much they associate with their partner (relative to other conspecifics) more than female juveniles do as time progresses (Figure 4b); in existing pairs, males associate proportionally more with their partner than females do through time (Figure 5). For newly-pairing adults, females increase the proportion of their opposite-sex associations that are with their partner more than males (Figure 6a). Our results also suggest that sex affects how much individuals change their social associations during pair bonding (Figure 1: trade-off #2). We show that

male juveniles have higher social association stability than female juveniles, across the whole winter, and weekend-by-weekend as a function of how associated the pair are (Figure 8b). We discuss these results in the context of pair bonding, the interplay of social and spatial behaviours, and how phenotypes can shape fine-scale social behaviour, impacting social structure.

For socially monogamous animals, pair bonding is often a necessary precursor for reproduction and pair behaviours (e.g. biparental care) (Roth *et al.*, 2021). Here, great tits increase affiliation to their partner as winter progresses and an individual's sex affects how much it associates with its future partner versus other conspecifics. Sex-based differences in pair bonding in birds and mammals have been previously reported, including partner preference development and affiliative behaviour frequency (Brusman *et al.*, 2022; Dolotovskaya *et al.*, 2020; Kubitza *et al.*, 2015). Why sex-based differences occur in our study population can be considered through social trade-off costs and benefits.

Animals can have valuable social relationships besides their partner. For example, stable female-female social bonds carry reproductive benefits in birds, dolphins and primates (Frère *et al.*, 2010; Riehl & Strong, 2018; Silk *et al.*, 2003). In existing great tit pairs, we show that males consistently associate with their partner in more of their flocking events than females (Figure 5). Previous research in this system has shown that for existing pairs, being familiar with nesting neighbours can improve reproductive success, but this acts through females (via clutch size and lay date) rather than males (Gokcekus *et al.*, 2023). Therefore, females may benefit from associating proportionally more with other long-term associates during winter more than males do, given winter social associations carry over to nest proximity (Firth & Sheldon, 2016).

We also find that for newly-pairing adults, females increase how much they associate with their partner compared to other opposite-sex birds (sex-based relative partner affiliation) more than males (Figure 6a). Underlying this, we found that throughout winter, c.44% of newly-pairing adult females' associations are with opposite-sex individuals; contrastingly, newly-pairing adult males initially have fewer observations with opposite-sex birds (37%), but this increases over time (Figure S3; Supplementary Results III). This growing association with females may contribute to a less pronounced increase in sex-based relative partner affiliation for males. For socially monogamous birds, having a lower proportion of female associates may lead to suboptimal partnerships, perhaps due to reduced mate sampling or increased mate competition, and may reduce opportunities for extra-pair copulations (Beck *et al.*, 2020; Culina *et al.*, 2015; Kempenaers *et al.*, 1992). Therefore, generally, pair bonding could trade off with mate choice processes.

Demonstrating that pair members have different social optima for pair bonding trade-offs suggests an area of potential conflict, if optima are incompatible. Interpreting conflict is however limited by our analyses focusing only on pairs which went on to breed; cases where social optima become too

incompatible for a pair to sustain until breeding, if existing, are not captured. Understanding drivers of phenotype-level differences in pair bonding trade-offs is also restricted by not knowing when pairs become fixed prior to breeding. Apparent quadratic effects (Figure S2) suggest increased relative partner affiliation occurs up to a point as time progresses. More broadly, this highlights the challenges of inferring complex social relationships in wild populations, where signals of dynamics and key transitions may be obscured in the data. Future research could explore whether association patterns at certain times predict long-term social outcomes, whilst considering the role of mortality and partner turnover. Addressing the fate of potential pairs that do not persist could provide insights into how demographic and phenotypic factors shape social trade-offs across socially monogamous systems.

Sex-based differences also exist in how great tits adjust social associations during pair bonding. Dynamism in fission-fusion societies enables individuals to reshape social networks, including altering associations to modulate mate competition (Oh & Badyaev, 2010). Social association changes result from interactions of spatial and social processes. Research from other systems show that changes in resource availability shape how individuals change their associations, and there is feedback between where individuals access resources and with whom they associate (Webber *et al.*, 2023). Social rewards also interact with resource use, as seen in jackdaws (Kings *et al.*, 2023) and great tits (Firth *et al.*, 2015). In the latter, associating with a partner can shift foraging locations, altering an individual's social environment (Firth *et al.*, 2015).

We found that a pair being more closely associated in a weekend is generally related to greater social association stability preceding it, implying pairs co-occur more when embedded in flocks with lower social turnover. Our results show that juvenile males, however, have higher social association stability than female juveniles for a given level of pair association (Figure 8b), and have higher social association stability across the winter when pairs have initially less similar associates (lower initial pair correlation) (Figure 7b). Dispersal is a spatial behaviour with social drivers and consequences that could influence such patterns (Webber *et al.*, 2023). Broadly, in birds, there are sex-based differences in dispersal behaviour, with females dispersing further than males (Greenwood, 1980). This holds true for great tits, with female juveniles dispersing further than male juveniles pre-winter (Greenwood *et al.*, 1979). This could mean that females are not selected to maintain social relationships whilst dispersing, unlike males, which may develop more stable non-partner social associations in this period. Stable non-partner social associations may also develop through juvenile great tits preferentially associating with spatially close conspecifics of a similar age, as they may hold the most relevant social information for that bird, and these stable associations can then carry over between seasons (Firth & Sheldon, 2016; Wild *et al.*, 2024). This pattern of juvenile males having higher social association stability than juvenile females diminishes as winter continues, however (Figure 9). Dispersal is one example of how the interplay between spatial and social behaviour can structure animal societies, yet observational data

alone often limit causal inference (Albery *et al*., 2024). Experimental approaches, such as manipulating resource availability or social environments, provide valuable tools to disentangle spatial and social effects and test predictions from observational studies (Farine & Whitehead, 2015; Firth & Sheldon, 2015). Future work across diverse systems could explore how individuals optimise social associations in response to ecological, social, and demographic pressures.

The observed foraging associations in this study system are known to be biologically and ecologically meaningful for other contexts too, such as nesting location and territory neighbours (Firth & Sheldon, 2016), mating decisions (Firth *et al*. 2015, 2018), and information spread and social learning (Aplin *et al*., 2015; Firth *et al*. 2016). Nevertheless, underpinning mechanisms of social patterns are difficult to tease out from observational data. For instance, individuals differ in their foraging tactics at feeders and how much they use feeders (Crates *et al*., 2016; Milligan *et al*., 2017). Variation in feeder use could be driven by social dynamics (e.g. visiting feeders to interact with key conspecifics) (Firth *et al*., 2015), but could also be affected by dominance, energy demands, or other foraging factors (Crates *et al*., 2016; Milligan *et al*., 2017). Our models captured individual variation in feeder use through a fixed effect ("Weekend count"; model Group 1), individual identity as a random effect (model Groups 1-5), and the number of datapoints in the model per individual (equalling the number of weekends that individual was recorded; model Groups 2, 3 & 5) (Table 1). Nevertheless, results of observational studies should be considered in the context of potential biases and their biological drivers.

Whilst our analyses capture fine-scale temporal changes in social associations, they do not explicitly separate within-individual allocation decisions from stable between-individual differences in overall social association patterns. As highlighted by van Noordwijk & de Jong (1986) and van de Pol & Wright (2009), this distinction is important for interpreting trade-offs. Our results therefore describe sex-specific patterns in social association dynamics consistent with trade-off hypotheses, rather than direct tests of individual-level allocation decisions.

Taking results together, we show there are sex-based differences in how great tits manage social trade-offs during pair bonding. These social trade-offs influence non-breeding season social networks, carrying forward to breeding season social structure. In turn, processes such as disease and information spread, cooperation, and selection emerge from the strengths and patterns of social connections (Brask *et al*., 2021; Cantor *et al*., 2021). The novel insights provided here therefore inform the feedback between individual behaviour and emergent processes, by identifying sources of variation in social strategies.

CONCLUSION

We demonstrate that an individual's sex affects how it trades off long-term benefits of pair bonding in winter with costs of reduced short-term benefits of associating with other conspecifics, in a model passerine population. We find that during winter pair bonding, in pre-existing pairs, males associate more with their partner compared to other birds than females. Our results also show that for adults forming a new pair, females increase how much they associate with their partner compared to other opposite-sex birds more than males. Considering juveniles, males increase their affiliation with their partner more than females, and males have higher social association stability. These results occur in the context of sex-dependent costs and benefits from social relationships other than the pair bond, and the interaction of spatial and social behaviours shaping how individuals change their associations. This provides new insights into sex-based differences in social strategies and a foundation for future research into social trade-offs in wild populations.

DATA AVAILABILITY

The datasets analysed in this study and associated code are fully available in this repository: https://figshare.com/projects/Sex-based_differences_in_social_trade-offs_in_a_wild_bird_society/248015.

DECLARATION OF INTEREST

The authors declare no competing interests.

