

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

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Social relationships of different types come with varied costs and benefits. Individuals in natural populations may experience selective pressure to optimize trade-offs between different social relationships. Specifically, individuals associate with conspecifics to varying extents; if social time is limited, individuals must trade off how much they invest in one social relationship versus another. The factors affecting how individuals manage social trade-off dynamics, however, remain largely untested in wild populations. We used a wild population of great tits, *Parus major*, as a model system to examine social trade-offs within social networks: specifically, how an individual's sex affected the trade-off between associating with a future breeding partner and associating with other conspecifics. We found that during the nonbreeding season (winter), both males and females increasingly associated with their future breeding partner but that there were sex-based differences in trade-off patterns. In existing breeding pairs, we found that males associated more with their partner than females did as a proportion of their total social associations. In new pairs, juvenile males increased their proportional association with their partner more than juvenile females did as winter progressed. Additionally, we found that juvenile males experienced less change in social group membership while accommodating pair bonding. These findings demonstrate how demographic characteristics shape fine-scale social behaviour, contributing to the biological processes that emerge from social structure.

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Diverse social relationships exist across animal societies. Previous research has reported a variety of benefits of sociality, including increased reproductive success associated with nonbreeding social relationships in greater anis, *Crotophaga major*, and chimpanzees, *Pan troglodytes* (Feldblum et al., 2021; Riehl & Strong, 2018). Conversely, sociality can be associated with costs, including competition (Ekanayake-Weber et al., 2024). Strong social relationships reduce life span and reproductive success in yellow-bellied marmots, *Marmota flaviventris*, and grooming adult conspecifics incurs aggression costs for juvenile Japanese macaques, *Macaca fuscata*, despite the 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 the costs and benefits of social relationships.

Social relationship trade-offs implicitly include opportunity costs if maintaining one relationship limits investment in another

because of 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 that jackdaws reshape social relationships to gain short-term benefits while maintaining strong bonds of longer-term value, highlighting how costs and benefits can occur over different timescales (Kings et al., 2023). How social trade-offs occur and why individuals manage them differently, however, remain largely untested in wild systems, despite such trade-offs contributing to social structure and emergent biological processes (Cantor et al., 2021).

One social relationship to which trade-offs can apply is the mating pair bond: a strong, selective association between a male and female that breed together, although the term is defined in diverse ways (Bales et al., 2021). In socially monogamous animals,

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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 against associating with other conspecifics. Pair bonds are expected to return benefits at a future time (during breeding), which imposes a strong temporal component to the social trade-off if pair bonding occurs well ahead of breeding (Culina et al., 2020; Teitelbaum et al., 2017). Additionally, there may be immediate pair bonding costs, including stress or energetic demands, that are traded off against future benefits (e.g. reproductive success: Campbell et al., 2009; Griffith et al., 2011).

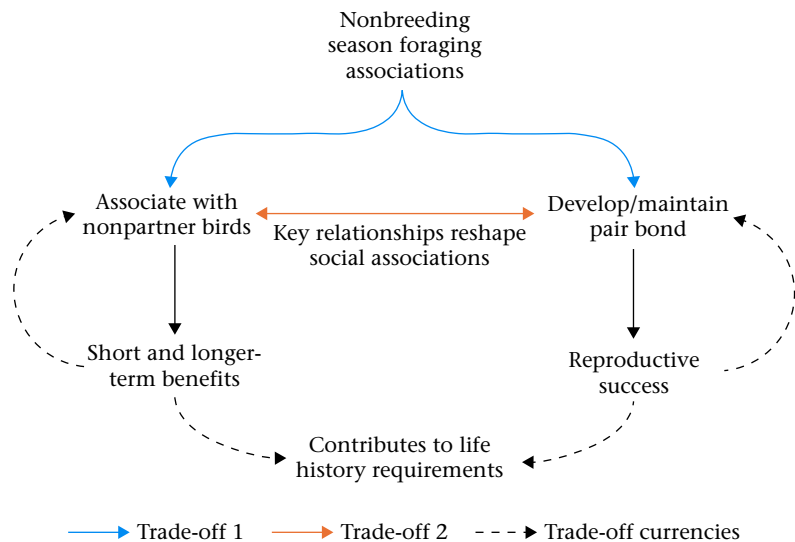
Opportunity costs arise if investing in a pair bond limits investment in other social relationships, as characterized by how much an individual associates with its partner relative to other conspecifics. Furthermore, pair bonding can reshape the identity of nonpair associates. For example, wild great tits, *Parus major*, may reshape their social connections to associate with their partner, despite experiencing a potentially suboptimal social environment (Firth et al., 2015). Opportunity costs arise because associating with others can provide benefits that are not available through the pair bond. In a variety of mammals and birds, 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 (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 sex-determined social patterns can be predicted (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*, males became less integrated than females in

grooming social networks during development, 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 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. We examined this in a wild model great tit population. During winter (nonbreeding 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 within pairs during winter, with a social relationship classified as a pair bond if the two birds subsequently breed together in the following spring (Abraham et al., 2025; Culina et al., 2020).

In this study, our aim was to assess how an individual's phenotype influenced 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 generalized linear mixed models (GLMMs). We considered two potential social trade-off scenarios faced by pair bonding great tits (Fig. 1). First, we predicted that during winter, an individual's sex would affect how much it associated with its future partner compared to other conspecifics. Additionally, social trade-offs may 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 would affect



**Figure 1.** Summary of the 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: the extent to which existing social relationships are changed or are lost during pair bonding. Males and females may experience different costs and benefits associated with different aspects of these trade-offs.

the extent to which it reshaped its social associations while associating with its partner during winter.

