REPRODUCTIVE CONSEQUENCES OF MATE RETENTION AND DIVORCE IN A SHORT-LIVED MIGRATORY PASSERINE

Daniel Ramírez Rodríguez-Solís[1], Iraida Redondo[1], Jesús Martínez-Padilla[2], Carlos Camacho[3], Jaime Potti[3], David Canal[1]

[1]Departament of Evolutionary Ecology, Museo Nacional de Ciencias Naturales (MNCN), CSIC, José Gutiérrez Abascal 2, E-28006 Madrid, Spain.

[2] Department of Biological Conservation and Ecosystem Restoration, Pyrenean Institute of Ecology (IPE-CSIC). Nuestra Señora de la Victoria, 16. 22700, Jaca, Spain.

[3] Department of Ecology and Evolution, Estación Biológica de Doñana (CSIC). Américo Vespucio, 26. 41092 Seville, Spain

*Corresponding author: Daniel Ramirez Rodriguez-Solis

* E-mail: daniel.ramirez@mncn.csic.es

Abstract

In socially monogamous birds, pair bond duration varies widely across species, from single-breeding associations to long-lasting, multi-year bonds. Studies on mate retention and divorce have predominantly focused on long-lived species, while research in short-lived and migratory species is limited. Consequently, the fitness consequences of divorce or remating in these species remain unclear. Here, we used a long term (1987–2023) and individual-based dataset to investigate the reproductive consequences of mate retention and divorce in pied flycatchers (*Ficedula hypoleuca*), a short-lived, long-distance migratory passerine. First, we described the overall patterns of divorce and remating within the population. Then, we analyzed whether reproductive success (laying date, clutch size and number of fledglings) differed between individuals that remate and those that divorce, while controlling for confounding factors, such as age or breeding dispersal. Specifically, we compared the reproductive consequences in the season before remating or divorce (year *t*) and the subsequent season (year *t+1*). We found that remating rates were low (3.52%) compared to divorces (26.8%), and both remained stable over the study period. In terms of reproductive performance, pair bond duration (remating vs. divorce) did not explain variation in laying date or clutch size. However, divorce was associated with an increase in the number of fledglings in the year following separation for both males and females, while remated individuals produced more fledglings in their first breeding season. The fitness consequences of divorce/remating persisted after accounting for confounding factors, supporting a direct influence of pairing status on reproductive success. These findings highlight the complex dynamics of mate relationships in short-lived migratory birds and emphasize the need for further research into the adaptive potential of pair-bond stability.

Key words: pair status, mate retention, breeding success, mate choice, pied flycatcher

Introduction

While social monogamy is the predominant mating system in birds, the duration of pair bond varies widely across species, from short associations limited to the parental care of a single breeding attempt to pair bonds that can last for multiple years (Black 1996, Kvarnemo 2018). The diversity in pair bond duration reflects the interplay between species-specific life-history strategies (e.g., investment in reproduction and survival) and ecological pressures (e.g., availability of breeding sites, food resources, predation risk), highlighting the importance of pair-bond strength in avian life histories. Since pair bond duration may strongly influence reproductive performance (Lack 1968, Bennett & Owens 2002), investigating its specific consequences on reproduction is essential to understanding its adaptive significance and evolutionary implications.

Retaining the same mate between successive breeding attempts may provide several advantages. Established pairs save the time and energy in finding a new partner and building a bond (Pampus *et al*. 2005, Gabriel & Black 2013, Culina *et al*. 2020, D'amelio *et al*. 2024). In addition, familiarity between partners can enhance their coordination in critical activities, as territory defense or offspring provisioning (Griggio & Hoi 2011, Gabriel & Black 2013, Sánchez-Macouzet *et al*. 2014, Culina *et al*. 2020, Botero-Delgadillo *et al*. 2024). Thus, remating may translate into increased reproductive success relative to newly formed pairs due to earlier breeding or higher fledgling success, although such benefits are not consistently supported (Rowley 1983, Choudhury 1995, Culina *et al*. 2015, Naves *et al*. 2007, Lv *et al*. 2016, Pitera *et al*. 2020, Dumas *et al*. 2024). Alternatively, individuals may switch mates between consecutive breeding seasons despite the former partner remaining alive, leading to "divorce". Divorce may arise from breeding dispersal or external constraints, such as differences in settlement time after migration, making it difficult for previous partners to overlap in space and time during the period of pair formation. Alternatively, divorce may result from adaptive decisions made by one or both pair members, as for example, when mate switching allows at least one member to improve their territory or mate quality (reviewed in Choudhury 1995).