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Supplementary Information

Sex-based differences in social trade-offs in a wild bird society

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Supplementary Methods

Supplementary Methods I

Glossary:

i) Social association: inferred social link from two individuals overlapping in space and time (Croft *et al.*, 2008)

ii) Social relationship: repeated association of individuals, involving relevant behaviours:

   a. Social association is proxy measure for social relationship; used if nature of interactions difficult to record, or associations inherently capture the relevant behaviour (e.g. feeding together)

iii) Social interaction: specific behaviour directed from actor to receiver

iv) Pair bond: strong selective association between a breeding male and female (Bales, 2021; although diversely defined in the literature)

v) Social network: representation of observed patterns of social associations (Farine & Whitehead, 2015)

vi) Social trade-off: trade-off of extent of one social relationship (association) versus another, considering costs and benefits of each social relationship (including opportunity costs, if developing one social relationship limits another)

For Hypothesis 1 models (Groups 1 and 2):

i) Successes: number of observations with partner in specified time period

ii) Failures: number of observations without partner in specified time period

iii) Seasonal partner affiliation: association with future breeding partner relative to other conspecifics over the whole winter. Measured as how many times a bird flocked with

(successes) and without (failures) its partner over the winter, from when the pair first flocked together that season.

iv) Weekly partner affiliation: association with future breeding partner relative to other conspecifics over the course of a single data recording weekend. Measured as how many times a bird flocked with (successes) and without (failures) its partner over the weekend, with weekends prior to the pair first observed flocking together that winter excluded.

v) Sex-based partner affiliation: the probability that if a bird is recorded with an opposite-sex bird, that bird is its partner.

vi) Sex-based Successes: number of observations with partner within weekend: equal to the number of flocking events (Successes, i)

vii) Sex-based Failures: number of observations with birds of the opposite sex within weekend (i.e. sum of all associations with opposite-sex birds)

viii) Weeks since meeting: number of weekends since breeding pair first observed in same flocking event (weekend of meeting = 0)

ix) Rescaled weeks since meeting: weeks since meeting centred and rescaled so mean = 0 and standard deviation = 1.

x) Pair status: as defined in Figure 2:
    a. Existing: Pair bred together in previous breeding season
    b. Ad-Ad: Newly pairing adults (following partner death or divorce) which pair with adult
    c. Juv-Juv: Juveniles which pair with juvenile
    d. MJuv-FAd: Male juveniles paired with newly pairing adult females
    e. FJuv-MAd: Female juveniles paired with newly pairing adult males

xi) Age: adult – more than one year old, not born in most recent breeding season; juvenile – first-year bird, born in most recent breeding season

xii) Partner's age: adult or juvenile

xiii) Immigration status: TRUE (bird was not born in Wytham Woods), FALSE (bird was born in Wytham Woods).

xiv) Year: 2012 (winter 2011-2012), 2013 (winter 2012-2013), 2014 (winter 2013-2014)

xv) ID: unique identification code of individual bird

xvi) Pair ID: unique identification code of each pair

xvii) Weekend location: each individual's preferred bird feeder site (most visited during weekend)

xviii) Location: preferred feeder site of individual for whole winter.

Additional variables for Hypothesis 2 models (Groups 4 and 5):

xix) Seasonal social association stability: for each individual, the correlation (ρ) of its association (SRI) with each individual from the weekend where it was first recorded flocking with its partner to the weekend where it was last recorded flocking with its partner, returning a single value for each individual for each winter (Ilany *et al*., 2021). Transformed to (0, 1) scale.

xx) Weekly social association stability: for each individual, the correlation (ρ) of its association (SRI) with each individual from one weekend to the next, returning a single value for each individual for each weekend (Ilany *et al*., 2021). Transformed to (0, 1) scale.

xxi) Initial pair correlation: how correlated an individual's associations were with its partner's social associations (correlation measured as above) when first recorded together, excluding the pair from the calculation.

xxii) Weekend pair correlation: how correlated an individual's associations were with its partner's social associations in weekend *t*, when being linked to the pair's association strength in weekend *t+1* (SRI)

Supplementary Methods II

Prediction 1: sex affects association with partner

Model Group 1: whole season GLMMs

Response variable: how many times a bird flocked with (successes (*k*)) compared to without (failures (*k* + *n*)) its partner over the whole non-breeding season, counting from when the pair first met. Seasonal partner affiliation.

Table S1: summary table of the structure of Group 1 models

Model name	Sample	Family	Fixed effects	Random effects	Zero-inflation
1.1	Males	Beta-binomial	pairing status + weekend count	(1 | Year) + (1 | ID) + (1 | Location)	No
1.2	Females	Beta-binomial	pairing status + weekend count	(1 | Year) + (1 | ID) + (1 | Location)	No
1.3	Newly pairing birds	Beta-binomial	sex + age + weekend count + immigration status	(1 | Year) + (1 | ID) + (1 | Location)	No
1.4	Existing pair birds	Binomial	sex + weekend count + immigration status	(1 | Year) + (1 | ID) + (1 | Location)	No
1.5	Juv-Juv pair birds	Beta-binomial	sex + weekend count + immigration status	(1 | Year) + (1 | ID) + (1 | Location)	No
1.6	New Ad-Ad pair birds	Beta-binomial	sex + weekend count + immigration status	(1 | Year) + (1 | ID) + (1 | Location)	No
1.7	MJuv-FAd pair birds	Beta-binomial	sex + weekend count + immigration status	(1 | Year) + (1 | ID) + (1 | Location)	No

1.8	FJuv-MAd pair birds	Binomial	sex + weekend count + immigration status	(1 | Year) + (1 | ID) + (1 | Location)	No

Model Group 2: temporal GLMMs

Response variable: how many times a bird flocked with (successes (*k*)) compared to without (failures (*k* + *n*)) its partner during a weekend. Weekends before a pair first met that season are excluded, as are records where a bird was not recorded in that weekend (i.e. 0 successes, 0 failures). Weekly partner affiliation.

Table S2: summary table of the structure of Group 2 models

Model name	Sample	Family	Fixed effects	Random effects	Zero-inflation
2.1	Males	Binomial	weeks since meeting * pairing status	(1 | Year) + (1 | ID) + (1 | Weekend Location)	Yes
2.2	Females	Binomial	pairing status * weekend count	(1 | Year) + (1 | ID) + (1 | Weekend Location)	Yes
2.3	Males	Binomial	rescaled weeks since meeting^2 + rescaled weeks since meeting * pairing status	(1 | Year) + (1 | ID) + (1 | Weekend Location)	Yes
2.4	Females	Binomial	rescaled weeks since meeting^2 + rescaled weeks since meeting * pairing status	(1 | Year) + (1 | ID) + (1 | Weekend Location)	Yes
2.5	Newly pairing birds	Binomial	weeks since meeting * sex * age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.6	Newly pairing juveniles	Binomial	weeks since meeting * sex + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.7	Newly pairing adults	Binomial	weeks since meeting * sex + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.8	Newly pairing juveniles	Binomial	rescaled weeks since meeting^2 + rescaled weeks since meeting * sex + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.9	Newly pairing adults	Binomial	rescaled weeks since meeting^2 + rescaled weeks since meeting * sex + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.10	Juvenile – juvenile pair birds	Binomial	weeks since meeting * sex + immigrant status	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.10.i	Juvenile – juvenile pair birds	Binomial	weeks since meeting + sex + immigrant status	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.11	New adult-adult pair birds	Binomial	weeks since meeting + sex + immigrant status	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes

2.12	Male juvenile – female adult pair birds	Binomial	weeks since meeting + sex + immigrant status	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.13	Female juvenile – male adult pair birds	Beta-binomial	weeks since meeting + sex + immigrant status	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.14	Existing pair birds	Beta-binomial	weeks since meeting + sex	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes
2.15	Existing pair birds	Beta-binomial	rescaled weeks since meeting^2 + rescaled weeks since meeting + sex	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	Yes

Group 3: sex based association GLMMs

Response variable: Sex-based successes (number of observations with partner within weekend) and sex-based failures (total observations with birds of the opposite sex within weekend). Weekends before a pair first met that season are excluded, as are records where a bird was not recorded in that weekend (i.e. 0 successes, 0 failures). Weekly sex-based partner affiliation.

Table S3: summary table of the structure of Group 3 models

Model name	Sample	Family	Fixed effects	Random effects	Zero-inflation
3.1	Existing pair birds	Binomial	weeks since meeting * sex	(1 | Year) + (1 | Pair ID / ID)	Yes
3.2	New pair birds	Binomial	weeks since meeting * age * sex	(1 | Year) + (1 | Pair ID / ID)	Yes

<u>Prediction 2: sex affects association changes during pair bonding</u>

Group 4: seasonal social association stability GLMMs

Response variable: seasonal social association stability: how correlated an individual's associations were from when it was first recorded with its partner, to the end of the non-breeding season.

Table S4: summary table of the structure of Group 4 models

Model name	Sample	Family	Fixed effects	Random effects	Zero-inflation
4.1	All birds	Beta	initial pair correlation + sex * age	(1 | Year) + (1 | Pair ID / ID) + (1 | Location)	No
4.2	New pair birds	Beta	initial pair correlation * sex * age	(1 | Year) + (1 | Pair ID / ID) + (1 | Location)	No
4.3	Existing pair birds	Beta	initial pair correlation + sex	(1 | Year) + (1 | Pair ID / ID) + (1 | Location)	No

4.4	Juvenile – juvenile pair birds	Beta	initial pair correlation + sex	(1 | Year) + (1 | Pair ID / ID) + (1 | Location)	No
4.5	New adult-adult pair birds	Beta	initial pair correlation * sex * immigrant status	(1 | Year) + (1 | Pair ID / ID) + (1 | Location)	No

Group 5: weekly social association stability GLMMs

Response variable: weekly social association stability: how correlated an individual's associations were from weekend *t* to weekend *t+1*.