## METHODS

### Study System

This research used the long-term study population of great tits at Wytham Woods (385 ha), Oxford, U.K. (51°46'N, 1°20'W). As in 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 approximately 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 exclusively in the woodland's 1020 nestboxes, facilitating long-term monitoring of breeding activity. 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 that approximately 90% of this population carries an RFID microchip, allowing extensive monitoring of social behaviour (Aplin et al., 2013).

### Social Association Data Collection

For three winters (December–March 2011–2012, 2012–2013 and 2013–2014), feeding stations were positioned throughout Wytham Woods at 65 fixed locations at approximately 250 m intervals. For 13 consecutive weekends each winter, feeders were available to birds, and antennae scanned for RFID tags 16 times/s from before dawn to after 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 conducted social network analysis in R version 4.2.2 using RStudio (Posit team, 2023) and the *igraph* (Csárdi et al., 2024) and *sna* (Butts, 2024) packages. To generate weighted social networks from flock memberships, we applied the 'gambit of the group', assuming that each bird in a flocking event was socially associated with every other bird in that flock at that specific time (Franks et al., 2010). Flock membership is strongly preferential in this population, reducing the impact of this assumption (Psorakis et al., 2012).

We quantified the association strength between two individuals (a dyad) using the simple ratio index (SRI; Cairns & Schwager, 1987), which ranges from zero (the dyad never co-occurred) to one (the 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 dyadic SRI values as measures of association strength between individuals (nodes). To capture temporal processes, we generated networks for each weekend of data collection following the discrete snapshot approach (Pinter-Wollman et al., 2014). Additionally, we generated networks for each full winter. We identified breeding pairs using data from the subsequent breeding season. We did not account for relatedness because 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

To measure relative partner affiliation (i.e. affiliation with a partner relative to affiliation with all other conspecifics), we quantified the number of flocking events in which each individual was observed with and without its partner. We modelled relative partner affiliation as binomial 'successes' (flocking events that included the partner) and 'failures' (flocking events that did not include the partner). We calculated this metric for each winter from the point at which the pair was first recorded together that season, thereby limiting analysis to the pair bonding period. We also calculated the metric for each weekend within the pair bonding period.

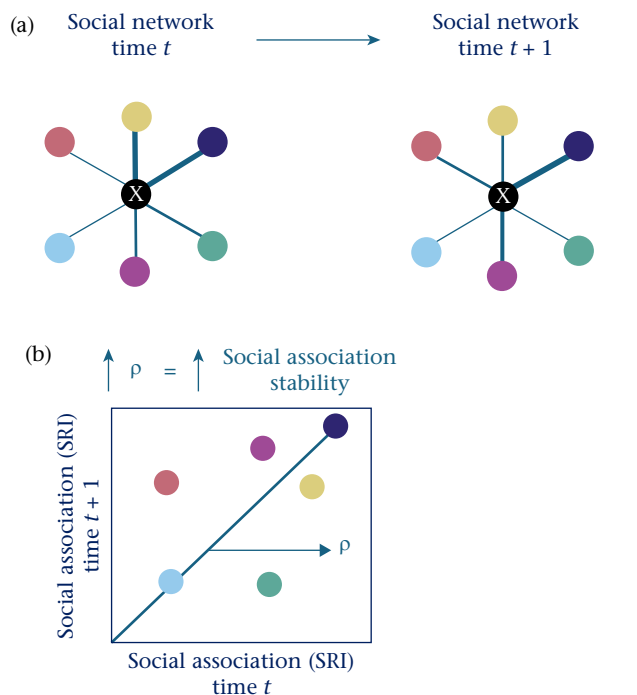
Additionally, the extent to which a great tit associates with its future partner relative to other opposite-sex individuals may reflect partner choice trade-offs (Culina et al., 2015). Therefore, we calculated, for each individual, the total number of observations with its future partner and the total number of observations with all opposite-sex conspecifics. This metric captured the probability that, when a bird was recorded with an opposite-sex individual, that individual was its future partner (sex-based relative partner affiliation). Here, 'successes' were the sum of observations in which the focal bird was observed with its partner, and 'failures' were the sum of observations in which the focal bird was observed with nonpartner opposite-sex individuals (i.e. summed across all opposite-sex individuals observed in the same flock as the focal bird).

### Social Association Stability

We predicted that an individual's sex would affect the stability of its social associations, as pair bonding has the potential to reshape its social environment (Firth et al., 2015). We quantified weekly social association stability for each individual as the correlation ( $\rho$ ) between its vector of SRI values with all other individuals from one weekend to the next, producing a single value for each individual for each weekend (Ilany et al., 2021; Fig. 2a and b). We also calculated seasonal social association stability using the same approach but measured between the weekends when the individual was first and last observed with its partner. In addition, we quantified initial pair correlation, defined as the correlation between the focal individual's social associations and those of its partner when first recorded together, excluding the focal dyad from the calculation. This metric captured the initial similarity in their social environments as a potential baseline for change.

### 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 the analysis on birds for which trade-offs could be quantified, we restricted analyses to individuals that:



**Figure 2.** Conceptual example. (a) Individual  $x$  changes its associations between time  $t$  and  $t+1$ . Colours denote different individuals, represented by nodes. Edge weights (line thickness) represent social association measured using the simple ratio index (SRI). (b) The resulting social association stability for individual  $x$  between time  $t$  and  $t+1$ . Each coordinate represents the association between individual  $x$  and individual  $y$  at time  $t$  ( $x$ -axis) and at time  $t+1$  ( $y$ -axis).

