Timing and social consequences of divorce in wild great tits: a phenomenological approach

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1 Abstract

Social behaviour is a key part of the life of many species. An example of an important social association is that between breeding partners – a key social connection in monogamously breeding species. The selection of a breeding partner begins well before reproduction for many species, and this process can have consequences for subsequent reproductive success. Thus, the non-breeding season can shape behaviour during the breeding season. However, it is currently unknown how outcomes in the breeding season can impact associate choice during the non-breeding season, as studying this has been limited due to requiring high volumes of individual social data across both contexts. This study used three years of wild great tit social data from Wytham Woods, Oxford, UK, to examine social associations between pairs classified with respect to prior and future

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relationship status. We found a distinct behavioural pattern in 'divorced' pairs, which was present from early in the winter, suggesting that the act of divorce occurs soon after the completion of the breeding season. Pairs forming for the first time behaved similarly to divorced pairs earlier in the season, but became similar to faithful pairs throughout the winter. On a finer spatiotemporal scale the behaviour of faithful and divorced birds diverged over the winter. These results provide the first evidence of when divorce occurs in paired great tits, while suggesting that different behaviours may drive behavioural divorce at different times.

2 Introduction

For many animals the social environment is a source of constant change, forcing individuals to make a variety of social decisions (Kurvers et al., 2014). Decisions about which and how many individuals to associate with may have wide-ranging fitness consequences for processes such as predation mortality (Alberts, 2018; Barocas et al., 2011; Montero et al., 2020), disease spread (Behringer et al., 2006; Evans et al., 2020; Stroeymeyt et al., 2018), and foraging activity (Lachlan et al., 1998; Machado et al., 2019). Research into these social processes has often defined sociality on the group level, for example by summarising an individual's associations across the population. However, the identity of those associations is another important aspect of social behaviour. For example, individuals may prioritise relationships with kin (Podgórski et al., 2014; Wilkinson et al., 2019), and long-term associations with specific individuals may have positive fitness impacts (Emery et al., 2007; Griffiths et al., 2004; Silk et al., 2009).

Mate choice is a particularly clear example of an important individual-level social choice, particularly in socially monogamous species. The potential fitness

consequences of mate choice have been widely discussed (Jennions and Petrie, 1997; Kokko et al., 2003), and many studies have shown that the decision to remate with a previous partner (pair fidelity) may have consequences for reproductive success (Black, 1996; Culina et al., 2015; Sánchez-Macouzet et al., 2014). However, this key process of selecting a mate is not only relevant during the breeding season. Indeed, social interaction with potential partners in a non-breeding period has been shown to influence mate choice (Cheetham et al., 2008; Senar et al., 2013; Yokoi et al., 2016) and familiarity with a mate in the non-breeding season may increase pair quality and reproductive success (Culina et al., 2020; Griggio and Hoi, 2011; Maldonado-Chaparro et al., 2021; Martin and Shepherdson, 2012; Montero et al., 2020). Further, how key breeding partner bonds persist after the breeding season, or if they dissolve during the non-breeding season, remains largely unknown in many monogamous species. These examples provide evidence that individual social associations are relevant across the breeding and non-breeding contexts, for example in great tits *Parus major*, who have higher fitness when in a pair that met earlier in the non-breeding season (Culina et al., 2020).

In species which live for over a year, breeding attempts will occur across multiple seasons. There are a number of studies showing that increased familiarity with a partner (i.e number of years having bred together) is associated with increased reproductive success (Culina et al., 2013, 2015; Gokcekus et al., 2023; Schieck and Hannon, 1998). At the same time, the chance of a pair divorcing often increases when their reproduction is less successful (Choudury, 1995; Linden, 1991). This suggests that individuals must weigh the benefits of remaining with a familiar partner against the costs of remaining with a potentially unsuitable one. There is limited research into how, in iterated breeding

attempts, individuals change their behaviour between years in order to manage these shifting relationships, particularly in social contexts outside of the breeding season. If the dyadic social behaviour of pairs which go on to be either faithful or divorced can be distinguished in the non-breeding season immediately after their first breeding attempt, that suggests that individuals adjust their social associations in response to information from the breeding season.

The social structure of great tits (*Parus major*) provides an opportunity to study this transition and interaction between breeding and non-breeding sociality. In the winter, great tits feed in loose fission-fusion flocks as they move around the woodland (Aplin et al., 2012). In the spring, they are territorial and socially monogamous, feeding and caring for a brood in a pair (Patrick et al., 2012). Further, there is much individual-level variation in pair bonding behaviour (Firth et al., 2018), and the timing of pairing appears to relate to breeding success (Culina et al., 2020). These findings suggest that there may be a fitness component to the transition between fission-fusion and monogamous sociality, and therefore that it may vary within the population, making them an interesting species in which to study this process.

In this research we combine two datasets from great tits (*Parus major*) in Wytham Wood, Oxford, UK. In the non-breeding season, social associations were inferred using visits of radio-frequency identification (RFID) tags to feeders. Paired birds were then observed during the breeding season, matching identities between the two seasons. We used this data to investigate the connection between spring and winter social behaviour. We focus on how pair outcomes in the spring relate to sociality between that pair in the winter, within their broader social context. This provides new insights into divorce and partner

choice in the wild, and a foundation for understanding how individual social associations transition across social structures and seasons.

3 Methods

3.1 Data preparation

The data for this analysis comes from a long-term study of great tits in Wytham Woods, Oxford, UK. Each spring, the tits breed almost exclusively in artificial nestboxes placed throughout the woods. These nestboxes are checked regularly (see Perrins, 1965) and breeding individuals identified using British Trust for Ornithology rings and PIT (passive integrated transponder) tags. Within the five years of breeding attempt data used in this analysis (2011-2015), both parents were successfully identified in 61.9% of nests with any eggs laid (1,330 of 2,148), and 85.4% of nests which produced fledglings (1,185 of 1,388).

During the winter season, 65 supplementary feeders were placed throughout the woods at approximately 250 m even grid spacing. For 13 weekends (Saturday and Sunday only) across three winter seasons (3 December 2011 to 26 February 2012; 1 December 2012 to 24 February 2013; 30 November 2013 to 23 February 2014), the feeders used RFID (radio frequency identification) antennae to identify bird PIT tags, recording each visit of tagged birds to the feeder. Feeders scanned for PIT tags every one-third of a second to obtain this data. Flocking events were identified from the feeder visit records using a Gaussian mixed model through the asnipe package (Farine, 2013), where clusters of visits to the feeder are identified as part of the same event. For a detailed description of this methodology, see Farine et al., 2015.

Pairs were defined by their relationship to three time periods. Chronologically, these were the previous breeding attempt, the focal winter, and the focal breeding attempt. Any observation of a pair breeding was a 'focal breeding'. The winter before that breeding was the focal winter, which was used for analysis. The status of the pair in the focal breeding was defined using the previous breeding. Pairs were only retained for analysis if both individuals in the pair had been observed at the feeders in the focal winter. The status of each pair was then classed into 6 categories, using these time periods. Only the following 4 categories were used for the analysis (Figure 1; see Appendix (A.1) for details of unused pair categories and pair categorisation):

Faithful The pair was observed together in the previous and focal breeding.

Divorced The pair was observed together in the previous breeding, and observed with other individuals in the focal breeding (or either individual was not observed in the focal spring, but observed alive at a later date, and therefore known to not have died, while their partner was observed with a different individual).

New Each member of the pair was observed with other individuals in the previous breeding, and observed together in the focal breeding. Alternatively, one pair member was observed with another individual in the previous breeding, and the other pair member was a juvenile.

There is overlap between 'Divorced' and 'New' pairs, with an individual able to be recorded twice in the same year, once as part of a 'Divorced' pair, and once as part of a 'New' pair. Across the pairs that were used for analysis (see Table 1), 27 individuals were observed as part of two pairs in the same year.

Juveniles Both individuals in the pair were born the previous year, and the focal

breeding was their first breeding season.

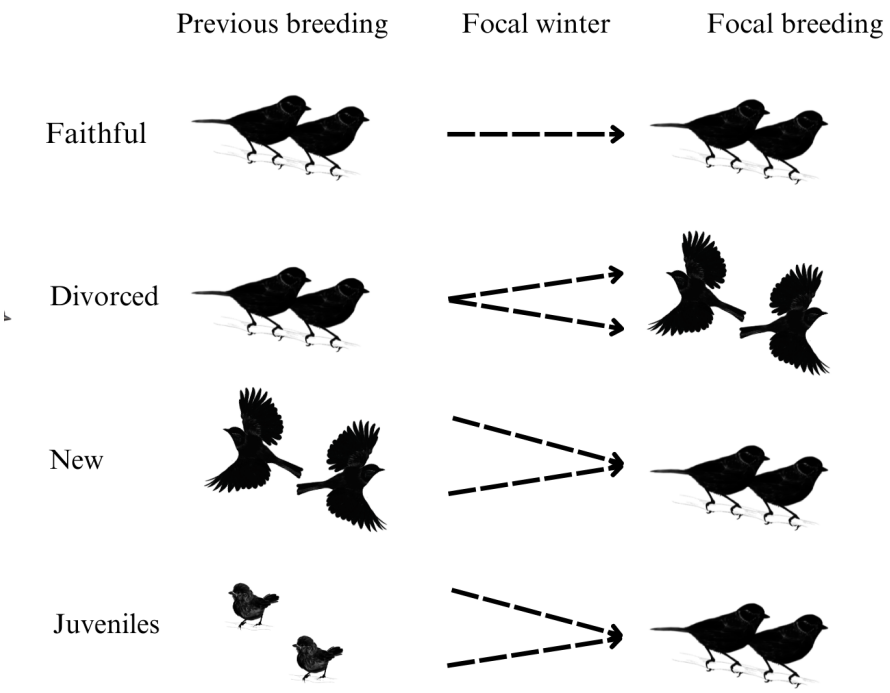

Figure 1: The relationship between pair status in subsequent breedings and pair status as used in the analysis. Focal winter refers to the winter in which behavioural indices for the pair are calculated.