Table S5: summary table of the structure of Group 5 models

Model name	Sample	Family	Fixed effects	Random effects	Zero-inflation
5.1	Existing pairs	Beta	simple ratio index + sex + weekend pair correlation + weeks since meeting	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	No
5.2	Newly-pairing adults	Beta	simple ratio index + sex + weekend pair correlation + weeks since meeting + immigration + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	No
5.3	Newly-pairing juveniles	Beta	simple ratio index + sex + weekend pair correlation + weeks since meeting + immigration + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	No
5.4	Existing pairs	Beta	simple ratio index + sex*weeks since meeting + weekend pair correlation	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	No
5.5	Newly-pairing adults	Beta	simple ratio index + sex*weeks since meeting + weekend pair correlation + immigration + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	No
5.6	Newly-pairing juveniles	Beta	simple ratio index + sex*weeks since meeting + weekend pair correlation + immigration + partner's age	(1 | Year) + (1 | Pair ID / ID) + (1 | Weekend Location)	No

Supplementary Methods III

Additional model details

Random effect selection

Single-sex models contained individual ID as a random effect, accounting for multiple records per individual. Despite only having three levels, potentially leading to inaccurate random effect variance estimates (Silk *et al.*, 2020), we included year as a random effect, accounting for annual variation and individuals' observations between years. To control for spatial variation we used a random effect of an individual's most-visited feeder (location), as habitat variation indirectly

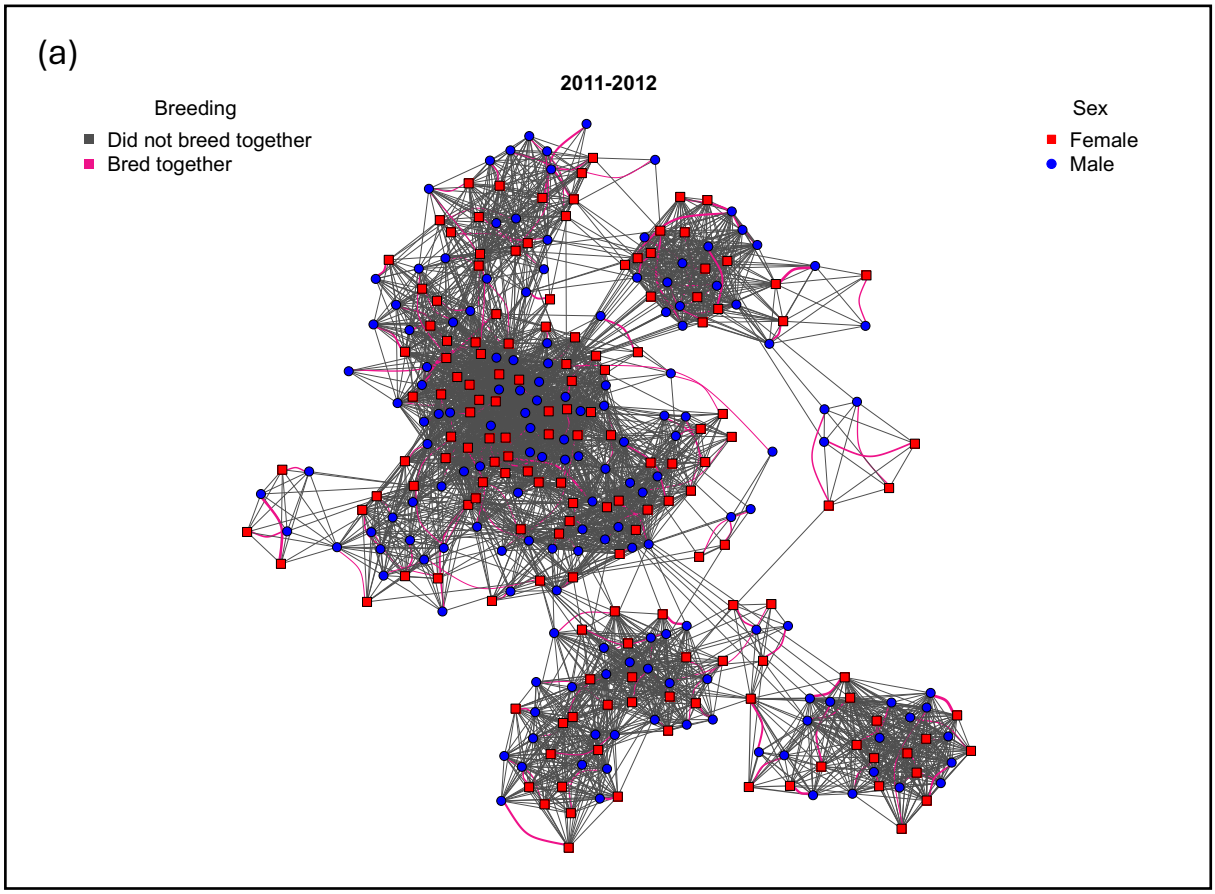
affects social structure in this population (Beck *et al*. 2023). On average, 78.9% of a bird's visits were to its preferred feeder that winter (Appendix D). We followed Barr *et al*. (2013), applying maximal random effects based on data collection.

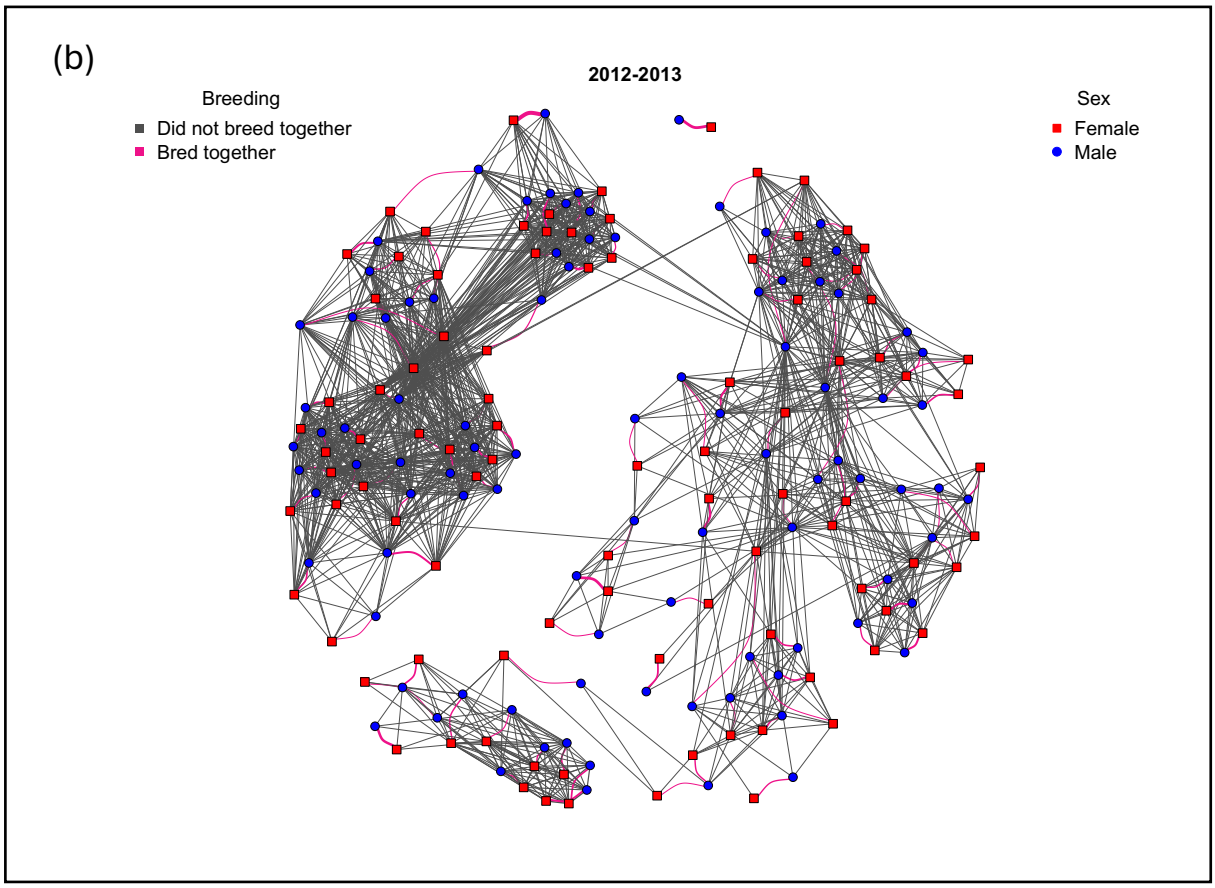
Technical model details

We built all models using *glmmTMB* (Brooks *et al*., 2024) in R (v.4.2.2) (R Core Team, 2022). We used Laplace approximation due to its relative accuracy and efficiency (Bolker *et al*., 2009). Using models to test hypotheses on the effect of sex and fixed effects to control for other factors, assessed models on their theoretical implications. We also used Akaike Information Criterion to consider model fit and complexity, following Sutherland *et al*. (2023). We used the *DHARMa* package to assess deviations from the expected distribution (dispersion, outliers), residuals patterns, and normal distribution of random effects (Hartig, 2022).