(1) had been confidently identified as either male or female ( $N = 1005$  in 2012;  $N = 831$  in 2013;  $N = 804$  in 2014); (2) were observed breeding in Wytham Woods in the following breeding season with an identified partner ( $N = 379$  in 2012;  $N = 247$  in 2013;  $N = 328$  in 2014); and (3) were recorded in more than one weekend per

winter and whose partner was also recorded in more than one weekend in the winter prior to breeding together ( $N = 311$  in 2012;  $N = 188$  in 2013;  $N = 219$  in 2014).

We classified breeding pairs as either existing pairs or new pairs, and, within the latter, by age (first year or adult) in relation to sex (Fig. 3). We expect behavioural differences between individuals forming and maintaining a pair bond, and age (including in relation to sex) is known to affect pair bond dynamics in some birds and mammals (Firth et al., 2018; Kelberman et al., 2024; Sánchez-Macouzet et al., 2014). The Supplementary Material contains social networks including only birds that fulfilled these model criteria (Supplementary Results I), demonstrating variation in the strength and number of social relationships and the emergence of pair bonds in networks (Figs. S1a, b, c).

## Statistical Analysis

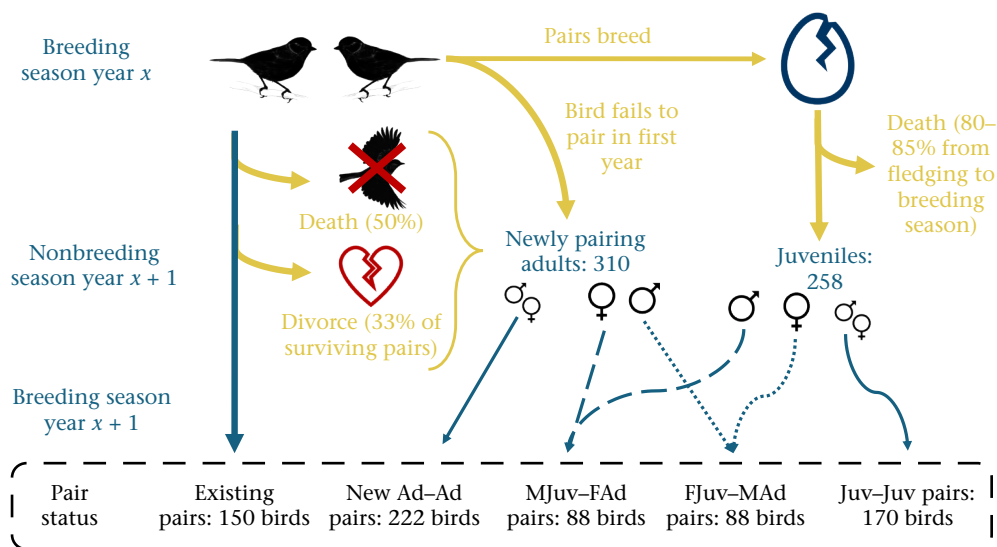
We used GLMMs, summarized in Table 1, to test the effect of sex on (1) association with a future breeding partner versus other conspecifics and (2) social association stability during pair bonding. See the Supplementary Material for full variable definitions (Supplementary Methods I) and further model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

## Prediction 1: Sex Affects Relative Partner Affiliation

### Group 1

We constructed GLMMs with a binomial response variable describing the number of times a bird flocked with (successes) and without (failures) its partner over the winter, from the point at which 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 the number of weekends a bird was recorded in that season.

Single-sex models included individual identity (ID) and year as random effects, and the individual's most frequently visited feeding station (location) to control for spatial habitat variation



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

**Table 1**  
Summary of model groups and their variables

| Group | Response                               | Subset                                       | Fixed effects included                                                                                                                                                             | Random effects                                                     |
|-------|----------------------------------------|----------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------|
| 1     | Seasonal relative partner affiliation  | Single sex models<br>Combined sex models     | Pairing status, weekend count<br>Sex, age, weekend count, immigration status                                                                                                       | Year, ID, location                                                 |
| 2     | Weekly relative partner affiliation    | Single sex models<br><br>Combined sex models | Weeks since meeting (plus rescaled for quadratic models), pairing status, weekend count<br>Weeks since meeting (plus rescaled for quadratic models), pairing status, weekend count | Year, ID, weekend, location<br>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                                |

Fixed effects include all variables that were used in final models for each group; not all models used all fixed effects. SRI = simple ratio index.

indirectly affecting social structure (Supplementary Material: 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 influence social network structure, including higher clustering coefficients (Beck et al., 2023). To analyse flocking event data, we used a binomial error distribution with a logit link function (MacKenzie et al., 2018). Where models were overdispersed (i.e. variance substantially exceeding that expected under the model) we refitted models using a beta-binomial error distribution (Harrison, 2015). To quantify the effect of sex, we fitted combined-sex models within each model set, 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). For newly forming pairs, 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 included random effects of location and year, as well as individual ID nested within pair ID to account for nonindependence within pairs.

#### Group 2

To examine how trade-offs vary over the winter season, we modelled the number of times a bird flocked with and without its partner in each weekend (weekly relative partner affiliation) as a function of time since pair formation that season. We excluded entries prior to the pair meeting and weekends in which a bird was not recorded. We included a zero-inflation term to account for entries in which a pair was not observed together (Supplementary Material: Supplementary Results III). We initially constructed single-sex models. In these models, pair status (Fig. 3) interacted with how long ago the pair met, and we specified the location random effect as the individual's most frequently visited feeder in that weekend (capturing 90.1% of visits; Supplementary Material: Supplementary Results IV). Differences in feeder use among individuals were accounted for by (1) the number of data points per individual, which scales with the number of weekends in which that individual was recorded and (2) including individual ID as a random effect, which models individual-level variation and reduces the influence of sparsely observed individuals.