All data preparation was done in R (Team, 2022) using the tidyverse (Wickham et al., 2019) and data table (Dowle and Srinivasan, 2023) packages. Models were run using the glmmTMB package in R (Brooks et al., 2017), with residuals checked used the DHARMa package (Hartig, 2022). Where models failed the residual assumption checks, they were further tested using non-parametric permutations, to also obtain permuted p-values for the results (p_{perm}). Details of model results, residual checks, and further discussion of permutation testing, are included in the Appendix.

Each of the two basic indices (see below) were calculated for each pair for every day both individuals were present within the season. Day is referred to as 'experimental day', where 1 represents the first day of data collection for a given year, to allow seasonal measures to align across years. While data was only collected on the weekends (to gain a snapshot of social structure at each time point), the experimental day variable represented the number of weekdays and weekends (i.e the second weekend was experimental days 8 and 9), in order to more accurately represent the scale of change over the season.

3.2 Shared flocking events

In order to estimate social associations we examined how individuals co-occurred across flocking events, following the gambit-of-the-group approach (Franks et al., 2010). For each pair, a winter association score was calculating using the daily proportion of shared flocking events (also known as simple ratio index (SRI)) using the following formula:

$$WA = \frac{x}{m + f + x}$$

where x is the number of shared flocking events between a pair, m is the number of flocking events observed to include the male but not the female, and f is the number of flocking events observed to include the female but not the male.

Shared flocking events were modelled using a k/n binomial generalised linear model, using x as successes (k) and $m + f + x$ as failures (n), in order to fit the score to the model structure. Pair status was the fixed effect, with year and pair id as intercept-level random effects. A 1:n overdispersion random effect and a zero-inflation term were included, as determined by AICc model selection

(Table A2). The model of shared flocking events over time was the same as this base model, but with the addition of a quadratic interaction term between pair status and day. The model was compared to a linearly modelled interaction using AICc, but the linear interaction model did not converge, so the quadratic model was retained.

3.3 Preferred partner

In order to investigate whether the behavioural differences we observed reflected a difference in general social behaviour or a specific difference in behaviour with an individual's partner, we analysed whether individuals' breeding season partner remained their 'preferred social partner' in the winter season. A preferred social partner was defined as the opposite-sex individual with the highest winter association score with the focal individual.

Modelling partner preference across the entirety of the winter was not possible with a logistic regression due to perfect separation of the divorced category (no divorced birds had their breeding partner as their preferred social partner). Due to the clear division of the data, no modelling was undertaken, and the more complex model of preferred partner over time was used to infer overall differences between the pair statuses.

Preferred partner was also calculated for each day. This was possible to model with a logistic regression, with pair status in interaction with a quadratic term for experimental day. Sex was included as a fixed effect, as well as year and pair id as random effects. This model was compared to a linear interaction model using AICc, and the quadratic model performed better so was retained (Table A12).

3.4 Visit adjacency

We also examined pairs' behaviour within flocking events. Daily visit adjacency was calculated only from records within flocking events that pairs shared. For each record, it was marked as adjacent if an individual visited the feeder within 3 seconds after their partner.

The amount of adjacent visits by a pair was estimated as a simple proportion, referred to from here as visit adjacency index (VAI):

$$VAI = \frac{m + f}{x + y}$$

where m is the number of male visit records adjacent to a female visit, f is the number of female visit records adjacent to a male visit, x and y are the total number of male and female visits respectively, and VAI is the visit adjacency index.

VAI was modelled using a k/n binomial generalised linear model. Pair status was included as a fixed effect, and year and pair id as intercept-level random effects. Average flock size was also included as a fixed effect, to account for follower proportion presumably being lower in larger flocks. A 1:n overdispersion random effect was included, as selected by AICc (Table A4). The model of visit adjacency over time was the same as the base model, but a quadratic interaction term was included between pair status and experimental day. The model was compared to a linearly modelled interaction using AICc, but the quadratic model performed better so was retained.

3.5 Non-pair associates

As an additional analysis we compared the winter association and visit adjacency scores of birds with their partner to the same scores with their other network associates. This was in order to understand whether any results observed might be due to a change in behaviour with all conspecifics, as opposed to just with the individual's partner. Details of model building and results for this analysis are included in A.3.

4 Results

Of 1,169 breeding pairs observed across three seasons, the total number of pairs which fulfilled the criteria for this analysis was 287 (24.6%). 635 pairs (54.3%) were ineligible because one or both individuals were not observed at the feeders in the focal winter, meaning no data was available for analysis, and 247 (21.1%) pairs were of an unused pair status due to uncertainty in the breeding status of one or more individual, meaning they couldn't be assigned to one of the four used pair statuses (Table A1). The number of analysed pairs of each status in each breeding season is presented in Table 1. Note that the relatively low number of pairs able to be used for analysis is expected due to the nature of wild system data, with many individuals being removed from the population due largely to mortality (as well as, potentially, emigration). The requirement for both individuals to survive two subsequent breeding attempts was a limitation on possible numbers. A full breakdown of the workflow for which pairs were and were not included is provided in A.1.

Table 1: The number of pairs in each pair category, across the three seasons, which were suitable for analysis. Pairs in 2012 were observed in the 2012 breeding season, and analysed using data from the 2011/2012 winter season, and so on for the following years.

Status/Year	2012	2013	2014	**Total**
Faithful	23	27	27	**77**
Divorced	9	12	5	**26**
New	30	29	34	**93**
Juvenile	44	8	39	**91**
Total	**106**	**76**	**105**	**287**

4.1 Shared flocking events

In a model without time, there was a significant difference between winter association score for each pair status (Table A3). With faithful as a reference value, new (coef=-0.54±0.15, $p<0.001$, $p_{perm}=0$), juvenile (coef =-0.88±0.15, $p<0.001$, $p_{perm}=0.01$), and divorced (coef=-1.31±0.23, $p<0.001$, $p_{perm}=0$) pairs all had significantly lower winter association. Faithful birds had significantly higher winter association score with their partner than with non-pair associates (coef=-1.08±0.04, $p<0.001$ (Table A13)), while divorced birds had similar winter association with their partner when compared to their non-pair associates (Figure A10).

Over time, faithful pairs showed a significant increase in winter association score (coef=0.24±0.02, $p<0.001$), with no significant quadratic effect (Figure 2). New pairs had a significant linear increase in winter association over time (0.14±0.03, $p<0.001$), with an n-shaped quadratic curve (-0.09±0.03, $p=0.006$). Juvenile pairs also had a significant linear increase (0.29±0.04, $p<0.001$), but in contrast, a u-shaped curve (0.09±0.04, $p=0.01$). Divorced pairs had a significant linear decrease in winter association score over time (-0.26±0.05, $p<0.01$), with no significant quadratic effect. A full model coefficient table is provided in the

Appendix (Table A7).

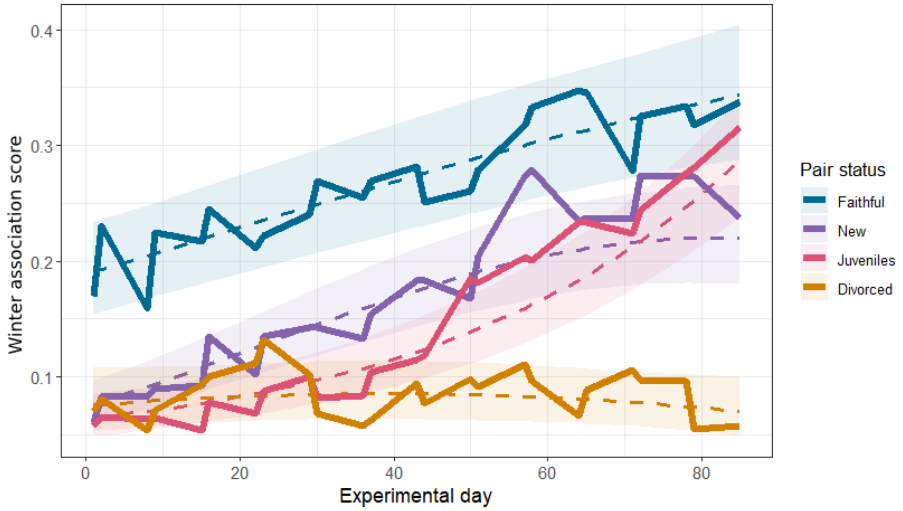

Figure 2: The predicted and observed association between experimental day and winter association score. Dashed lines represent the predicted value from a binomial GLMM with a quadratic interaction term, and ribbons a 95% confidence interval around that prediction. Predictions are made for each pair status at each relevant value of experimental day, averaged across random effect groups and conditioned on the zero-inflation term (Lüdecke, 2018). Solid lines are the average values from the raw data.

4.2 Preferred partner

There was a large difference between the pairing categories in the number of individuals which had the highest association with their breeding partner. As discussed in the methods, we could not model this due to perfect separation of the divorced category, which suggests that this difference may be a significant one. However, the overall effect can be extracted from the model of partner presence over time.