Supplementary Results

Supplementary Results I





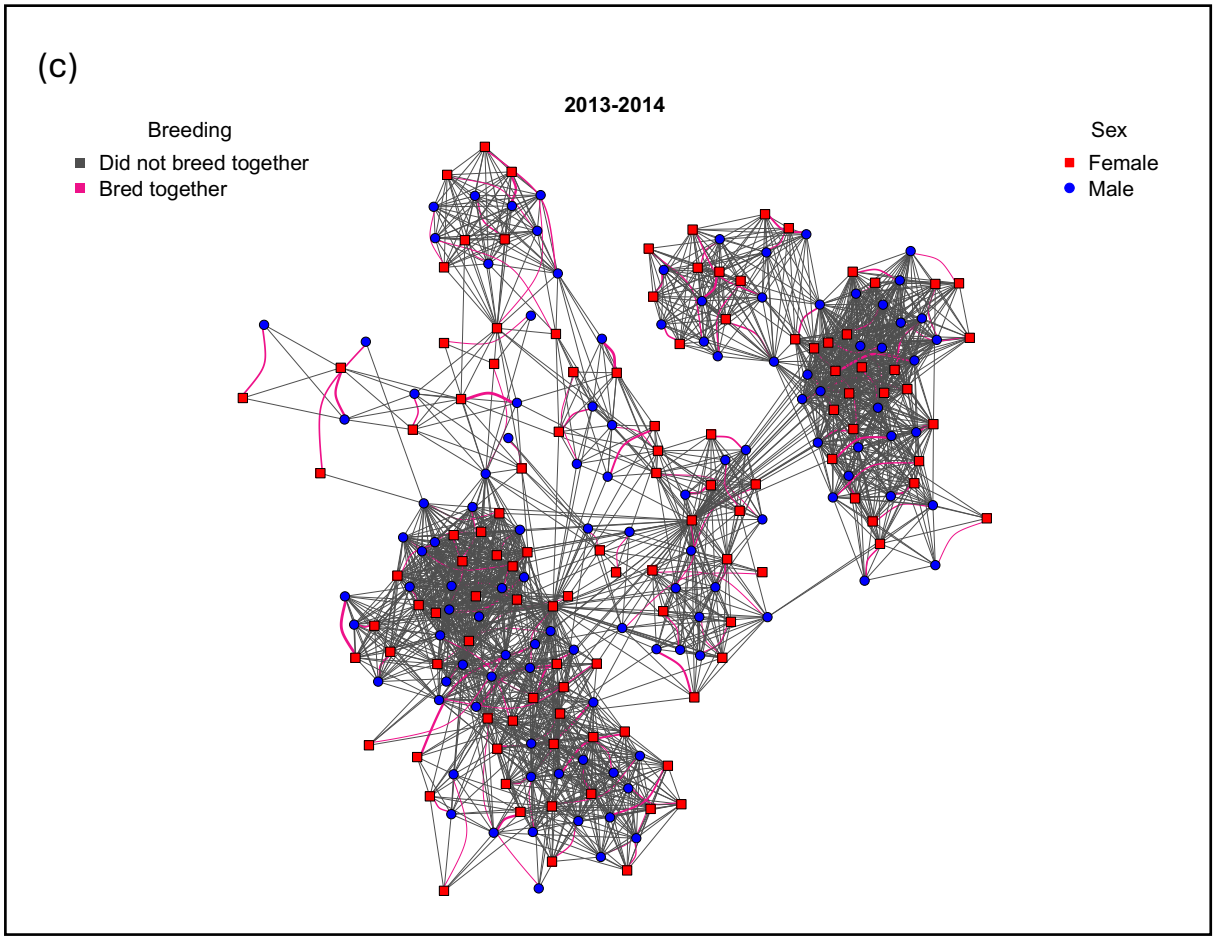


Figure S1: Illustrative social networks for winters 2011-2012, 2012-2013, and 2013-2014. These networks only include birds which fulfilled model criteria, for illustrative purposes, showing variation in the strength and number of individuals' relationships and the emergence of pair bonds within networks. Note: metric calculations and networks used to calculate correlation of associations (for modelling) incorporated associations with all birds recorded, not just those which fulfilled model criteria. Nodes represent individuals (coloured by sex), and the thickness of edges (lines between nodes) represents the strength of association between two individuals (Simple Ratio Index). Edges are coloured (pink) and curved if the dyad went on to be a breeding pair the following breeding season. Relative position of nodes is for display and does not reflect any spatial positioning.

Supplementary Results II

Group 1

Model 1.1:

AIC = 3757.8; observations = 357

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.580	0.177	-3.276	0.001
Pairing status (existing)	0.273	0.101	2.721	0.007
Pairing status (FJuv-MAd)	0.040	0.131	0.308	0.758
Pairing status (Juv-Juv)	-0.173	0.105	-1.645	0.100
Pairing status (MJuv-FAd)	-0.306	0.127	-2.416	0.016
Weekend count	0.007	0.014	0.549	0.583

Random effect term	Variance	Standard deviation
Location (intercept)	0.017	0.131
Year (intercept)	0.002	0.047
ID (intercept)	0.134	0.366

Model 1.2:

AIC = 3700.7; observations = 355

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.536	0.149	-3.606	<0.001
Pairing status (existing)	0.188	0.096	1.956	0.051
Pairing status (FJuv-MAd)	-0.185	0.125	-1.474	0.140
Pairing status (Juv-Juv)	-0.157	0.096	-1.632	0.103
Pairing status (MJuv-FAd)	-0.178	0.116	-1.538	0.124
Weekend count	0.008	0.011	0.702	0.482

Random effect term	Variance	Standard deviation
Location (intercept)	7.039e-02	2.653e-01
Year (intercept)	6.341e-10	2.518e-05
ID (intercept)	7.260e-02	2.694e-01

Model 1.3:

AIC = 5925.4; observations = 564

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.428	0.134	-3.192	0.001
Sex (male)	-0.017	0.059	-0.287	0.774
Age (juvenile)	-0.153	0.062	-2.464	0.014
Weekend count	-0.005	0.010	-0.469	0.639
Immigrant	-0.041	0.062	-0.651	0.515

Random effect term	Variance	Standard deviation
Location (intercept)	8.826e-02	2.971e-01
Year (intercept)	8.348e-09	9.137e-05
ID (intercept)	5.974e-02	2.444e-01

Model 1.4:

AIC = 1486.3; observations = 148

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.011	0.179	-5.648	<0.0001
Sex (male)	0.042	0.076	0.555	0.579
Weekend count	0.064	0.013	4.773	<0.0001
Immigrant	-0.051	0.084	-0.604	0.546

Random effect term	Variance	Standard deviation
Location (intercept)	0.084	0.289
Year (intercept)	0.0001	0.012
ID (intercept)	0.165	0.405

Model 1.5:

AIC = 1769; observations = 170

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.803	0.241	-3.335	<0.0001
Sex (male)	-0.075	0.121	-0.622	0.534
Weekend count	0.021	0.020	1.077	0.282
Immigrant	-0.151	0.144	-1.051	0.293

Random effect term	Variance	Standard deviation
Location (intercept)	0.219	0.468
Year (intercept)	0.007	0.084
ID (intercept)	0.008	0.090

Model 1.6:

AIC = 2323.1; observations = 220

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.287	0.208	-1.374	0.169
Sex (male)	-0.018	0.074	-0.244	0.807
Weekend count	-0.026	0.017	-1.519	0.129
Immigrant	0.138	0.082	1.688	0.092

Random effect term	Variance	Standard deviation
Location (intercept)	9.039e-02	3.006e-01
Year (intercept)	6.729e-10	2.594e-05
ID (intercept)	1.063e-02	1.031e-01

Model 1.7

AIC = 995.6; observations = 98

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.411	0.241	-1.698	0.089
Sex (male)	-0.105	0.113	-0.932	0.351
Weekend count	-0.032	0.019	-1.662	0.096
Immigrant	-0.103	0.121	-0.851	0.395

Random effect term	Variance	Standard deviation
Location (intercept)	3.175e-01	5.635e-01
Year (intercept)	1.543e-09	3.928e-05
ID (intercept)	1.569e-02	1.252e-01

Model 1.8

AIC = 798.8; observations = 76

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.517	0.351	-1.473	0.141
Sex (male)	0.206	0.128	1.609	0.108
Weekend count	-0.031	0.028	-1.109	0.286
Immigrant	0.096	0.141	0.682	0.495

Random effect term	Variance	Standard deviation
Location (intercept)	0.231	0.481
Year (intercept)	0.020	0.141
ID (intercept)	0.265	0.515

Group 2

Model 2.1

AIC = 24502.8; observations = 3399

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.731	0.076	-9.566	<0.0001
Weeks since met	0.074	0.003	23.810	<0.0001
Pairing status (existing)	0.378	0.045	8.339	<0.0001
Pairing status (FJuv-MAd)	0.296	0.063	4.693	<0.0001
Pairing status (Juv-Juv)	-0.067	0.059	-1.155	0.248
Pairing status (MJuv-FAd)	-0.013	0.080	-8.413	<0.0001
Weeks since met*Pairing status (existing)	-0.013	0.006	-2.617	0.009
Weeks since met*Pairing status (FJuv-MAd)	-0.027	0.007	-3.857	<0.0001
Weeks since met*Pairing status (Juv-Juv)	0.035	0.006	6.330	<0.0001
Weeks since met*Pairing status (MJuv-FAd)	0.031	0.007	4.429	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	0.002	0.046
ID (intercept)	0.396	0.629
Weekend location (intercept)	0.145	0.381