To test whether birds nonlinearly increased their relative partner affiliation as winter progressed, we fitted models including a quadratic effect of the number of weeks since meeting (standardized to mean = 0 and SD = 1), to examine whether 'u' or 'n' shaped relationships existed (Salinas Ruíz et al., 2023).

We fitted combined-sex models restricted by pairing status, including both linear and quadratic versions. For newly forming pairs, we additionally split models by age. We constructed separate models for each pair type (Fig. 3).

#### Group 3

To examine partner choice aspects of nonbreeding season social trade-offs, we modelled the extent to which an individual associated with its partner versus other opposite-sex birds, using observations with the partner as successes and observations with opposite-sex conspecifics as failures (sex-based relative partner affiliation). This metric was calculated for each weekend. To address model nonconvergence, we excluded the weekend-level 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 individuals' social association stability as the response variable, defined as the correlation ( $\rho$ ) between an individual's vector of SRI values with all other individuals at time  $t$  and time  $t+1$ . This was measured (1) between the weekend when an individual was first observed with its partner and the weekend when it was last observed with its partner that winter (seasonal social association stability) and (2) between consecutive weekends (weekly social association stability). We transformed all correlations from  $[-1, 1]$  to  $[0, 1]$  using  $\frac{\rho+1}{2}$  and then adjusted values to lie within the open interval  $(0, 1)$  by subtracting  $\epsilon$  ( $1 \times 10^{-10}$ ) from all values; no values were  $\leq 0$ . This transformation allowed the use of GLMMs with a beta error distribution and logit link function for model groups 4 and 5. All subsequent analyses used the transformed values.

#### Group 4

When modelling seasonal social association stability, we allowed the effect of sex to depend on age and controlled for initial pair correlation, defined as the correlation between an individual's associations and those of its partner when they were first recorded flocking together. For newly forming pairs, we included a three-way interaction between sex, age and initial pair correlation, allowing the sex\*age interaction to vary with initial pair correlation. We fitted separate combined-sex models for each pair status.

#### Group 5

To link changes in social associations to pair bonding, we modelled an individual's weekly social association stability as a function of the pair's association strength (SRI) in weekend  $t+1$  and tested for an effect of sex. For existing pairs, we controlled for time since meeting that winter and weekend pair correlation, defined as the correlation between an individual's social associations and those of its partner in weekend  $t$ . Pair correlation could not be calculated for weekends in which one member of the pair

was absent in the previous weekend, so these entries were excluded. For newly forming pairs, we fitted separate models by age and additional models testing whether the effect of sex varied with time since pair formation.

#### Ethical Note

We conducted our study following the ASAB Ethical Committee/ABS Animal Care Committee guidelines (<https://doi.org/10.1016/j.anbehav.2005.10.001>). All work was approved by the ethics review committee Animal Welfare and Ethical Review Board at the Department of Zoology, University of Oxford (approval number: APA/1/5/ZOO/NASPA/SHELDON/TitBreedingEcology). Birds were caught in the wild using mist nests in the winter (on weekdays with suitable weather conditions from September to February) and nestboxes during spring (adults on day 12 after the eggs hatched onwards, and chicks on day 15) using spring traps that block the entrance when birds return to the nest after foraging, following longstanding procedures of the Wytham tit study. Mist nests and nestboxes were checked approximately every 10–15 min and birds were retrieved to ensure trapping time was minimized. All bird ringing and tagging was carried out under standard licensing permissions from the British Trust for Ornithology (BTO A5435). Captured birds were handled by trained ringers following techniques of the British Trust of Ornithology and released immediately back into the wild after the necessary measurements were taken. The PIT tags were approximately 0.13 g, which is smaller than the natural diurnal variations in great tits' weight ( $1.1 \pm 0.02$  g, [Macleod et al., 2005](#)). The added weight was found to have no significant adverse effects on survival or body condition ([Nicolaus et al., 2008](#)).

## RESULTS

Winter social networks contained 1079 individuals in 2011–2012, 720 in 2012–2013 and 773 in 2013–2014. These social networks were built from 242 041 flocking events across the 3 years, with a mean ( $\pm$  SE) flock membership of  $9.040 \pm 0.013$  individuals. Across years, 557 individuals were included in the models. Of these, birds spent  $10.8 \pm 0.117$  weekends in Wytham Woods each winter and encountered  $70.5 \pm 1.41$  individuals (network degree). Twenty-six individuals appeared in all 3 years and 100 appeared in 2 years. Model outputs can be found in the Supplementary Material (Supplementary Results II). Models were fitted as described in the Methods and values are reported throughout as logit transformed coefficient estimates  $\pm$  SE and model  $P$  values.

#### 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 its partner relative to other conspecifics) over the whole winter. This was true for both new pairs (Supplementary Material: Model 1.3; sex: estimate =  $-0.017 \pm 0.134$ ,  $P = 0.773$ ) and existing pairs (Supplementary Material: Model 1.4; sex: estimate =  $0.042 \pm 0.076$ ,  $P = 0.579$ ). Single-sex models predicted similar values for both pairing types in males and females (Supplementary Material: Model 1.1 and Model 1.2, Supplementary Results II).

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

Over time, birds increased affiliation with their future breeding partner ([Figs. 4–6](#)). For new pairs, the effect of sex depended on

age and time since meeting their partner (Supplementary Material: Model 2.5; weeks since meeting\*sex\*age: estimate =  $0.043 \pm 0.007$ ,  $P < 0.0001$ ). Additionally, we split newly pairing birds by age to determine whether the effect of sex on relative affiliation with their new partner through time differed between juveniles and adults.