Across the season, new (coef=-0.76±0.17, $p<0.001$), juvenile (-1.09±0.18, $p<0.001$), and divorced (-2.84±0.41, $p<0.001$) individuals were significantly less likely than faithful individuals to have the highest association with their breeding partner

(Figure 3). Faithful individuals had a significantly increased likelihood over time (0.38±0.05, p<0.001), with their rate of increase slightly decreasing towards the end of the winter (-0.13±0.06, p=0.02). New individuals had a significant linear increase over time (0.27±0.09, p=0.002) and a similar decrease in rate, causing an n-shaped curve (-0.23±0.09, p=0.01). Individuals in juvenile pairs significantly increased the chance that their partner was their highest association over time (0.71±0.11, p<0.001), with no significant quadratic effect. Divorced individuals were significantly less likely to have the highest association with their partner over time (-0.67±0.23, p=0.003), but with no significant quadratic effect. There was no effect of sex. A full model coefficient table is provided in the Appendix (Table A12).

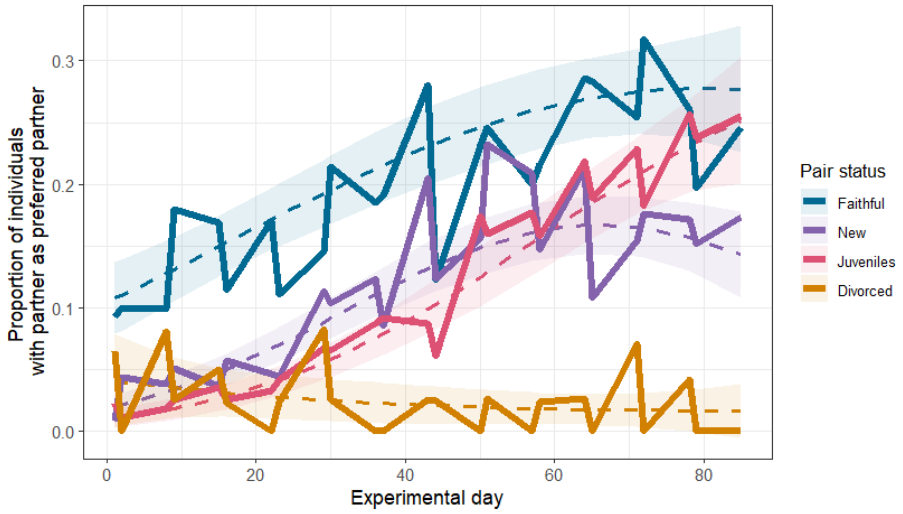

Figure 3: The predicted and observed association between experimental day and whether an individual had the highest winter association score with their breeding partner. Dashed lines represent the predicted value from a logistic GLMM with a quadratic interaction term, and ribbons a 95% confidence interval around that prediction. Predictions are made for each pair status at each relevant value of experimental day, averaged across random effect groups and conditioned on the zero-inflation term (Lüdecke, 2018). Solid lines are the average values from the raw data.

4.3 Visit adjacency

Examining behaviour within flocking events, we found no significant difference between overall visit adjacency index for faithful, new (coef=0.05±0.06, p=0.42), and juvenile (0.08±0.07, p=0.28) pairs. However, divorced pairs had significantly lower visit adjacency index (-0.54±0.12, p<0.001) (Table A5). Faithful birds had significantly visit adjacency index with their partner than with non-pair associates (coef=-0.42±0.04, p=<0.001 (Table A14)), while divorced birds had similar visit adjacency index with their partner when compared to their non-pair associates (Figure A13)

In a quadratic interaction model between pair status and time, there was a slight but significant linear increase in visit adjacency index over the winter for faithful (coef=0.05±0.02, p=0.03) and juvenile (0.10±0.04, p=0.01) pairs (Figure 4). There was a significant linear decrease in visit adjacency index for divorced pairs (-0.23±0.08, p=0.006). New pairs did not have a significant linear change over time (0.06±0.04, p=0.1). Despite the quadratic interaction model outperforming a linear model, none of the quadratic effects in the model were significant. The conclusions drawn from the linear interaction model coefficients were the same as the quadratic model. Full model coefficient tables (quadratic and linear model results) are provided in the Appendix (Table A9, Table A10).

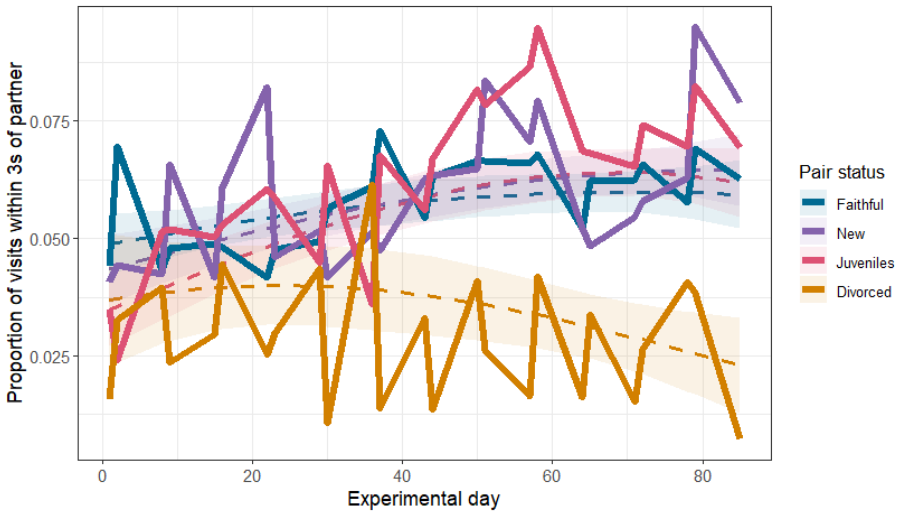

Figure 4: The predicted and observed association between experimental day and visit adjacency index. Dashed lines represent the predicted value from a binomial GLMM with a quadratic interaction term, and ribbons a 95% confidence interval around that prediction.Predictions are made for each pair status at each relevant value of experimental day, averaged across random effect groups and conditioned on the zero-inflation term (Lüdecke, 2018). Solid lines are the average values from the raw data.

5 Discussion

We show how breeding relationships shape future winter flocking behaviour, and find that social behaviour during the non-breeding winter season is strongly associated with breeding status in the neighbouring springs in a wild population of great tits. Specifically, we report clear evidence for divorce to have taken place from early in the winter, as well as demonstrating that new partnerships are beginning to form by this point. We showed that across the winter as a whole, faithful pairs of wild great tits shared the most flocking events with their breeding partners, and divorced pairs the least. These differences are present in both absolute winter association score between a pair, and the chance of an individual having the highest winter association score with their breeding part-

ner, suggesting an active adjustment of time spent with a partner, as opposed to a change in behaviour with all conspecifics. Within those shared events, pairs which were together in the subsequent spring (faithful, new, and juvenile) had considerably more visits to the feeder immediately after their partner, when compared to pairs which were divorced.

The distinction between faithful and divorced pairs from the very beginning of the winter period provides new insights suggesting that information from the breeding season almost immediately influences individual social associations during the winter non-breeding season. This finding, that divorce is behaviourally observable from the beginning of the season, with divorced pairs being no different to any pair of opposite sex birds, suggests that to great tits, an unsuitable partner may be worse than no partner at all. However, the different pattern observed in visit adjacency means that there may be causal differences underlying the results at different spatiotemporal levels of behaviour. Shared flocking events are inherently spatial, as it is impossible for birds to share a flocking event if they are not in the same location. It is also uncertain to what extent shared flocking events reflect social decision making as opposed to simply non-deliberate spatial co-occurrence (for discussions of spatial and social effects in this system see Aplin et al., 2015; Farine and Sheldon, 2019; Firth and Sheldon, 2016). In comparison, pair closeness within flocking events reflects a more direct social decision at a fine spatiotemporal scale, therefore representing social behaviour over and above spatiotemporal location. It may be that at the beginning of the season the difference between faithful pairs and other pairs is spatially determined, while social decision-making becomes more important throughout the season. This may represent a general insight into the processes that determine pair bonding and fidelity. In order to investigate this further, ex-

periments which separate individual feeding locations during the non-breeding season are now needed, to separate social behaviour from spatial feeding behaviour (see Firth and Sheldon, 2015 for an example of a feeder segregation experiment).

These findings demonstrate that social associations in one context (breeding season) carry over to another context (non-breeding season), suggesting an important role of the individual identity of associates. The great tits in our study showed a difference in their social behaviour with a previous partner related to whether they would go on to breed together again. A potential explanation for this difference could be that birds which are more likely to divorce are birds which already have some distinct pattern of social behaviour, such as having a less strong pair bond with their partner even before breeding (Choudury, 1995). Alternatively, it could be that divorce leads to a change in overall behaviour, not just behaviour with a previous partner, such as an increased number of weaker social bonds as an individual searches for a new partner (this has been shown in humans (Milardo, 1987)). Further research into this behavioural process may help to disentangle these potential explanations.

In sum, we provide new insights into the timing of divorce and new partnership formation in a wild population, and demonstrate how social relationships during the breeding season shape non-breeding winter sociality in great tits, and shows how winter social decisions in terms of group membership and behaviour within flocking events may be connected to breeding pair relationships. To our knowledge, this is the first work identifying the fine-scale timing of divorce using distinct behavioural patterns. Future examinations focusing on investigating the causal relationships behind the observed associations in this and broader

systems would now be of much interest.

6 Acknowledgments

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7 Author contributions

All authors contributed to the ideas of this study. ADA completed the statistical analyses with methodology assistance from JF and BCS. ADA drafted the manuscript, with feedback and input from JF and BCS throughout.

References

Alberts, S. (2018). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology*, *88*, 47–66.

Anderson, M., & Braak, C. (2003). Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation*, *73*, 85–113.

Anderson, M. J., & Legendre, P. (1999). An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *Journal of Statistical Computation and Simulation*, *62*, 271–303.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & BC., S. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4199–4205.

Aplin, L. M., Firth, J., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Psorakis, I., et al. (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour*, *108*, 117–127.

Barocas, A., Ilany, A., Koren, L., Kam, M., & Geffen, E. (2011). Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE*, *6*.