Model 2.2

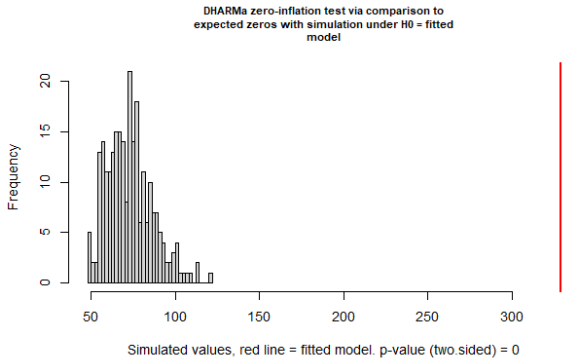
AIC = 24256.6; observations = 3359

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.987	0.101	-9.805	<0.0001
Weeks since met	0.080	0.003	25.641	<0.0001
Pairing status (existing)	0.497	0.046	10.805	<0.0001
Pairing status (FJuv-MAd)	0.370	0.071	5.246	<0.0001
Pairing status (Juv-Juv)	0.151	0.059	2.544	0.011
Pairing status (MJuv-FAd)	-0.176	0.064	-2.751	0.006
Weeks since met*Pairing status (existing)	-0.014	0.005	-3.010	0.003
Weeks since met*Pairing status (FJuv-MAd)	-0.016	0.007	-2.413	0.016
Weeks since met*Pairing status (Juv-Juv)	-0.005	0.006	-0.942	0.346
Weeks since met*Pairing status (MJuv-FAd)	0.016	0.007	2.331	0.020

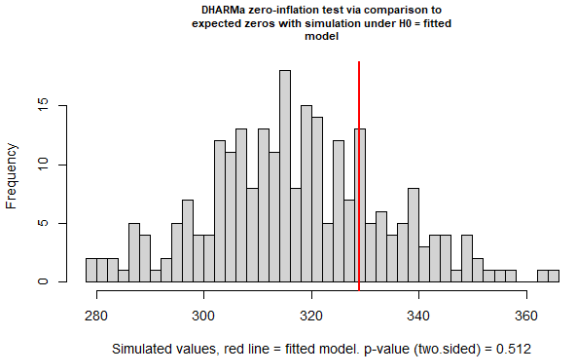
Random effect term	Variance	Standard deviation
Year (intercept)	0.008	0.089
ID (intercept)	0.545	0.738
Weekend location (intercept)	0.261	0.512

Zero-inflation test:

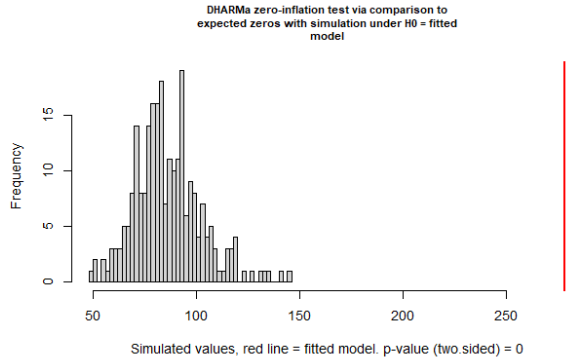
For Model 2.1 but without zero-inflation term:



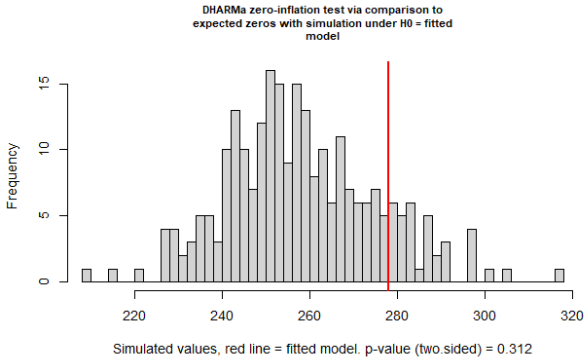
For Model 2.1 with zero-inflation term:



For Model 2.2 but without zero-inflation term:



For Model 2.2 but with zero-inflation term:



These examples highlight that including the zero-inflation term (zi =~1) is beneficial in models considering week-by-week social trade-offs. This improves model performance and potentially captures zero-generating processes (e.g. technical failures, absence of partner from system).

Model 2.3

AIC = 24446.3; observations = 3399

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.212	0.071	-2.859	0.004
(Rescaled weeks since met)^2	-0.058	0.008	-7.634	<0.0001
Rescaled weeks since met	0.285	0.012	24.709	<0.0001
Pairing status (existing)	0.300	0.032	9.288	<0.0001
Pairing status (FJuv-MAd)	0.122	0.048	2.522	0.011
Pairing status (Juv-Juv)	0.148	0.049	3.025	0.002
Pairing status (MJuv-FAd)	-0.463	0.070	-6.589	<0.0001
Rescaled weeks since met *Pairing status (existing)	-0.044	0.017	-2.519	0.012
Rescaled weeks since met *Pairing status (FJuv-MAd)	-0.109	0.025	-4.339	<0.0001
Rescaled weeks since met *Pairing status (Juv-Juv)	0.116	0.020	5.732	<0.0001
Rescaled weeks since met *Pairing status (MJuv-FAd)	0.100	0.026	3.882	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	0.002	0.049
ID (intercept)	0.384	0.619
Weekend location (intercept)	0.140	0.374

Model 2.4

AIC = 24198.9; observations = 3359

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.430	0.099	-4.326	<0.0001
(Rescaled weeks since met)^2	-0.058	0.007	-7.724	<0.0001
Rescaled weeks since met	0.307	0.012	26.502	<0.0001
Pairing status (existing)	0.409	0.034	12.088	<0.0001
Pairing status (FJuv-MAd)	0.262	0.057	4.577	<0.0001
Pairing status (Juv-Juv)	0.118	0.049	2.408	0.016
Pairing status (MJuv-FAd)	-0.070	0.049	-1.426	0.154
Rescaled weeks since met *Pairing status (existing)	-0.050	0.017	-2.925	0.003
Rescaled weeks since met *Pairing status (FJuv-MAd)	-0.069	0.024	-2.803	0.005
Rescaled weeks since met *Pairing status (Juv-Juv)	-0.029	0.020	-1.406	0.160
Rescaled weeks since met *Pairing status (MJuv-FAd)	0.046	0.026	1.801	0.072

Random effect term	Variance	Standard deviation
Year (intercept)	0.008	0.091
ID (intercept)	0.540	0.735
Weekend location (intercept)	0.259	0.510

Model 2.5

AIC = 5143; observations = 5143

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.898	0.086	-10.449	<0.0001
Weeks since met	0.085	0.003	30.030	<0.0001
Sex (male)	0.127	0.045	2.815	0.005
Age (juv)	-0.016	0.059	-0.276	0.782
Weeks since met* Sex (male)	-0.013	0.004	-3.205	0.001
Weeks since met* Age (juv)	-0.006	0.005	-1.199	0.230
Sex (male)*Age (juv)	-0.308	0.072	-4.246	<0.0001
Weeks since met* Sex (male)* Age (juv)	0.043	0.007	6.585	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	1.210e-08	0.0001
ID/Pair ID (intercept)	7.215e-02	0.269
Pair ID (intercept)	4.851e-01	0.696
Weekend location (intercept)	2.562e-01	0.506

Model 2.6

AIC = 15431.4; observations = 2116

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.045	0.140	-7.505	<0.0001
Weeks since met	0.078	0.004	20.681	<0.0001
Sex (male)	-0.190	0.052	-3.644	0.0003
Partner's age (juv)	0.091	0.150	0.608	0.543
Weeks since met* Sex (male)	0.031	0.005	5.896	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	3.452e-08	0.0002
ID/Pair ID (intercept)	5.773e-02	0.240
Pair ID (intercept)	8.420e-01	0.918
Weekend location (intercept)	3.860e-01	0.621

Model 2.7

AIC = 21091.5; observations = 3027

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.870	0.087	-9.968	<0.0001
Weeks since met	0.084	0.003	29.349	<0.0001
Sex (male)	0.127	0.052	2.458	0.014
Partner's age (juv)	0.055	0.088	0.629	0.529
Weeks since met* Sex (male)	-0.012	0.004	-3.056	0.002

Random effect term	Variance	Standard deviation
Year (intercept)	1.536e-08	0.0001
ID/Pair ID (intercept)	1.054e-01	0.325
Pair ID (intercept)	2.422e-01	0.492
Weekend location (intercept)	1.913e-01	0.437

Model 2.8

AIC = 15393.9; observations = 2116

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.543	0.139	-3.918	<0.0001
(Rescaled weeks since met)^2	-0.059	0.009	-6.280	<0.0001
Rescaled weeks since met	0.297	0.014	21.535	<0.0001
Sex (male)	-0.017	0.045	-0.385	0.700
Partner's age (juv)	0.101	0.149	0.677	0.498
Rescaled weeks since met * Sex (male)	0.105	0.018	5.753	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	4.135e-08	0.0002
ID/Pair ID (intercept)	5.690e-02	0.239
Pair ID (intercept)	8.355e-01	0.914
Weekend location (intercept)	3.979e-01	0.631