*New pairs: the effect of sex changes over time for juveniles.* Male juveniles increased their relative partner affiliation (the proportion of flocking events shared with their partner relative to their total flocking events) significantly more than female juveniles during winter (Supplementary Material: Model 2.6; weeks since meeting\*sex: estimate =  $0.031 \pm 0.005$ ,  $P < 0.0001$ ; [Fig. 4b](#)). This was despite male juveniles initially flocking proportionally less with their partner (sex: estimate =  $-0.190 \pm 0.052$ ,  $P < 0.001$ ).

By contrast, newly pairing adult females initially flocked proportionally less with their partner (Supplementary Material: Model 2.7; sex: estimate =  $0.127 \pm 0.052$ ,  $P = 0.014$ ) and also increased their relative partner affiliation significantly more than adult males during winter (weeks since meeting\*sex: estimate =  $-0.012 \pm 0.004$ ,  $P = 0.002$ ; [Fig. 4a](#)). Therefore, in newly pairing adults, the effect of sex was reversed relative to that observed in juveniles, although the magnitude of the effect was smaller.

Additionally, we fitted quadratic models to test whether great tits increase their relative partner affiliation nonlinearly. A quadratic effect was significant for juveniles, and male juveniles again increased their relative partner affiliation significantly more per week than female juveniles (Supplementary Material: Model 2.8; (rescaled weeks since meeting)<sup>2</sup>: estimate =  $-0.059 \pm 0.009$ ,  $P < 0.0001$ ; rescaled weeks since meeting\*sex: estimate =  $0.105 \pm 0.018$ ,  $P < 0.0001$ ; [Fig. S2](#)). Therefore, juvenile males increased their relative partner affiliation (potentially nonlinearly) week-on-week more than juvenile females.

*Existing pairs: males associated proportionally more with their partner.* In existing pairs, males consistently associated relatively more with their partner (relative partner affiliation) than females did (Supplementary Material: Model 2.14; sex: estimate =  $0.089 \pm 0.047$ ,  $P = 0.057$ ; [Fig. 5](#)), but there was no support for a quadratic effect (Supplementary Material: Model 2.15; (rescaled weeks since meeting)<sup>2</sup>: estimate =  $-0.007 \pm 0.018$ ,  $P = 0.705$ ).

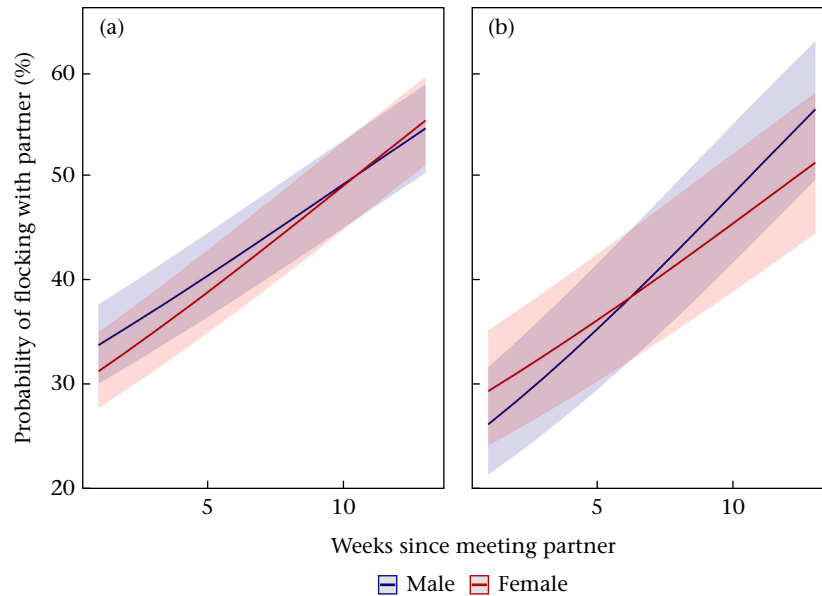
##### Group 3: sex-based relative partner affiliation

*New pairs: age, sex and time interacted to shape sex-based relative partner affiliation.* For new pairs, the proportion of opposite-sex associations with the partner was significantly related to the weeks since meeting\*sex\*age interaction (Supplementary Material: Model 3.2; estimate =  $0.043 \pm 0.012$ ,  $P < 0.001$ ; [Fig. 6](#)). That is to say, the effect of time on sex-based relative partner affiliation depended on both sex and age. The effect of sex was pronounced in newly pairing adults, with a steeper increase in sex-based relative partner affiliation for females than males (weeks since met\*sex (male): estimate =  $-0.034 \pm 0.003$ ,  $P < 0.0001$ ; [Fig. 6a](#)).