Behringer, D. C., Butler, M. J., & Shields, J. (2006). Avoidance of disease by social lobsters. *Nature*, *441*, 421.

Black, J. (1996). *Partnerships in birds: The study of monogamy*. Oxford Univ. Press.

Brooks, M., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Maechler, M., & Bolker, B. (2017). Glmmtmb balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Cheetham, S. A., Thom, M. D., Beynon, R. J., & JL., H. (2008). The effect of familiarity on mate choice. In H. JL, R. Beynon, S. C. Roberts, & T. Wyatt (Eds.), *Chemical signals in vertebrates 11*. Springer.

Choudury, S. (1995). Divorce in birds: A review of the hypotheses. *Animal Behaviour*, *50*, 413–429.

Culina, A., Firth, J., & Hinde, C. A. (2020). Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, *287*(20201), 554.

Culina, A., Lachish, S., Pradel, R., Choquet, R., & BC., S. (2013). A multi-event approach to estimating pair fidelity and heterogeneity in state transitions. *Ecology and Evolution*, *3*, 4326–4338.

Culina, A., Lachish, S., & Sheldon, B. (2015). Evidence of a link between survival and pair fidelity across multiple tit populations. *Journal of Avian Biology*, *46*, 507–515.

Dowle, M., & Srinivasan, A. (2023). Data.table: Extension of data.frame. *R package version*, *1*(14), 8. https://CRAN.R-project.org/package=data.table

Emery, N. J., Seed, A. M., von Bayern Amp, & NS., C. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 489–505.

Evans, J., Silk, M., Boogert, N., & Hodgson, D. (2020). Infected or informed? social structure and the simultaneous transmission of information and infectious disease. *Oikos*, *129*.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in r using asnipe. *Methods in Ecology and Evolution*, *4*(12), 1187–1194. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12121

Farine, D. R., Firth, J., Aplin, L. M., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Milligan, N. D., Psorakis, I., et al. (2015). The role of social and ecological processes in structuring animal

populations: A case study from automated tracking of wild birds. *Royal Society Open Science 7*, *2*, 15005.

Farine, D. R., & Sheldon, B. (2019). *Stable multi-level social structure is maintained by habitat geometry in a wild bird population* [BioRxiv. Preprint].

Firth, J., Cole, E. F., Ioannou, C. C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K., & Sheldon, B. (2018). Personality shapes pair bonding in a wild bird social system. *Nature Ecology & Evolution*, *2*, 1696–1699.

Firth, J., & Sheldon, B. (2015). Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Royal Society Proceedings B*, *282*.

Firth, J., & Sheldon, B. (2016). Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. *Ecology Letters*, *19*(11), 1324–1332.

Franks, D., Ruxton, G., & James, R. (2010). Sampling animal association networks with the gambit of the group. *Behavioural Ecology and Sociobiology*, *64*.

Gokcekus, S., Firth, J., Regan, C., Cole, E. F., Sheldon, B., & GF., A. (2023). Social familiarity and spatially variable environments independently determine reproductive fitness in a wild bird. *The American Naturalist*, *201*, 813–824.

Griffiths, S. W., Brockmark, S., H?jesj?, J., & JI., J. (2004). Coping with divided attention: The advantage of familiarity. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *271*, 695–699.

Griggio, M., & Hoi, H. (2011). An experiment on the function of the long-term pair bond period in the socially monogamous bearded reedling. *Animal Behaviour*, *82*, 1329–1335.

Hartig, F. (2022). Dharma: Residual diagnostics for hierarchical (multi-level / mixed) regression models. *R package version 0.*, *4*, 6. https://CRAN.R-project.org/package=DHARMa

Hope, A. (1968). A simplified monte carlo significance test procedure. *Journal of the Royal Statistical Society: Series B (Methodological)*, *30*, 582–598.

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews*, *72*, 283–327.

Kennedy, P., & Cade, B. (1996). Randomization tests for multiple regression. *Communications in Statistics - Simulation and Computation*, *25*, 923–936.

Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *270*, 653–664.

Kurvers, R., Krause, J., Croft, D. P., Adm, W., & Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: Emerging issues. *Trends in Ecology & Evolution*, *29*, 326–335.

Lachlan, R. F., Crooks, L., & Laland, K. (1998). Who follows whom? shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, *56*, 181–190.

Linden, M. (1991). Divorce in great tits – chance or choice? an experimental approach. *The American Naturalist*, *138*, 1039–1048.

Lüdecke, D. (2018). Ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

Machado, A. M., Cantor, M., Costa, A. P., Righetti, B. P., Bezamat, C., Valle-Pereira, J. V., Simões-Lopes, P. C., Castilho, P. V., & FG., D.-J. (2019).

Homophily around specialized foraging underlies dolphin social preferences. *Biology Letters*, *15*(20180), 909.

Maldonado-Chaparro, A., Forstmeier, W., & Farine, D. R. (2021). Relationship quality underpins pair bond formation and subsequent reproductive performance. *Animal Behaviour*, *182*, 43–58.

Manly, B. (2007). *Randomization, bootstrap, and monte carlo methods in biology. 3rd ed.* Chapman & Hall.

Martin, M. S., & Shepherdson, D. (2012). Role of familiarity and preference in reproductive success in ex situ breeding programs. *Conservation Biology*, *26*, 649–656.

Milardo, R. (1987). Changes in social networks of women and men following divorce: A review. *Journal of Family Issues*, *8*, 78–96.

Montero, A. P., Williams, D. M., Martin, J., & Blumstein, D. (2020). More social female yellow-bellied marmots, marmota flaviventer, have enhanced summer survival. *Animal Behaviour*, *160*, 113–119.

Patrick, S. C., Chapman, J. R., Dugdale, H. L., Quinn, J. L., & BC., S. (2012). Promiscuity, paternity and personality in the great tit. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1724–1730.

Perrins, C. (1965). Population fluctuations and clutch-size in the great tit, *Parus major L. The Journal of Animal Ecology*, *34*, 601.

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., & B, J. (2014). Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. *PLoS ONE*, *9*.

Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: Pair bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society B: Biological Sciences*, *281*(20132), 843.

Schieck, J., & Hannon, S. (1998). Breeding site fidelity in willow ptarmigan: The influence of previous reproductive success and familiarity with partner and territory. *Oecologia*, *81*, 465–472.

Senar, J. C., Mateos-Gonzalez, F., Uribe, F., & Arroyo, L. (2013). Familiarity adds to attractiveness in matters of siskin mate choice. *Proceedings of the Royal Society B: Biological Sciences*, *280*(20132), 361.

Silk, J., Beehner, J., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & DL., C. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3099–3104.

Stroeymeyt, N., Grasse, A. V., Crespi, A., Mersch, D. P., Cremer, S., & Keller, L. (2018). Social network plasticity decreases disease transmission in a eusocial insect. *Science*, *362*, 941–945.

Team, R. C. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wilkinson, G. S., Carter, G., Bohn, K. M., Caspers, B., Chaverri, G., Farine, D. R., Günther, L., Kerth, G., Knörnschild, M., Mayer, F., et al. (2019). Kinship, association, and social complexity in bats. *Behavioral Ecology and Sociobiology*, *73*.

Yokoi, S., Ansai, S., Kinoshita, M., Naruse, K., Kamei, Y., Young, L. J., Okuyama, T., & Takeuchi, H. (2016). Mate-guarding behavior enhances male reproductive success via familiarization with mating partners in medaka fish. *Frontiers in Zoology*, *13*.

A Appendix

A.1 Pair categories

Pair categories for a given breeding season were calculated based on the following variables:

1. Whether the pair was observed during the focal breeding
2. Whether the female was observed in the focal breeding
3. Whether the male was observed in the focal breeding
4. Whether the pair was observed in the previous breeding
5. Whether the female was observed in the previous breeding
6. Whether the male was observed in the previous breeding
7. Whether the female is a juvenile (born in the previous breeding season)
8. Whether the male is a juvenile
9. Whether the male was observed alive in any later season
10. Whether the female was observed alive in any later season

The combination of these variables determined the status of the pair. Certain combinations were 'impossible' (e.g pair observed in a year but the female not observed) and were used to identify and correct errors in data entry.

The full list of pair categories, based on the above variables, is as follows:

Faithful A pair was 'faithful' if they were observed in the focal breeding (1=TRUE), and observed in the previous breeding (4=TRUE).

Divorced A pair was 'divorced' if the pair was not observed in the focal breeding (1=FALSE), but both individuals were (2&3 = TRUE), and the pair had been observed in the previous breeding (4=TRUE). Alternatively, if one individual was not observed in the focal breeding (2 XOR 3=FALSE) but they were observed alive at a later date (9 XOR 10=TRUE), they would still be recorded as divorced.

New A pair was 'new' if they were observed in the focal breeding (1=TRUE), not observed in the previous breeding (4=FALSE), but both individuals were observed in the previous breeding (5&6=TRUE). Pairs were also classified as new if one but not both individuals were a juvenile (7 XOR 8=TRUE).

Juveniles A pair were 'juveniles' if they were observed in the focal year (1=TRUE) and both individuals were juveniles (7&8=TRUE).

Split A pair was 'split' where they were no longer breeding together, but the fate of one or both birds was unknown so it was unclear whether the split was due to divorce or death. This was the case where they were not observed in the focal breeding (1=FALSE) but were observed in the previous breeding (4=TRUE) and one or both individuals were not observed in the focal breeding (2/3=FALSE) and not observed alive at a later date (9/10=FALSE). This category was not included in analysis.

New (unknown) A pair was 'new unknown' where they were breeding together, but their status in the previous breeding was unknown, so it was unclear whether they were a faithful or new pair. This was the case where they were observed in the focal breeding (1=TRUE) but were not observed in the pre-

vious breeding (4=FALSE) and one or both individuals were not observed in the previous breeding (5/6=FALSE). This category was not included in analysis.