Model 2.9

AIC = 20998.3; observations = 3027

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.257	0.087	-2.969	0.003
(Rescaled weeks since met)^2	-0.079	0.008	-9.748	<0.0001
Rescaled weeks since met	0.318	0.011	30.154	<0.0001
Sex (male)	0.050	0.045	1.115	0.265
Partner's age (juv)	0.058	0.088	0.658	0.511
Rescaled weeks since met * Sex (male)	-0.044	0.015	-2.993	0.003

Random effect term	Variance	Standard deviation
Year (intercept)	1.870e-08	0.0001
ID/Pair ID (intercept)	1.042e-01	0.323
Pair ID (intercept)	2.421e-01	0.492
Weekend location (intercept)	1.969e-01	0.444

Model 2.10

AIC = 9364.4; observations = 1360

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.177	0.217	-5.418	<0.0001
Weeks since met	0.084	0.005	17.434	<0.0001
Sex (male)	-0.188	0.058	-3.227	0.001
Immigrant	-0.055	0.071	-0.782	0.434
Weeks since met * Sex (male)	0.024	0.006	3.759	0.0002

Random effect term	Variance	Standard deviation
Year (intercept)	1.579e-07	0.0004
ID/Pair ID (intercept)	6.351e-02	0.252
Pair ID (intercept)	1.658	1.288
Weekend location (intercept)	1.164	1.079

Model 2.10.i

AIC = 9376.5; observations = 1360

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.241	0.215	-5.773	<0.0001
Weeks since met	0.096	0.003	27.779	<0.0001
Sex (male)	-0.062	0.047	-1.295	0.195
Immigrant	-0.057	0.071	-0.811	0.417

Random effect term	Variance	Standard deviation
Year (intercept)	1.446e-07	0.0004
ID/Pair ID (intercept)	6.384e-02	0.253
Pair ID (intercept)	1.639	1.280
Weekend location (intercept)	1.146	1.079

Model 2.11

AIC = 15634; observations = 2303

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.921	0.093	-9.890	<0.0001
Weeks since met	0.080	0.002	34.760	<0.0001
Sex (male)	0.044	0.045	0.970	0.332
Immigrant	0.096	0.062	1.540	0.123

Random effect term	Variance	Standard deviation
Year (intercept)	8.014e-09	8.952e-05
ID/Pair ID (intercept)	9.301e-02	3.050e-01
Pair ID (intercept)	1.741e-01	4.173e-01
Weekend location (intercept)	1.923e-01	4.385e-01

Model 2.12

AIC = 5513; observations = 766

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.207	0.154	-7.838	<0.0001
Weeks since met	0.105	0.004	21.816	<0.0001
Sex (male)	-0.061	0.061	-1.009	0.313
Immigrant	0.084	0.088	0.959	0.337

Random effect term	Variance	Standard deviation
Year (intercept)	1.598e-08	0.0001
ID/Pair ID (intercept)	6.213e-02	0.249
Pair ID (intercept)	6.399e-01	0.800
Weekend location (intercept)	1.863e-01	0.432

Model 2.13

AIC = 4538.7; observations = 714

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.194	0.189	-6.296	<0.0001
Weeks since met	0.071	0.009	7.561	<0.0001
Sex (male)	0.102	0.063	1.610	0.107
Immigrant	0.075	0.079	0.949	0.343

Random effect term	Variance	Standard deviation
Year (intercept)	1.221e-08	0.0001
ID/Pair ID (intercept)	1.101e-02	0.105
Pair ID (intercept)	4.254e-01	0.652
Weekend location (intercept)	4.802e-01	0.693

Model 2.14

AIC = 9445.1; observations = 1615

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.739	0.093	-7.941	<0.0001
Weeks since met	0.063	0.004	14.579	<0.0001
Sex (male)	0.090	0.047	1.907	0.056

Random effect term	Variance	Standard deviation
Year (intercept)	0.008	0.089
ID/Pair ID (intercept)	0.0367	0.191
Pair ID (intercept)	0.142	0.377
Weekend location (intercept)	0.058	0.242

Model 2.15

AIC = 9447, observations = 1615

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.314	0.091	-3.457	0.001
(Rescaled weeks since met)^2	-0.007	0.018	-0.379	0.705
Rescaled weeks since met	0.234	0.016	14.537	<0.0001
Sex (male)	0.090	0.047	1.908	0.056

Random effect term	Variance	Standard deviation
Year (intercept)	0.008	0.089
ID/Pair ID (intercept)	0.0367	0.191
Pair ID (intercept)	0.142	0.377
Weekend location (intercept)	0.058	0.242

<u>Group 3</u>

Model 3.1

AIC = 13546; observations = 1618

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-1.774	0.195	-9.102	<0.0001
Weeks since met	0.033	0.003	11.034	<0.0001
Sex (male)	0.266	0.063	4.196	<0.0001
Weeks since met*sex (male)	-0.020	0.004	-4.778	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	0.088	0.297
ID/Pair ID (intercept)	0.091	0.301
Pair ID (intercept)	0.420	0.648

Model 3.2

AIC = 42564; observations = 5164

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-2.055	0.086	-23.926	<0.0001
Weeks since met	0.048	0.002	20.347	<0.0001
Age (juvenile)	-0.056	0.056	-1.003	0.316
Sex (male)	0.320	0.042	7.600	<0.0001
Weeks since met*age (juvenile)	0.003	0.004	0.647	0.518
Weeks since met*sex (male)	-0.034	0.003	-10.178	<0.0001
Age (juvenile)*sex (male)	-0.365	0.068	-5.352	<0.0001
Weeks since met*sex (male)*age (juvenile)	0.044	0.006	7.885	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	0.012	0.111
ID/Pair ID (intercept)	0.070	0.264
Pair ID (intercept)	0.572	0.756

Group 4

Model 4.1

AIC = -1201.1; observations = 658

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.439	0.193	-2.276	0.023
Initial pair correlation	1.841	0.215	8.573	<0.0001
Sex (male)	-0.037	0.044	-0.829	0.407
Age (juvenile)	-0.071	0.065	-1.095	0.273
Sex (male)*age (juvenile)	0.188	0.080	2.367	0.018

Random effect term	Variance	Standard deviation
Year (intercept)	2.285e-03	4.781e-02
ID/Pair ID (intercept)	4.922e-10	2.219e-05
Pair ID (intercept)	1.921e-01	4.383e-01
Location (intercept)	4.096e-02	2.024e-01

Model 4.2

AIC = -931.3; observations = 516

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.344	0.310	-1.112	0.266
Initial pair correlation	1.684	0.354	4.762	<0.0001
Sex (male)	0.280	0.335	0.837	0.403
Age (juvenile)	-0.727	0.405	-1.795	0.073
Initial pair correlation*sex (male)	-0.336	0.386	-0.871	0.384
Initial pair correlation*age (juvenile)	0.853	0.472	1.807	0.071
Sex (male)*age (juvenile)	1.004	0.482	2.083	0.037
Initial pair correlation*sex (male)*age (juvenile)	-1.050	0.567	-1.853	0.064

Random effect term	Variance	Standard deviation
Year (intercept)	1.677e-03	0.041
ID/Pair ID (intercept)	7.894e-10	2.81e-05
Pair ID (intercept)	1.747e-01	0.418
Location (intercept)	4.624e-02	0.215

Model 4.3

AIC = -298.9; observations = 142

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.456	0.533	-0.857	0.392
Initial pair correlation	2.025	0.588	3.443	0.001
Sex (male)	-0.082	0.068	-1.214	0.225

Random effect term	Variance	Standard deviation
Year (intercept)	2.281e-14	1.510e-07
ID/Pair ID (intercept)	4.776e-10	2.185e-05
Pair ID (intercept)	4.472e-01	6.687e-01
Location (intercept)	2.508e-02	1.584e-01

Model 4.4

AIC = -223.7; observations = 154

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.487	0.402	-1.211	0.226
Initial pair correlation	1.872	0.478	3.916	<0.0001
Sex (male)	0.173	0.086	2.004	0.045

Random effect term	Variance	Standard deviation
Year (intercept)	9.215e-17	9.600e-09
ID/Pair ID (intercept)	1.178e-09	3.433e-05
Pair ID (intercept)	2.806e-01	5.297e-01

Model 4.5

AIC = -421.9, 208 observations

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	1.889	0.564	2.107	0.035
Initial pair correlation	-0.074	0.633	-0.116	0.907
Sex (male)	-1.809	0.596	-3.037	0.002
Immigrant	-1.647	0.590	-2.791	0.005
Initial pair correlation*sex (male)	2.018	0.671	3.008	0.003
Initial pair correlation*immigrant	1.921	0.666	2.882	0.004
Sex (male)*immigrant	3.269	0.766	4.269	<0.0001
Initial pair correlation*sex (male)*immigrant	-3.665	0.870	-4.212	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	3.732e-12	1.932e-06
ID/Pair ID (intercept)	2.345e-09	4.843e-05
Pair ID (intercept)	1.901e-01	4.360e-01
Location (intercept)	3.992e-02	1.998e-01

Group 5

Model 5.1

AIC = -3073, 1242 observations

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.552	0.150	-3.689	0.0002
SRI	1.368	0.135	10.141	<0.0001
Sex (male)	0.029	0.031	0.943	0.346
Weeks since meeting	0.012	0.005	2.216	0.027
Weekly pair correlation	1.810	0.148	12.217	<0.0001