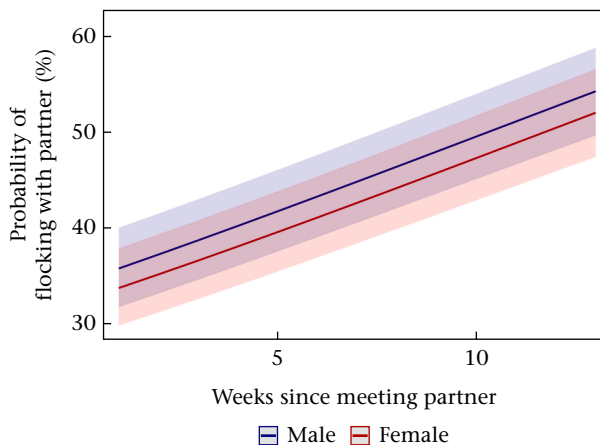
#### Prediction 2: Sex Affects Social Association Stability During Pair Bonding

##### Group 4: seasonal social association stability

*The effect of sex depended on age.* The effect of sex on a great tit's seasonal social association stability, the correlation ( $\rho$ ) of its association (SRI) with each other individual from first to last recorded flocking with its partner in a winter, depended on age (Supplementary Material: Model 4.1; sex\*age: estimate =  $0.188 \pm 0.080$ ,  $P = 0.018$ ). Within juvenile–juvenile pairs, males had higher correlations (Supplementary Material: Model 4.4; sex: estimate =  $0.173 \pm 0.086$ ,  $P = 0.045$ ). To assess whether the effects of sex and age on seasonal social association stability



**Figure 4.** Probability of (a) newly pairing adults and (b) juveniles flocking with their partner relative to the time since meeting their partner. Lines show predicted values from zero-inflated binomial generalized linear mixed models: model 2.7 for (a) and model 2.6 for (b). Ribbons show 95% confidence intervals around the model predictions. Model details are provided in the Supplementary Material.



**Figure 5.** Probability of individuals in existing pairs flocking with their partner relative to the time since meeting their partner. Lines show predicted values from a zero-inflated beta-binomial generalized linear mixed model (model 2.14). Ribbons show 95% confidence intervals around the model predictions. Model details are provided in the Supplementary Material.

depended on how correlated a pair's associations were when they met (initial pair correlation), we tested a three-way interaction for new pairs (initial pair correlation\*sex\*age; Supplementary Material: Model 4.2) and a two-way interaction for existing pairs (initial pair correlation\*sex; Supplementary Material: Model 4.3). This interaction was not significant for either group (existing: estimate =  $0.654 \pm 0.538$ ,  $P = 0.22$ ; new: estimate =  $-1.05 \pm 0.567$ ,  $P = 0.064$ ; Fig. 7).

#### Group 5: weekly social association stability

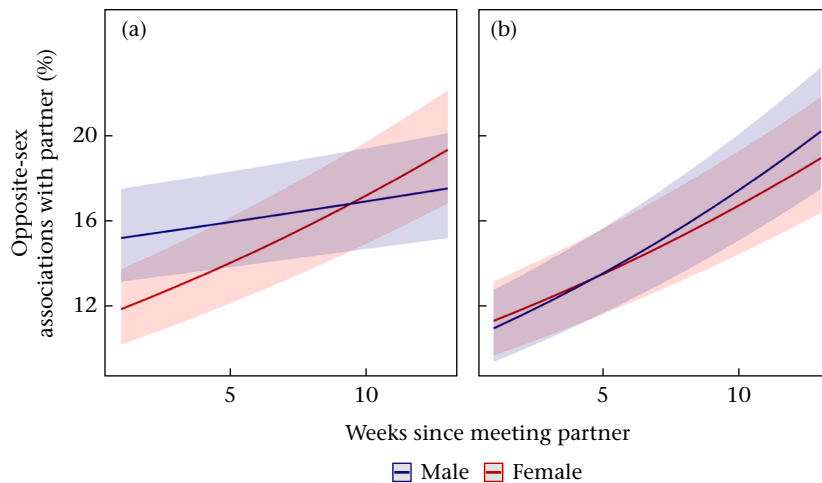
Males had higher weekly social association stability for a given level of pair association. Seasonal social consistencies may, however, reflect broader patterns. Individuals with higher initial correlations with their partner's associations (initial pair correlation) also had higher seasonal social association stability, suggesting that pairs may form from relatively stable flocks. Therefore, we

modelled social association stability between weekends (weekend  $t$  and  $t+1$ ) as a function of the pair's association (SRI) in weekend  $t+1$  and tested for sex differences.

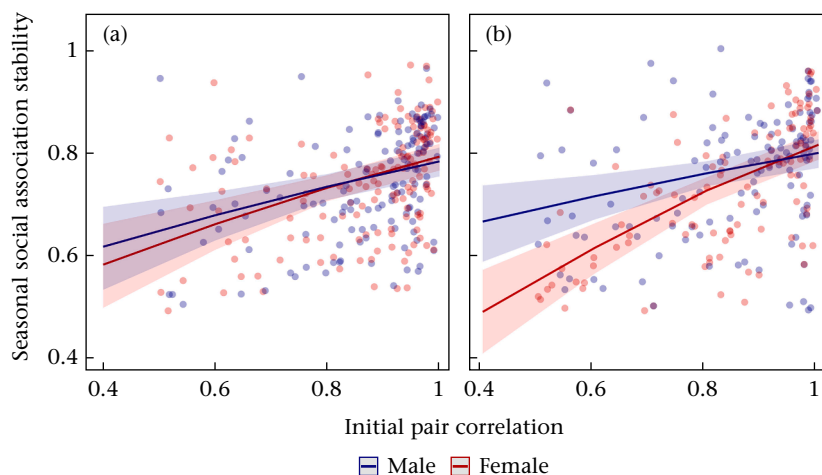
Being more associated with its partner was related to an individual having a higher weekly social association stability (Fig. 8). There was no significant effect of a bird's sex for either existing pairs (Supplementary Material: Model 5.1; sex: estimate =  $0.029 \pm 0.030$ ,  $P = 0.345$ ) or newly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