Table A1: The number of breeding pairs of each status across each of the three study years. As these totals include birds which did not have movement data from the previous winter, and therefore could not be included in the analysis, totals for the faithful, divorced, new, and juvenile statuses may be higher than in Table 1. Pairs in 2012 were observed in the 2012 breeding season, and analysed using data from the 2011/2012 winter season, and so on for the following years.

Status/Year	2012	2013	2014	**Total**
Faithful	27	29	30	**86**
Divorced	12	16	5	**33**
New	47	50	52	**149**
Juveniles	78	17	84	**179**
Split	171	218	118	**507**
New (unknown)	111	58	46	**215**
Total	**446**	**388**	**335**	**1169**

Figure A1 provides an example of how individuals may be assigned to different pair statuses. Due to the individually-focused approach, numbers in the diagram may differ from those in other tables, but it should demonstrate how the number of pairs usable in analysis may reduce dramatically.

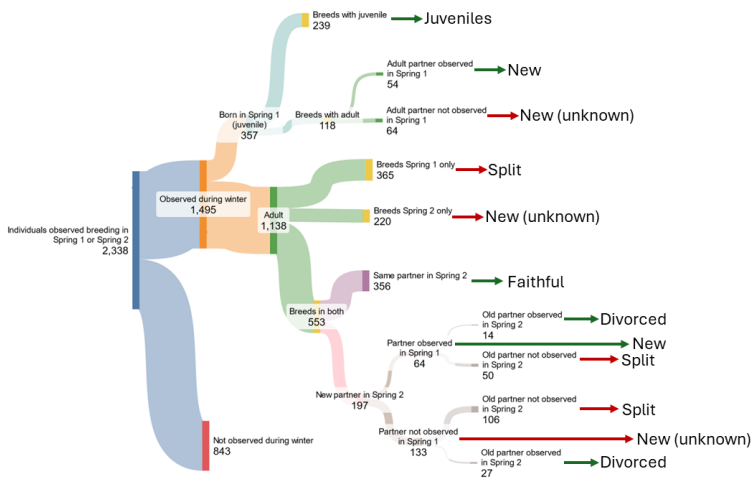

Figure A1: Number of individuals in the data at each stage of pair classification. Pair statuses denoted with a green arrow are those included in the final analysis, while ones with red arrows were not. Note that as an individual's partner has to be observed in the winter to be included in the final analysis, numbers may differ from those included in other tables.

A.2 Model checking and detailed results

A.2.1 Suitability of permutation testing

In cases where error distributions appear not to follow assumptions of normality, permutation testing is a possible non-parametric solution. It tests whether the observed results differ from the distribution of the values estimated when the data is 'shuffled' - if they do, it suggests that any significant relationship found from the original model did not arise by chance. The probability of obtaining the observed value from the permuted distribution provides a new p-value.

While this method is very well accepted for models with a single predictor, it is debated whether it remains suitable for models with multiple predictors, random effects, or repeated samples (Kennedy and Cade, 1996). This is because the shuffling may break relationships within the data, making the randomised

dataset not a relevant comparison to the original. There are a number of ways to perform a permutation test, as any combination of parameters can be permuted.

Theoretically, permutation of the residuals constrained by model groups would provide the most reliable results (M. Anderson and Braak, 2003; Manly, 2007). However, limitations on permutation from using binomial models with a limited number of constrained permutations (possible combinations within groups) mean that permuting the raw data was the most suitable for my analysis. Following the procedure from Hope, 1968 and M. J. Anderson and Legendre, 1999, we assessed the results of the permutation from the Z-score of the coefficients, as opposed to the raw coefficient values. An exact permutation test was not possible, as that would require all possible permutations, and therefore 534! at minimum for my models. Instead, we conducted randomisation tests, where a large random sample of possible permutations were used.

Where residual assumptions were not met for a model, I used the following procedure, for a k/n binomial model.

1. Randomise k/n pairs across the dataset.
2. Run original model structure using randomised dataset.
3. Extract model coefficient Z-values.
4. Repeat 1-3 5000 times.
5. Compare the absolute distributions of the coefficient Z-values from the permuted models to the coefficient Z-values from the original model, in order to obtain a two-tailed p-value.

In interpreting the results of the permutation tests it is important to note that small changes in how the permutations are performed may change the power

of the analysis, and that in some cases permutation tests can still be affected by nonhomogeneity of variance. Therefore, where possible, we still attempted to adjust the initial model in order to fulfil residual distribution assumptions, or make breaches of the residual assumptions as minor as possible.

A.2.2 Shared flocking events

Model selection

Table A2: AICc model selection results for a model of simple ratio index by pair status. The model used in analysis is italicised.

Model number	**Fixed effects**	**Random effects**	**Zero-inflation**	**AICc**	**Δ AICc**
1	Pair status	Year + Pair ID	-	4397.49	1226.81
2	Pair status	Year + Pair ID + 1:n	-	3233.64	62.96
3	Pair status	Year + Pair ID	∼1	3948.10	777.42
4	*Pair status*	*Year + Pair ID + 1:n*	*∼1*	*3170.68*	*0*

Model residuals

The residuals from the selected model showed significant deviations from assumptions (Figure A2). To investigate these deviations as a potential explanation for observed effects, a permutation test was conducted.

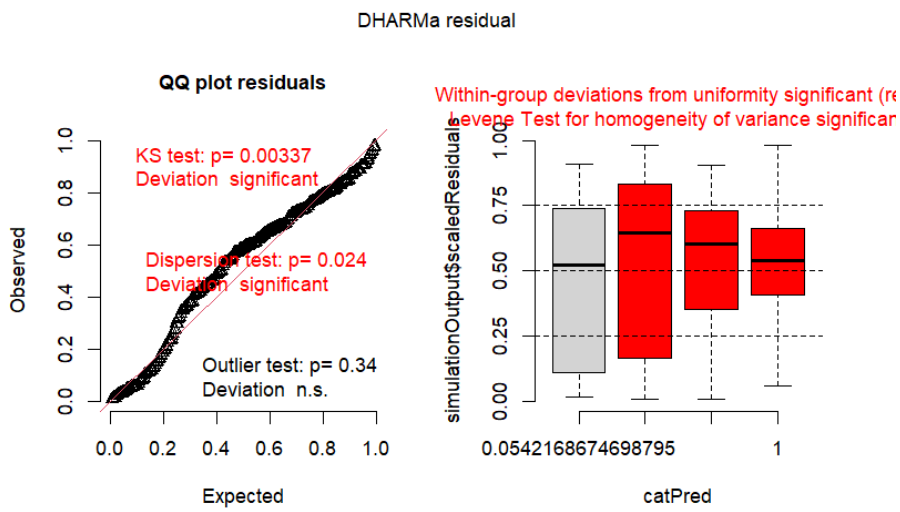

Figure A2: The model residuals (estimated with DHaRMa) from a binomial GLMM of the effect of pair status on simple ratio index.

Permutation test

A permutation test was conducted, with 5000 randomisations of the response. 5.98% of the models did not converge, meaning a Z-score value was unable to be extracted. The two-sided permutation p-values supported the results from the original model (Figure A3).

Coefficient table

Table A3: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair status on simple ratio index. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**	**Permuted p-value**
Intercept	*-1.10*	*0.11*	*<0.001*	*0.03*
Pair status New	*-0.54*	*0.15*	*<0.001*	*0.015*
Pair status Juveniles	*-0.88*	*0.15*	*<0.001*	*0.012*
Pair status Divorced	*-1.31*	*0.23*	*<0.001*	*0.01*

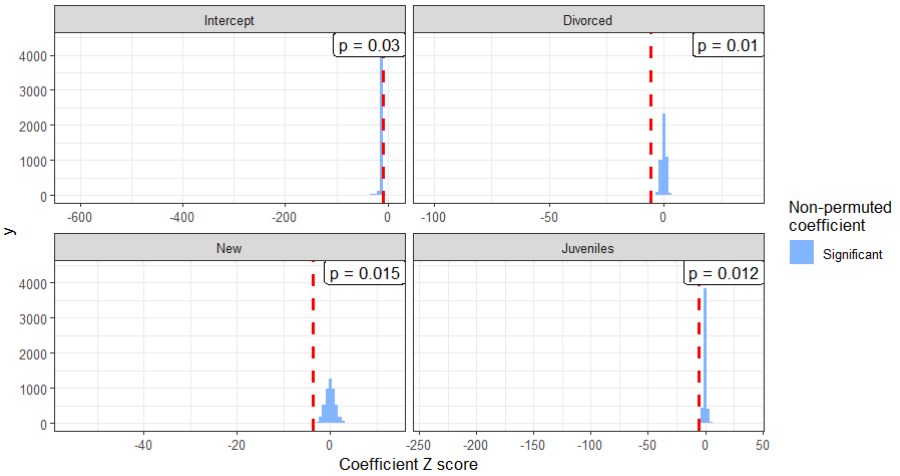

Figure A3: The result of a permutation test of a model of the effect of pair status on simple ratio index. Non-converged models with NA Z-score values are not included.

A.2.3 Visit adjacency

Model selection

Table A4: AICc model selection results for a model of visit adjacency index by pair status. The model used in analysis is italicised.

Model number	Fixed effects	Random effects	Zero-inflation	AICc	Δ AICc
1	Pair status + Average flocksize	Year + Pair ID	-	2135.68	44.36
2	*Pair status + Average flocksize*	*Year + Pair ID + 1:n*	-	*2091.31*	*0*
3	Pair status + Average flocksize	Year + Pair ID	∼1	2137.80	46.49
4	Pair status + Average flocksize	Year + Pair ID + 1:n	∼1	2093.45	46.49

Model residuals

The model residuals showed no significant deviation from assumptions (Figure A4).