Random effect term	Variance	Standard deviation
Year (intercept)	7.362e-10	2.713e-05
ID/Pair ID (intercept)	5.430e-04	2.330e-02
Pair ID (intercept)	6.465e-02	2.543e-01
Weekend location (intercept)	8.959e-02	2.993e-01

Model 5.2

AIC = -3375, 1239 observations

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.668	0.149	-4.491	<0.0001
SRI	0.888	0.134	6.603	<0.0001
Sex (male)	0.114	0.035	3.257	0.001
Weeks since meeting	0.017	0.006	2.841	0.005
Weekly pair correlation	2.160	0.152	14.197	<0.0001
Partner's age (juvenile)	0.151	0.066	2.283	0.022
Immigrant	0.072	0.046	1.577	0.115

Random effect term	Variance	Standard deviation
Year (intercept)	2.129e-03	0.046
ID/Pair ID (intercept)	1.005e-09	3.17e-05
Pair ID (intercept)	8.354e-02	0.289
Weekend location (intercept)	6.440e-02	0.254

Model 5.3

AIC = -4973, 1929 observations

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.234	0.138	-1.691	0.091
SRI	0.812	0.110	7.350	<0.0001
Sex (male)	0.019	0.026	0.740	0.459
Weeks since meeting	0.016	0.004	3.633	<0.001
Weekly pair correlation	1.705	0.134	12.716	<0.0001
Partner's age (juvenile)	0.108	0.059	1.815	0.070
Immigrant	0.026	0.036	0.729	0.466

Random effect term	Variance	Standard deviation
Year (intercept)	2.333e-03	0.048
ID/Pair ID (intercept)	6.864e-10	2.62e-05
Pair ID (intercept)	7.980e-02	0.282
Weekend location (intercept)	5.989e-02	0.245

Model 5.4

AIC = -3072, observations = 1242

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.527	0.153	-3.450	0.001
SRI	1.368	0.135	10.142	<0.0001
Sex (male)	-0.019	0.067	-0.280	0.780
Weeks since meeting	0.008	0.007	1.135	0.256
Weekly pair correlation	1.810	0.148	12.210	<0.0001
Sex (male)*weeks since meeting	0.008	0.009	0.800	0.423

Random effect term	Variance	Standard deviation
Year (intercept)	8.572e-10	2.928e-05
ID/Pair ID (intercept)	5.092e-04	2.257e-02
Pair ID (intercept)	6.453e-02	2.540e-01
Weekend location (intercept)	8.960e-02	2.993e-01

Model 5.5

AIC = -3379.3, observations = 1239

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.747	0.152	-4.932	<0.0001
SRI	0.905	0.135	6.725	<0.0001
Sex (male)	0.251	0.065	3.857	<0.0001
Weeks since meeting	0.029	0.008	3.768	<0.001
Weekly pair correlation	2.165	0.152	14.265	<0.0001
Partner's age (juvenile)	0.153	0.066	2.305	0.021
Immigrant	0.074	0.046	1.633	0.102
Sex (male)*weeks since meeting	-0.024	0.010	-2.496	0.013

Random effect term	Variance	Standard deviation
Year (intercept)	1.963e-03	4.430e-02
ID/Pair ID (intercept)	6.253e-10	2.501e-05
Pair ID (intercept)	8.345e-02	2.889e-01
Weekend location (intercept)	6.678e-02	2.584e-01

Model 5.6

AIC = -4972, observations = 1929

Term	Estimate	Standard error	*Z*-value	*P*-value
Intercept	-0.254	0.140	-1.809	0.070
SRI	0.811	0.110	7.341	<0.0001
Sex (male)	0.061	0.056	1.085	0.278
Weeks since meeting	0.019	0.006	3.295	0.001
Weekly pair correlation	1.706	0.134	12.727	<0.0001
Partner's age (juvenile)	0.109	0.059	1.836	0.066
Immigrant	0.025	0.036	0.683	0.495
Sex (male)*weeks since meeting	-0.006	0.008	-0.838	0.402

Random effect term	Variance	Standard deviation
Year (intercept)	2.375e-03	4.873e-02
ID/Pair ID (intercept)	6.490e-10	2.548e-05
Pair ID (intercept)	7.960e-02	2.821e-01
Weekend location (intercept)	6.023e-02	2.454e-01

455 Supplementary Results III

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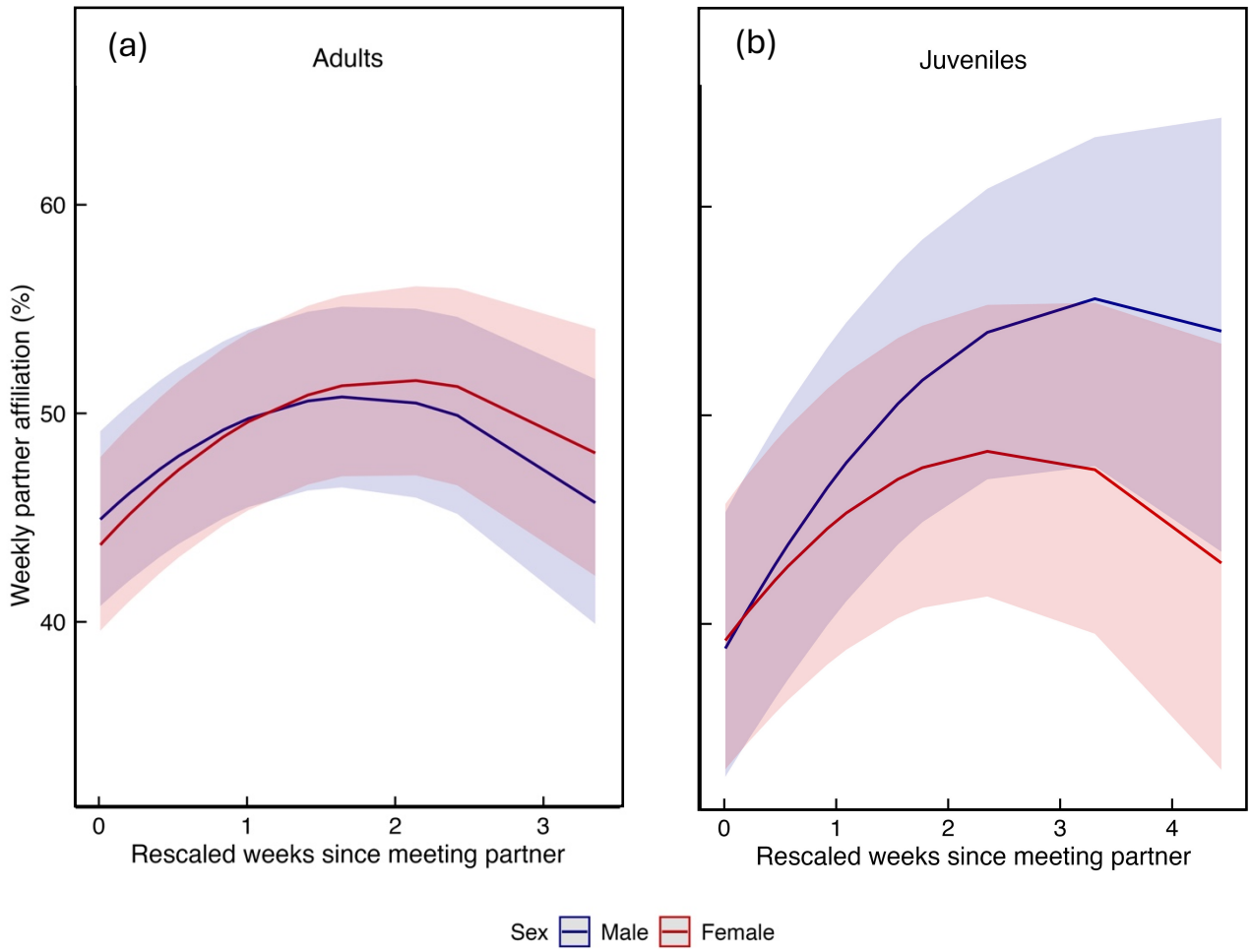

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Figure S2: newly-pairing birds may increase partner affiliation non-linearly and male juveniles do so more than female juveniles as time progresses. Lines show predicted values from zero-inflated binomial GLMMs; ribbons show 95% confidence intervals around model predictions. (a): Model 2.9, newly-pairing adults, 3027 observations and (b): Model 2.8, juveniles, 2116 observations: (successes, failures) ~ (rescaled weeks since meeting)^2 + rescaled weeks since meeting*sex + partner's age + (1|year) + (1|pair ID/individual ID) + (1|weekend location).