## DISCUSSION

We used a large wild bird data set and social network analyses to provide new insights into how sex affects social trade-offs in a socially monogamous passerine. During the nonbreeding season (winter), great tits associating with conspecifics at foraging sites face a social trade-off: developing pair bonds of long-term value (pair bonds with future breeding partners) at the potential expense of losing the short-term benefit of other social relationships (Fig. 1: trade-off 1). We found sex-specific patterns in social associations. Juvenile males increased the proportion of their associations that were with their partner (relative to other conspecifics) more than juvenile females did as time progressed (Fig. 4b); in existing pairs, males associated proportionally more with their partner than females did over time (Fig. 5). Among newly pairing adults, females increased the proportion of their opposite-sex associations that were with their partner more than males did (Fig. 6a). Our results also suggest that sex affects the extent to which individuals change their social associations during pair bonding (Fig. 1: trade-off 2). We show that male juveniles had higher social association stability than female juveniles, across the whole winter and from weekend to weekend as a function of pair association strength (Fig. 8b). We discuss these results in the



**Figure 6.** Percentage of opposite-sex interactions at weekends that were with an individual's partner relative to the time since first meeting that partner for (a) newly pairing adults and (b) juveniles. Lines show predicted values from a zero-inflated beta-binomial generalized linear mixed model (model 3.2). Ribbons show 95% confidence intervals around the model predictions. Model details are provided in the Supplementary Material.



**Figure 7.** Seasonal social association stability relative to the correlation between the focal individual's social associations and those of its partner when first recorded together (initial pair correlation) for (a) newly pairing adults and (b) juveniles. Lines show predicted values of seasonal social association stability for each group across values of initial pair correlation from a beta generalized linear mixed model (model 4.2). Ribbons show 95% confidence intervals for the predicted values. Points represent the raw data. Model details are provided in the Supplementary Material.

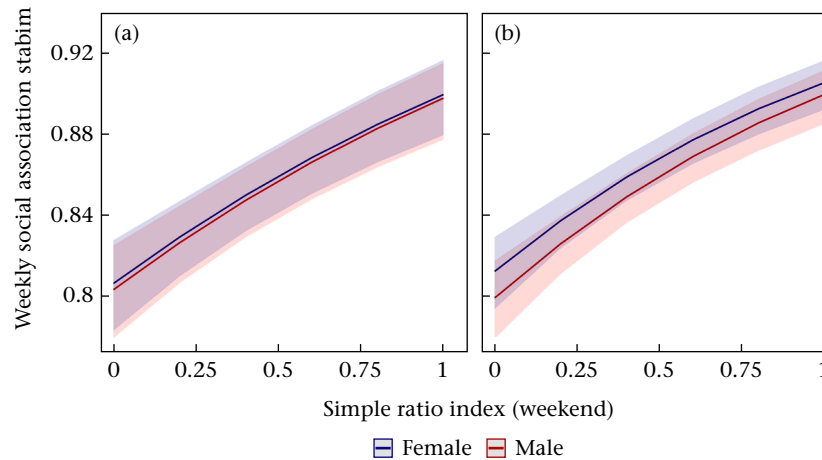
context of pair bonding, the interplay between social and spatial behaviours and how phenotypes can shape fine-scale social behaviour, thereby influencing social structure.

In socially monogamous animals, pair bonding is often a necessary precursor to reproduction and pair behaviours (e.g. biparental care: Roth et al., 2021). Here, we showed that great tits increased affiliation with their partner as winter progressed and an individual's sex affected the extent to which it associated with its future partner rather than other conspecifics. Sex-based differences in pair bonding in birds and mammals have been reported previously, including differences in partner preference development and the frequency of affiliative behaviours (Brusman et al., 2022; Dolotovskaya et al., 2020; Kubitza et al., 2015). The sex-based differences that occurred in our study population may be explained by the costs and benefits associated with social trade-offs.

Animals can have valuable social relationships with individuals other than their partner. For example, stable female–female social bonds carry reproductive benefits in bottlenose dolphins, *Tursiops* sp., greater anis, *Crotophaga major*, and yellow baboons, *Papio cynocephalus* (Frère et al., 2010; Riehl & Strong, 2018; Silk et al.,

2003). In existing great tit pairs, we showed that males consistently associated with their partner in a greater proportion of flocking events than females (Fig. 5). Previous research in this system has shown that, for existing pairs, familiarity with nesting neighbours can improve reproductive success, but this effect acts through females (via clutch size and lay date) rather than males (Gokcekus et al., 2023). Therefore, females may benefit more than males from associating proportionally more with other long-term associates during winter, given that winter social associations carry over to nest proximity (Firth & Sheldon, 2016).

We also found that among newly pairing adults, females increased the extent to which they associated with their partner compared to other opposite-sex birds (sex-based relative partner affiliation) more than males did (Fig. 6a). Underlying this pattern, we found that throughout winter, approximately 44% of newly pairing adult females' associations were with opposite-sex individuals. By contrast, newly pairing adult males initially had a lower percentage of observations with opposite-sex individuals (37%), but this percentage increased over time (Supplementary Material: Supplementary Results III; Fig. S3). This increase in



**Figure 8.** Weekly social association stability relative to the simple ratio index (SRI) for (a) newly pairing adults and (b) juveniles. Lines show predicted values from beta (logit link) generalized linear mixed models: model 5.2 for (a) and model 5.3 for (b). Ribbons show 95% confidence intervals around the model predictions. Model details are provided in the Supplementary Material.