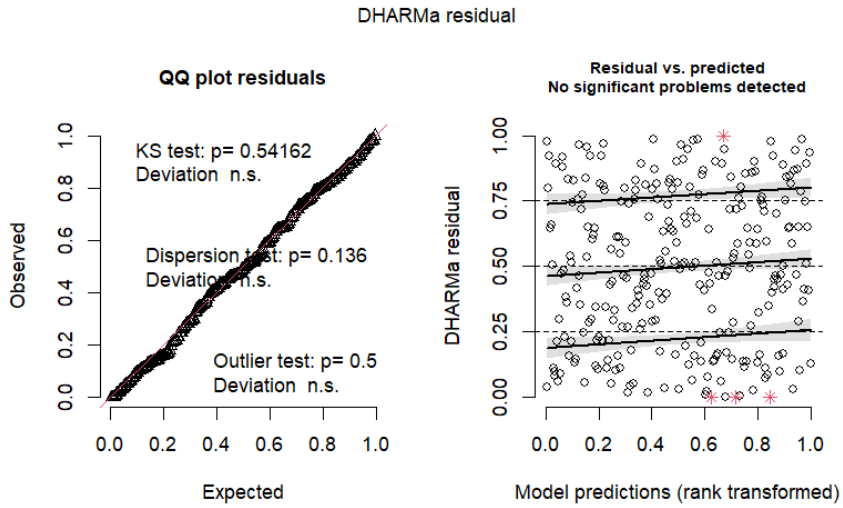

Figure A4: The model residuals (estimated with DHaRMa) from a binomial GLMM of the effect of pair status on visit adjacency index.

Coefficient table

Table A5: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair status on visit adjacency index. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**
Intercept	*-2.45*	*0.09*	*<0.001*
Pair status New	0.05	0.06	0.416
Pair status Juveniles	0.08	0.07	0.280
Pair status Divorced	*-0.54*	*0.12*	*<0.001*
Average flocksize	*-0.03*	*0.01*	*<0.001*

A.2.4 Shared flocking events by time

Model selection

Table A6: AICc model selection results for a model of winter association score by pair status and experimental day. The model used in analysis is italicised.

Model number	**Fixed effects**	**Random effects**	**Zero-inflation**	**AICc**	**Δ AICc**
1	Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2	Year + Pair ID	-	38036.86	9698.97
2	Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2	Year + Pair ID + 1:n	-	29227.10	889.21
3	Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2	Year + Pair ID	∼1	30651.73	2313.84
4	*Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2*	*Year + Pair ID + 1:n*	*∼1*	*28337.89*	*0*
5	Pair status + Day + Pair status*Day	Year + Pair ID + 1:n	∼1	28359.61	21.73

Model residuals

The residuals for the selected model show a number of deviations from assumptions (Figure A5). To test these deviations as a potential explanation for the model results, a permutation test was conducted.

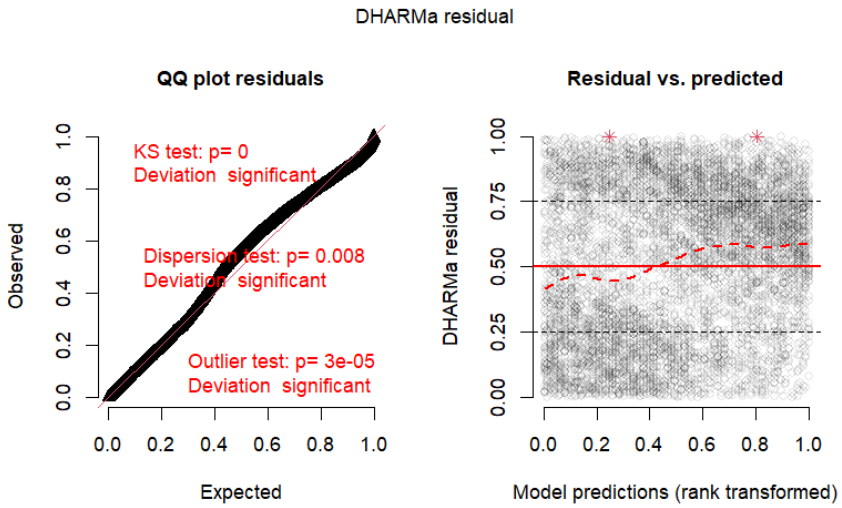

Figure A5: The model residuals (estimated with DHaRMa) from a binomial GLMM of the effect of pair status and day on winter association score.

Permutation test

A permutation test was conducted, with 5000 randomisations of the response. 3.25% of models did not converge so a Z score was unable to be extracted. The two-sided permutation p-values supported the results from the original model, except for the significance of the Intercept result, with the permutation test suggesting that there may not be statistical evidence that the Intercept value differs from zero (Figure A6). This difference largely doesn't impact the interpretation of the results.

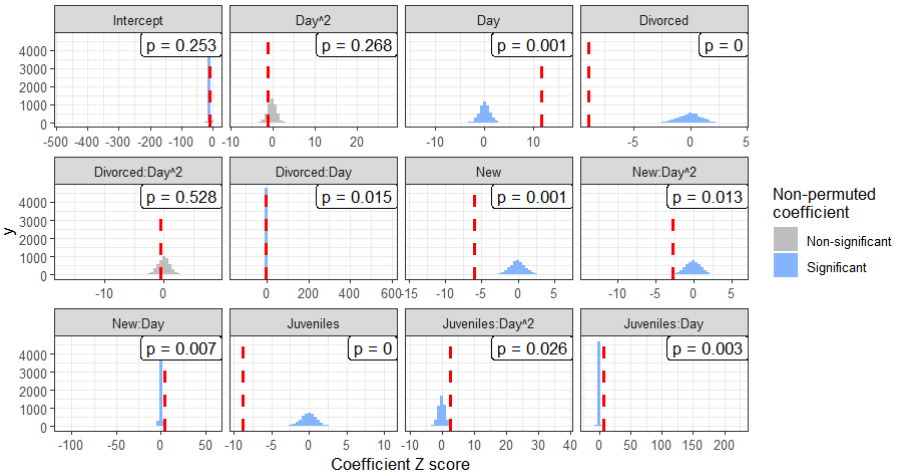

Figure A6: The result of a permutation test of a model of the effect of pair status and day on winter association score. Non-converged models with NA Z-score values are not included.

Coefficient table

Table A7: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair status and day on winter association score. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**	**Permuted p-value**
Intercept	*-0.98*	*0.12*	*<0.001*	*0.253*
Pair status New	*-0.58*	*0.10*	*<0.001*	*0.001*
Pair status Juveniles	*-1.01*	*0.11*	*<0.001*	*0*
Pair status Divorced	*-1.40*	*0.16*	*<0.001*	*0*
Day	*0.24*	*0.02*	*<0.001*	*0.001*
Day^2	-0.03	0.02	0.25	0.268
*Pair status New*Day*	*0.14*	*0.03*	< 0.001	*0.007*
*Pair status Juveniles*Day*	*0.29*	*0.04*	*<0.001*	*0.003*
*Pair status Divorced*Day*	*-0.26*	*0.05*	*<0.001*	*0.015*
*Pair status New*Day*^{2}	*-0.09*	*0.03*	*0.005*	*0.0013*
*Pair status Juveniles*Day*^{2}	*0.09*	*0.04*	*0.014*	*0.026*
Pair status Divorced*Day^2	-0.03	0.06	0.547	0.528

A.2.5 Visit adjacency by time

Model selection

Table A8: AICc model selection results for a model of visit adjacency index by pair status and experimental day. The model used in analysis is italicised. Models which did not converge were not assessed using AICc, so have an AICc value of NA.

Model number	**Fixed effects**	**Random effects**	**Zero-inflation**	**AICc**	**Δ AICc**
1	Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2 + Average flocksize	Year + Pair ID	-	15739.36	804.37
2	*Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2 + Average flocksize*	*Year + Pair ID + 1:n*	-	*14934.99*	*0*
3	Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2 + Average flocksize	Year + Pair ID	∼1	15589.54	654.55
4	Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2 + Average flocksize	Year + Pair ID + 1:n	∼1	NA	NA
5	Pair status + Day + Pair status*Day	Year + Pair ID + 1:n + Average flocksize	-	14938.95	3.95

Model residuals

Model residuals for the selected model are presented below (Figure A7). There is evidence of over or under dispersion, and patterns in the residuals. While these deviations are relatively minor, a permutation test was conducted to check these residual patterns as a potential explanation for the observed results.

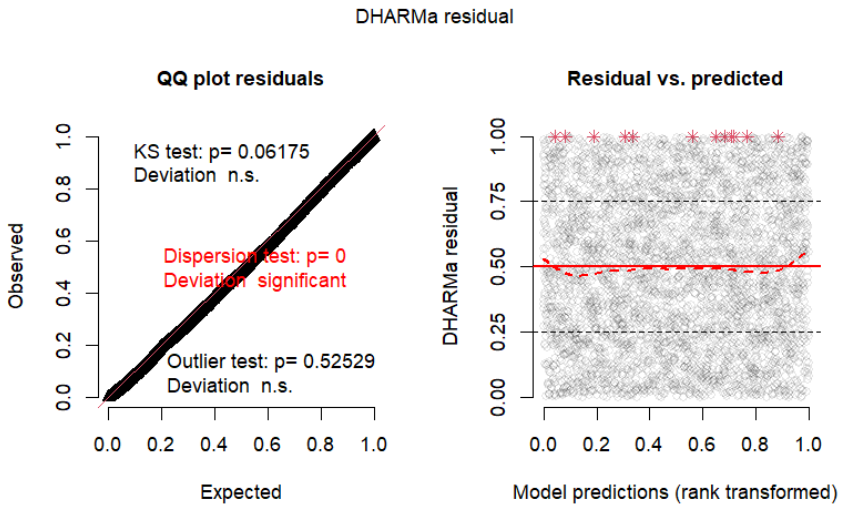

Figure A7: The model residuals (estimated with DHaRMa) from a binomial GLMM of the effect of pair status and day on visit adjacency index.