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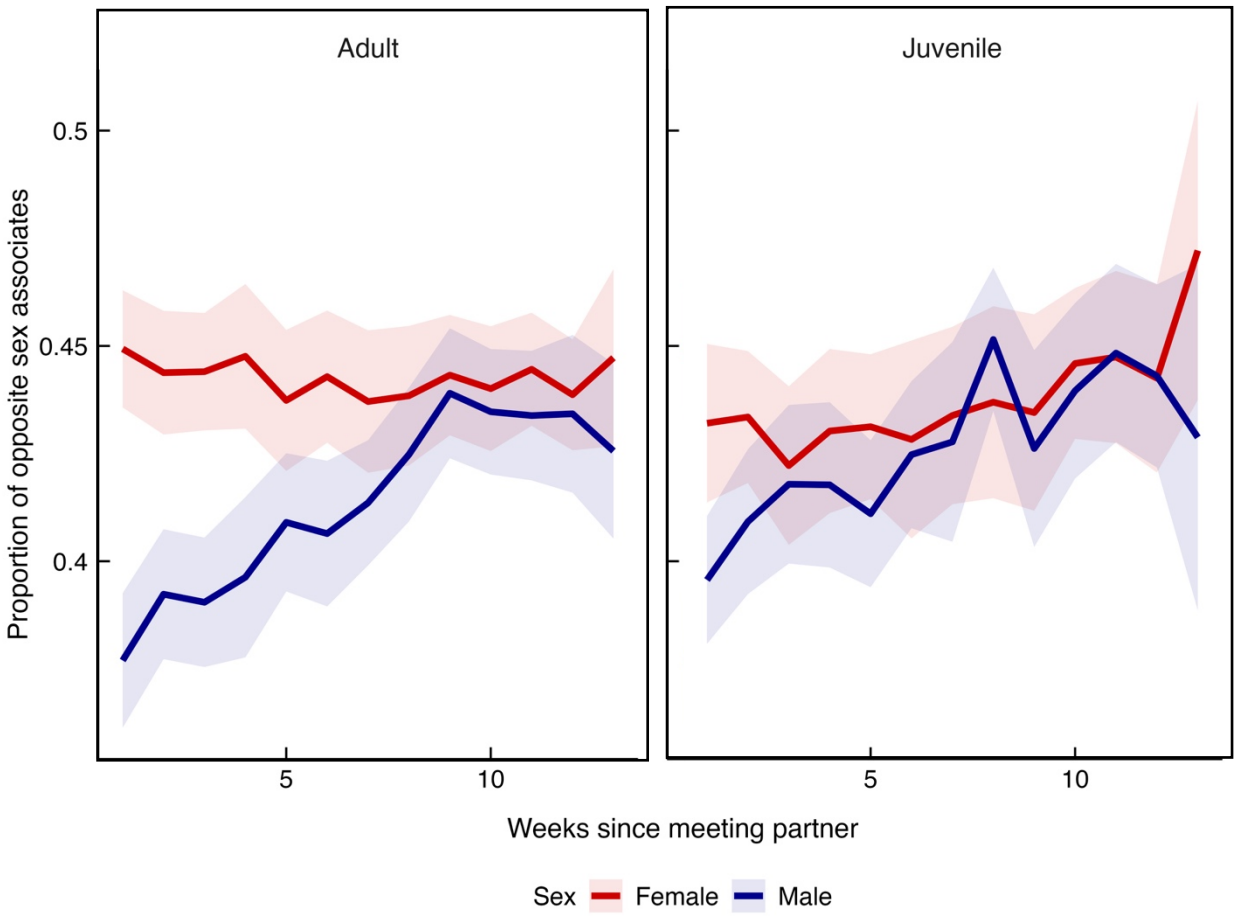


Figure S3: opposite-sex proportion of social environment for newly-pairing birds through time since meeting partner. Lines show mean average proportion of associations which are with opposite sex, for each weekend since meeting their partner. Ribbons show 95% confidence intervals for each weekend. Note that some birds are unsexed in winter social associations; these are excluded. NB: this figure shows summary of raw data, not a model.

Supplementary Results IV

Classifying spatial activity as an individual's preferred feeder site captured the majority of feeder visits.

Whole season: (1 | Location)

Proportion of an individual's total feeder visits to its preferred feeder:

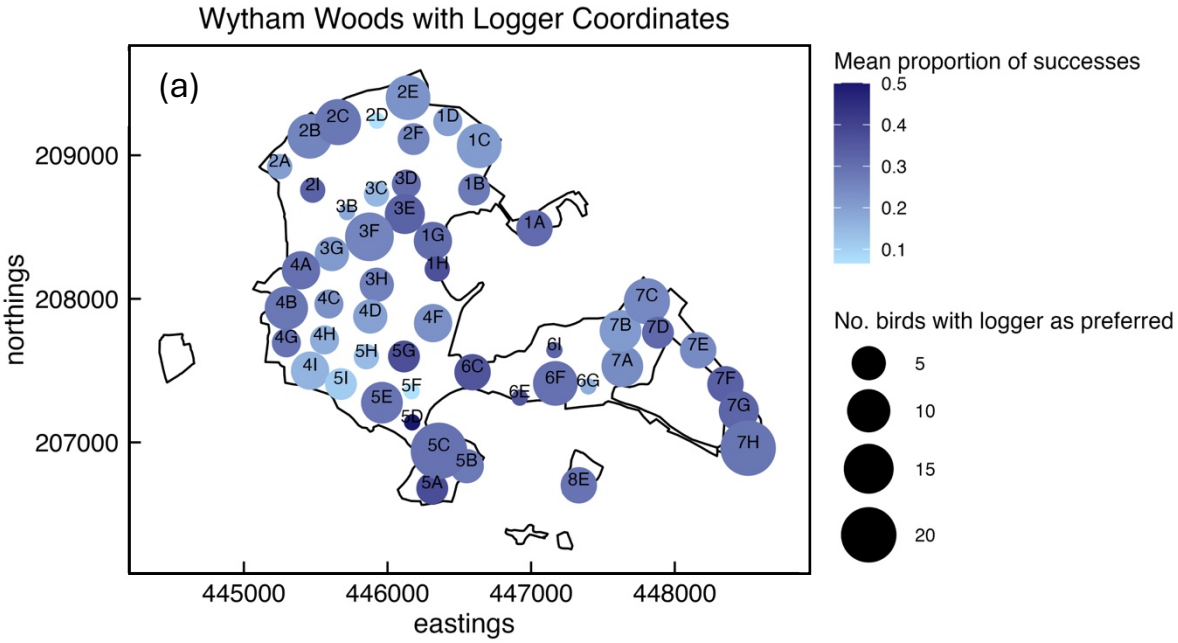
- For total population: 0.808
- For population that fulfils model criteria: 0.789

Temporal: (1 | Weekend location)

Proportion of an individual's total feeder visits in a weekend to its preferred feeder for that weekend:

- For total population: 0.904
- For population that fulfils model criteria: 0.901

Figure S4 a & b display spatial variation in social association metrics.



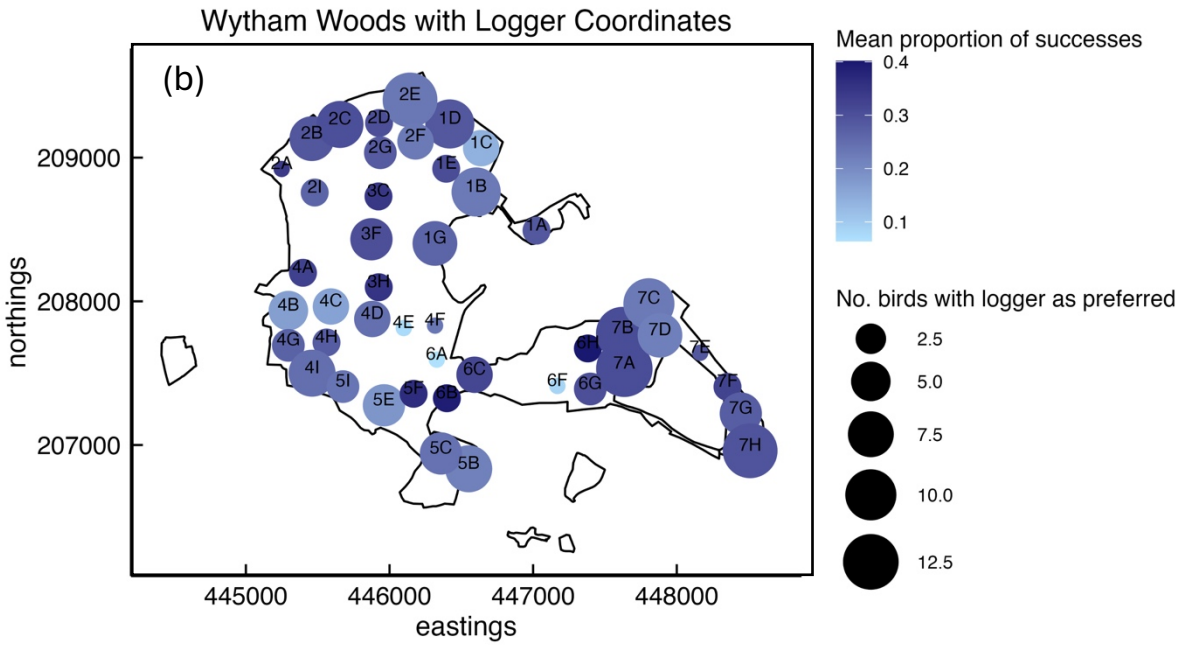


Figure S4: (a): Spatial variation of partner association; Winter 2011-2012. Birds classified according to their single most preferred feeder (most visited across whole non-breeding season). Size of point associated with each feeder site shows how many birds had that feeder as their preferred site. Colour of point denotes the mean average proportion of flocking events with their partner across the whole season, for birds that have that feeder as their preferred site. (b): Spatial variation of partner association; Winter 2013-2014. Purpose of additional figure is to demonstrate year-by-year variation in spatial activity. Birds classified according to their single most preferred feeder (most visited across whole non-breeding season). Size of point associated with each feeder site shows how many birds had that feeder as their preferred site. Colour of point denotes the mean average proportion of flocking events with their partner across the whole season, for birds that have that feeder as their preferred site.

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