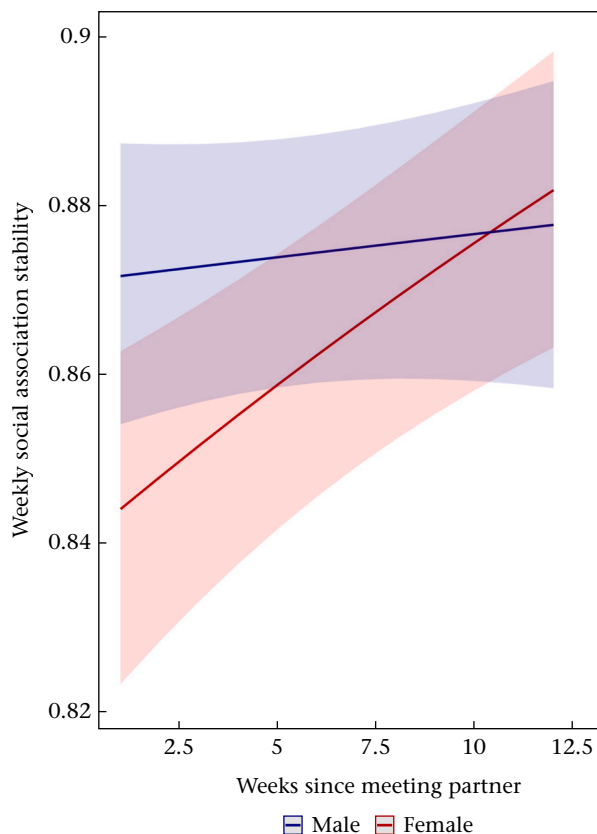
associations with females may contribute to the less pronounced increase in sex-based relative partner affiliation observed in males. In socially monogamous birds, having a lower proportion of female associates may lead to suboptimal partnerships, perhaps because of reduced mate sampling or increased mate competition, and may reduce opportunities for extrapair copulations (Beck et al., 2020; Culina et al., 2015; Kempenaers et al., 1992). Therefore, 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 these optima are incompatible. However, interpretation of conflict is limited because our analyses focused only on pairs which went on to breed; cases where social optima become too incompatible for a pair to sustain until breeding, if they existed, were not captured. Understanding the drivers of phenotype-level differences in pair bonding trade-offs is also restricted by not knowing when pairs became fixed prior to breeding. Apparent quadratic effects (Fig. S2) suggest that increased relative partner affiliation occurred up to a point as time progressed. 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 roles 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). Changes in social associations result from interactions between spatial and social processes. Research from other systems shows that changes in resource availability shape how individuals adjust 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, thereby altering an individual's social environment (Firth et al., 2015).

We found that greater pair association within a weekend was generally related to greater social association stability preceding it, implying that pairs co-occur more when embedded in flocks with lower social turnover. Our results show that juvenile males, however, had higher social association stability than juvenile females for a given level of pair association (Fig. 8b) and had higher social association stability across the winter when pairs initially had less similar associates (lower initial pair correlation; Fig. 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 farther than males (Greenwood, 1980). This holds true for great tits, with juvenile females dispersing farther than juvenile males prewinter (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 nonpartner social associations during this period. Stable nonpartner social associations may also develop through juvenile great tits preferentially associating with spatially close conspecifics of similar age, as these individuals may hold the most relevant social information, and these stable associations can then carry over between seasons (Firth & Sheldon, 2016; Wild et al., 2024). However, this pattern of juvenile males having higher social association stability than juvenile females diminishes as winter continues (Fig. 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 optimize 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 in 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, the underlying mechanisms of social patterns are difficult to tease apart from observational data. For instance, individuals differ in their foraging tactics at feeders and



**Figure 9.** Weekly social association stability relative to the time since meeting their partner for newly paired juveniles. Lines show predicted values from a beta (logit link) generalized linear mixed model (model 5.6). Ribbons show 95% confidence intervals around the model predictions. Model details are provided in the Supplementary Material.

in 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' in model group 1), individual identity as a random effect (model groups 1–5) and the number of data points per individual (equalling the number of weekends that individual was recorded in model groups 2, 3 and 5; Table 1). Nevertheless, results from 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 and De Jong (1986) and Van De Pol and Wright (2009), this distinction is important for interpreting trade-offs. Our results therefore describe sex-specific patterns in social association dynamics that are consistent with trade-off hypotheses, rather than direct tests of individual-level allocation decisions.

Taking the results together, we showed that there are sex-based differences in how great tits manage social trade-offs during pair bonding. These social trade-offs influence nonbreeding season social networks, carrying forward into 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 demonstrated that an individual's sex affected how it traded off long-term benefits of pair bonding in winter with the costs of reduced short-term benefits of associating with other conspecifics in a model passerine population. We found that during winter pair bonding in pre-existing pairs, males associated more with their partner compared to other birds than females did. Our results also showed that among adults forming a new pair, females increased the extent to which they associated with their partner compared to other opposite-sex birds more than males did. In juveniles, males increased their affiliation with their partner more than females did, and males had 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 between 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.

### Author Contributions

**George H.T. Rabin:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Adelaide D. Abraham:** Writing – review & editing, Supervision, Conceptualization. **Taylor Bi:** Writing – review & editing. **Keith McMahon:** Writing – review & editing, Data curation. **Ben C. Sheldon:** Writing – review & editing, Resources, Funding acquisition. **Josh A. Firth:** Writing – review & editing, Supervision, Conceptualization.

### Data Availability

The data sets analysed in this study and associated code are available here: [https://figshare.com/projects/Sex-based\\_differences\\_in\\_social\\_trade-offs\\_in\\_a\\_wild\\_bird\\_society/248015](https://figshare.com/projects/Sex-based_differences_in_social_trade-offs_in_a_wild_bird_society/248015).

### Declaration of Interest

None.

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### Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2026.123681>.

The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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