Permutation test

A permutation test was conducted, with 1000 randomisations of the response. 58.6% of permuted models did not converge, so a Z-score was unable to be extracted. The two-sided permutation p-values supported the significance of all the coefficients which were found to be significant in the original model (Figure A8). However, the coefficient New:Day which was found to be non-significant in the original model was significant based on the permuted p-values. As this effect being significant would only strengthen the conclusions of our research, we chose to err on the side of caution, and continued to interpret this coefficients as non-significant based on the more conservative results of the original model.

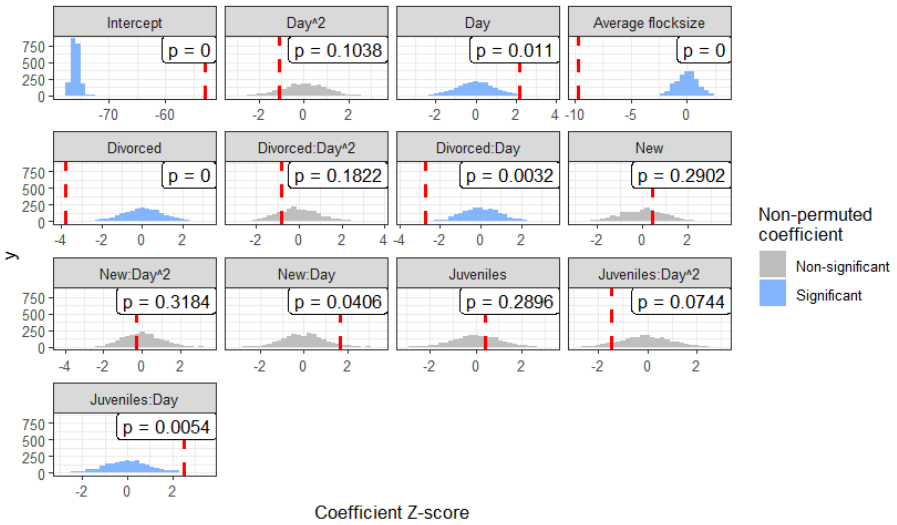

Figure A8: The result of a permutation test of a model of the effect of pair status and day on visit adjacency index. Non-converged models with NA Z-score values are not included.

Coefficient table

Table A9: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair status and day on visit adjacency index. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**	**Permuted p-value**
Intercept	*-2.93*	*0.06*	*<0.001*	*0*
Pair status New	0.03	0.07	0.68	0.29
Pair status Juveniles	0.03	0.08	0.67	0.29
Pair status Divorced	*-0.49*	*0.13*	*<0.001*	*0*
Day	*0.05*	*0.02*	*0.03*	*0.01*
Day^2	-0.03	0.03	0.27	0.10
Average flocksize	*-0.18*	*0.02*	*<0.001*	*0*
Pair status New*Day	0.06	0.04	0.102	0.04
*Pair status Juveniles*Day*	*0.10*	*0.04*	*0.013*	*0.01*
*Pair status Divorced*Day*	*-0.23*	*0.08*	*0.006*	*0.003*
Pair status New*Day^2	-0.01	0.03	0.757	0.32
Pair status Juveniles*Day^2	-0.06	0.04	0.150	0.07
Pair status Divorced*Day^2	-0.07	0.08	0.412	0.18

While the model with quadratic terms outperformed the linear model in model selection, none of the quadratic terms are significant in the final model. The non-quadratic model coefficient table is provided here for comparison.

Table A10: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair status and day on visit adjacency index. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**
Intercept	*-2.96*	*0.05*	*<0.001*
Pair status New	0.02	0.06	0.74
Pair status Juveniles	-0.03	0.06	0.70
Pair status Divorced	*-0.55*	*0.11*	*<0.001*
Day	*0.06*	*0.02*	*0.008*
Average flocksize	*-0.18*	*0.02*	*<0.001*
Pair status New*Day	0.06	0.04	0.120
*Pair status Juveniles*Day*	*0.08*	*0.04*	*0.029*
*Pair status Divorced*Day*	*-0.20*	*0.08*	*0.008*

A.2.6 Preferred partner by time

Model selection

Table A11: AICc model selection results for a model of partner preference by pair status and experimental day. The model used in analysis is italicised.

Model number	**Fixed effects**	**Random effects**	**Zero-inflation**	**AICc**	**Δ AICc**
1	*Pair status + Day + Day^2 + Pair status*Day + Pair status*Day^2 + Sex*	*Year + Pair ID*	-	*7357.12*	*0*
2	Pair status + Day + Pair status*Day + Sex	Year + Pair ID	-	7388.70	31.58

Model residuals

The residuals for the partner preference model are shown below (Figure A9). The Kolmogorov-Smirnov test shows significant deviation - however, this test is very sensitive to deviation at high sample sizes, so a permutation test was not conducted.

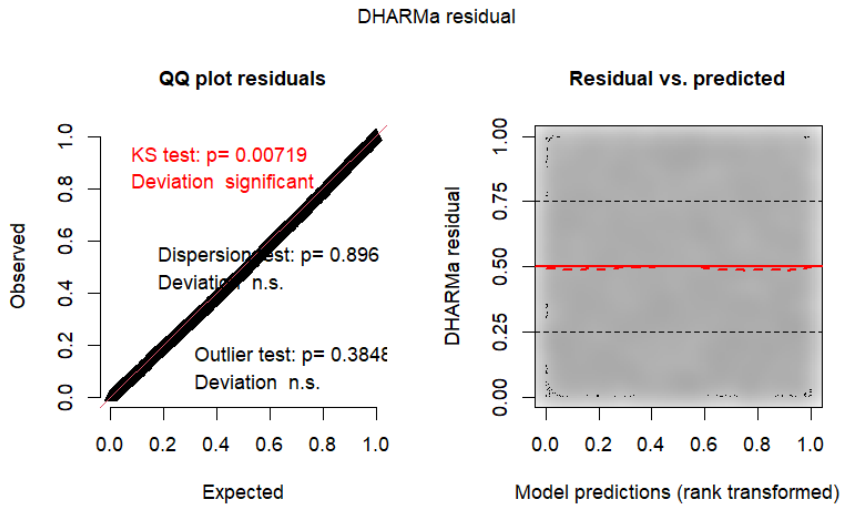

Figure A9: The model residuals (estimated with DHaRMa) from a binomial GLMM of the effect of pair status and day on partner preference.

Coefficient table

Table A12: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair status and day on partner preference. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**
Intercept	*-1.38*	*0.13*	*<0.001*
Pair status New	*-0.76*	*0.17*	*<0.001*
Pair status Juveniles	*-1.09*	*0.18*	*<0.001*
Pair status Divorced	*-2.84*	*0.41*	*<0.001*
Day	*0.05*	*0.38*	*<0.001*
Day^2	*-0.13*	*0.06*	*0.02*
Sex Male	-0.09	0.06	0.14
*Pair status New*Day*	*0.27*	*0.09*	*0.002*
*Pair status Juveniles*Day*	*0.71*	*0.11*	*<0.001*
*Pair status Divorced*Day*	*-0.67*	*0.23*	*0.003*
*Pair status New*Day*^{2}	*-0.23*	*0.09*	*0.012*
Pair status Juveniles*Day^2	-0.08	0.10	0.455
Pair status Divorced*Day^2	0.21	0.25	0.389

A.3 Non-pair associates

As an additional analysis we also investigated how a bird's winter association and visit adjacency scores with its partner compared to the same scores with its network associates.

For each focal bird from the analysis, we found each bird that it had been observed sharing a flocking event with and then estimated winter association score and visit adjacency index using the same methods as in the other models. These estimates were then modelled, with methods and results presented below.

A.3.1 Methods

Winter association score was modelled using a generalised linear mixed model with a binomial response distribution. Pair type (original or associate) was used in interaction with pair status as a predictor, with year, pair, and a 1:n overdispersion term as random effects. A zero-inflation term was included, which was allowed to vary by pair type, as the selection of associates using shared flocking events meant that zeroes were only possible for 'original' pairs. A permutation test was conducted to check for robustness of the results to violations of some residual assumptions.

Visit adjacency index was also modelled with a binomial GLMM, with pair status and type in interaction as fixed effects, as well as year, pair, and a 1:n overdispersion term as random effects. Average flock size was also included as a fixed effect predictor. AICc indicated no need to include a zero-inflation term. Visual analysis of the residuals using DHARMa showed no need for a permutation test.

A.3.2 Results

Winter association score

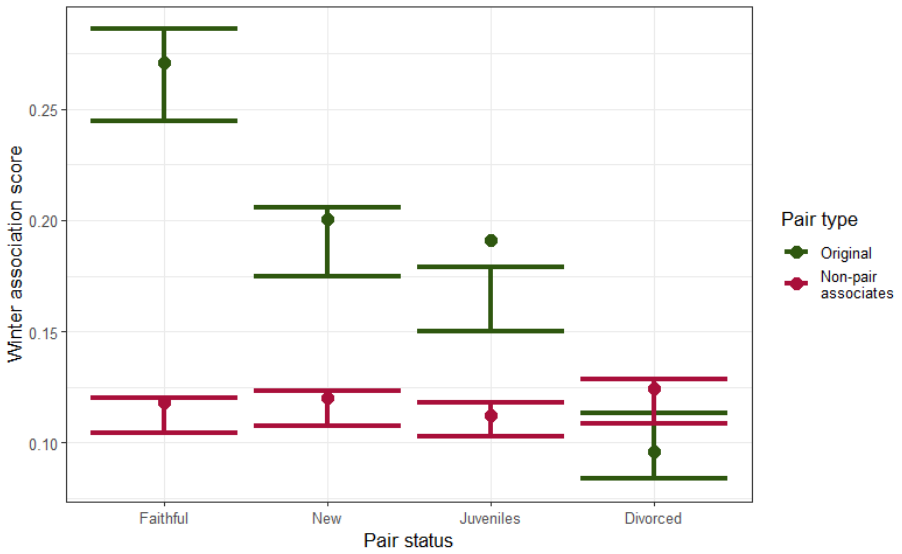

Figure A10: The winter association score of birds with their breeding partner ('Original') compared to their other network associates ('Non-pair associates'). Points represent means in the raw data, while error bars are the 95% prediction confidence interval calculated using ggeffects, averaged across random effect groups and conditioned on a zero-inflation term (Lüdecke, 2018).

For faithful (coef=1.05±0.04, p=<0.001), new (Figure A10), and juvenile pairs (Figure A10), winter association scores with an individual's breeding partner were significantly higher than winter association scores with their non-pair associates. For divorced pairs, there was no significant difference (Figure A10).

Table A13: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair type and pair status on winter association score. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**
Intercept	*-1.02*	*0.05*	*<0.001*
Pair status New	*-0.43*	*0.06*	*<0.001*
Pair status Juveniles	*-0.61*	*0.06*	*<0.001*
Pair status Divorced	*-1.21*	*0.09*	*<0.001*
Non-pair associates	*-1.05*	*0.04*	*<0.001*
*Pair status New*Non-pair associates*	*0.46*	*0.05*	*<0.001*
*Pair status Juveniles*Non-pair associates*	*0.59*	*0.05*	*<0.001*
*Pair status Divorced*Non-pair associates*	*1.26*	*0.08*	*<0.001*

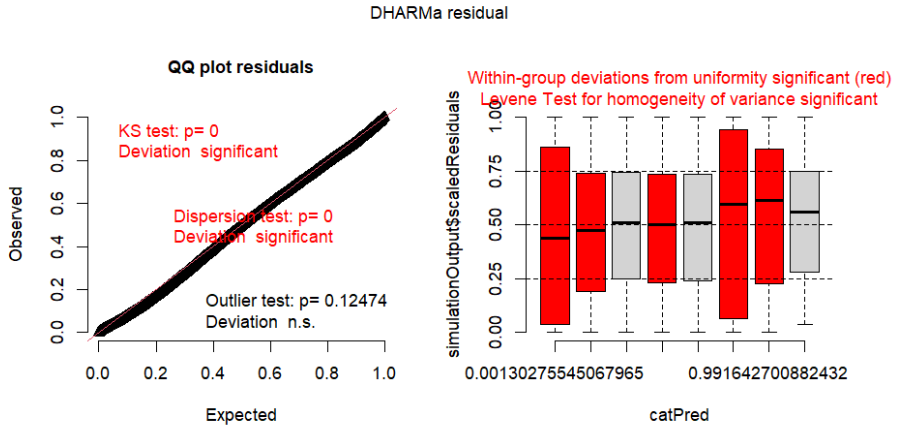

Figure A11: The residuals for a binomial GLMM model of the effect of pair type and pair status on winter association score. Residuals calculated using the DHARMa package (Hartig, 2022).

The model failed some checks of residual assumptions. While the likelihood of failing these checks increases at high sample sizes (n=20,418), a permutation test was conducted to be certain of model conclusions, following the methodol-

ogy described in A.2.1. As shown in A12, the permutation test results concur with the results from the original model.

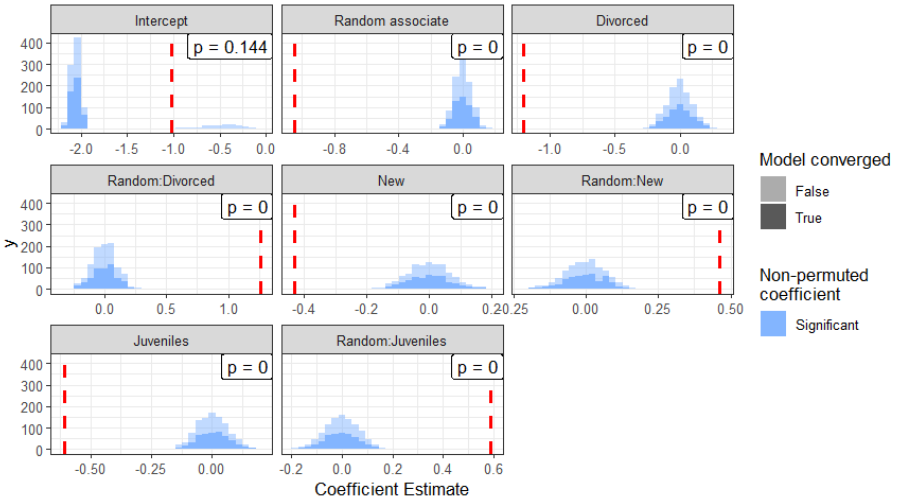

Figure A12: The results of a permutation test for the coefficients in a binomial GLMM of the effect of pair type and pair status on winter association score. Histograms represent the results from 1000 models of a randomly permuted dataset, while the red line represents the result from the original model.

Visit adjacency index

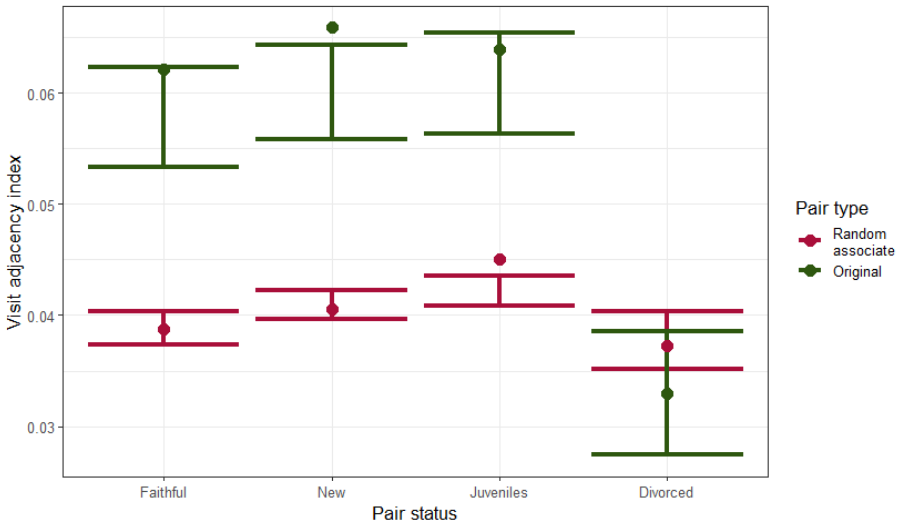

Figure A13: The visit adjacency index of birds with their breeding partner ('Original') compared to their other network associates ('Non-pair associates'). Points represent means in the raw data, while error bars are the 95% prediction confidence interval calculated using ggeffects, averaged across random effect groups and conditioned on a zero-inflation term (Lüdecke, 2018).

For faithful (coef=-0.42±0.04, p=<0.001), new (Figure A13), and juvenile pairs (Figure A13), visit adjacency index with an individual's breeding partner was significantly higher than visit adjacency index with their non-pair associates. For divorced pairs, there was no significant difference (Figure A13).

Table A14: Fixed effect coefficient estimates from a binomial GLMM of the effect of pair type and pair status on winter association score. Significant coefficients are indicated in italics.

Coefficient	**Estimate**	**Standard error**	**p-value**
Intercept	*-2.70*	*0.06*	*<0.001*
Pair status New	0.04	0.06	0.482
Pair status Juveniles	0.06	0.06	0.360
Pair status Divorced	*-0.59*	*0.10*	*<0.001*
Non-pair associates	*-0.42*	*0.04*	*<0.001*
Flocksizes	*-0.0.1*	*0.001*	*<0.001*
Pair status New*Non-pair associates	0.01	0.05	0.793
Pair status Juveniles*Non-pair associates	0.03	0.06	0.579
*Pair status Divorced*Non-pair associates*	*0.56*	*0.09*	*<0.001*

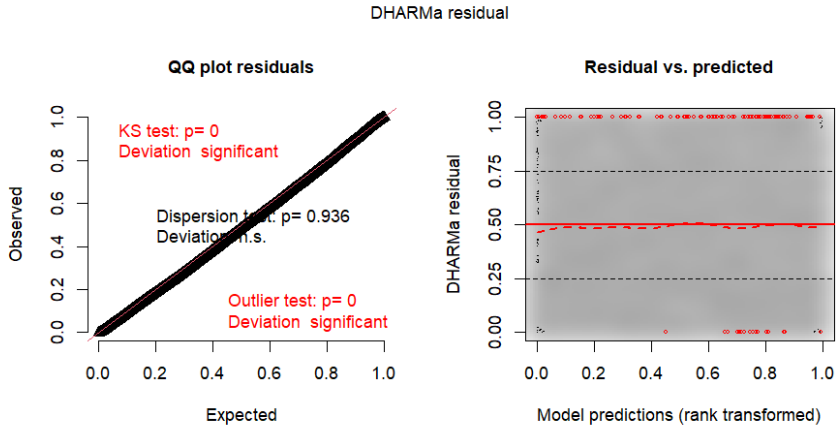

Figure A14: The residuals for a binomial GLMM model of the effect of pair type and pair status on winter association score. Residuals calculated using the DHARMa package (Hartig, 2022).

The model failed some residual assumption checks. However, a visual analysis suggests that this is due to the high sample size (n=20,388), so no permutation test was conducted.