Empirical studies on mate retention and divorce have primarily focused on long-lived species, while studies focused on short-lived and migratory species are much scarcer (e.g., Botero-Delgadillo *et al*. 2024). Yet, short- and long-lived species face distinct ecological pressures that may profoundly influence pair bond dynamics (Covas & Griesser 2007, Tarwater & Arcese 2017). Further, differences in reproductive performance between remated and divorced pairs may not be a consequence of the breeding strategy itself, but rather confounded by factors such as age or individual quality (Lv *et al*. 2016). For example, newly formed pairs may consist of young or low-quality individuals. However, longitudinal analyses controlling for those confounding factors are scarce in the literature (reviewed in Culina *et al*. 2015, Botero-Delgadillo *et al*. 2024, Dumas *et al*. 2024). Lastly, as explained above, divorce may be a consequence of mismatches in spatial or temporal arrival patterns from migration, rather than from active behavioral decisions (Choudhury 1995). Nevertheless, previous work has rarely differentiated these scenarios by considering all instances of divorce together (i.e., individuals overlapping or not spatiotemporally), which may bias our understanding of the adaptive value of mating strategies.

Here, we take advantage of a 36-year (1987–2023), individual-based dataset to investigate the reproductive consequences of mate retention and divorce in the pied flycatcher (*Ficedula hypoleuca*), a short-lived, long-distance migratory passerine. This study first explores the patterns of remating and divorce across the population. Subsequently, using a longitudinal framework, we assessed whether breeding success - measured as laying date, clutch size and number of fledglings the season before (year t) and after (year *t+1)* remating or divorce- differed between males and females based on their pairing status. Based on the literature (Choudhury 1995, Cézilly *et al*. 2000, Culina *et al*. 2015, Lv *et al*. 2016, Pitera *et al*. 2021, Botero-Delgadillo *et al*. 2024), we predict that divorce may be favored in the short term over remating due to the high mortality risk between breeding seasons, which could reduce the benefits of pair bond stability.

Materials and Methods

Ethical Note and Animal Care

Adults were captured during incubation or using a conventional spring trap, which is a harmless design (Friedman *et al*. 2008). Standardized ringing protocols and measurements were carried out for all captured individuals. We have a long experience in this procedure, the time required for it was restricted to a minimum (mostly less than 15 min), and it was carried out as cautiously and efficiently as possible.

All applicable international, national and/or institutional guidelines for the capture and ringing of animals were followed and the study was approved by the Spanish institutional authorities. Doñana Biological Station-CSIC and Autonomous Communities of Madrid and Castilla-La Mancha provided capture and ringing licences. Field procedures were approved by the CSIC Ethical Committee for the following projects (refs. PAC05-006-2, CGL2006-07481/BOS, CGL2009-10652, CGL2011-29694, CGL2014-55969-P and PID2022-141763NA-I00) and, more recently, by the Autonomous Community of Madrid (Ref.: PROEX 068.6/24 to DC) guaranteeing that they comply with Spanish and European legislation on the protection of animals used for scientific purposes.

Study species and population

The pied flycatcher is a small-sized (11-13 gr), hole-nesting, insectivorous passerine. It is a trans-Saharan migrant that breeds in the temperate forests of Eurasia (Lundberg & Alatalo 1992), occupying a wide variety of woodlands, both deciduous and coniferous. During the breeding season, pied flycatchers show sexual dimorphism in plumage, with females displaying a greyish-brown plumage in contrast to the black and white pattern of males (Lundberg & Alatalo 1992, Potti et al. 2014). Males arrive from the wintering areas before females, establish a territory around a nesting site, and try to attract a female. This species shows high natal and breeding philopatry (Camacho *et al*. 2013, 2016), is single-brooded and predominantly monogamous, although some males become socially polygamous (Lundberg & Alatalo 1992, Canal *et al*. 2020).

Data were collected between 1987 and 2023 in a population of pied flycatchers breeding in nest boxes near La Hiruela (41°04' N, 3°27' W, central Spain). The population occupies two distinct habitat plots that differ markedly in vegetation composition and structure: a deciduous oak forest covering 9.3 ha (*Quercus pyrenaica*), and a mixed coniferous plantation (predominantly *Pinus sylvestris)* of 4.8 ha, 1.1 km apart. There are 239 nest boxes, 156 in the oak forest and 83 in the coniferous plot, spaced approximately 20 ± 9.2 meters apart from one another. The study area and field methodologies have been described in detail elsewhere (Camacho *et al*. 2018, Potti *et al*. 2018).

General field procedures

Breeding season begins approximately the second week of April (before the first males arrive from migration) and ends in early July. During this period, we routinely check to monitor occupancy by pied flycatchers and other species (see Potti *et al.* 2021). Once a nest was occupied, we conducted daily inspections to record laying date (first laid egg), clutch size (typically, 5-7 eggs), and the number of fledglings (at 13 days old). Adult birds were captured during incubation (females) or while feeding the nestlings (both sexes) around 8 days post-hatching. The exact age of many individuals (ca. 53%) was known because all nestlings are ringed before fledging (Potti & Montalvo 1991) and local recruitment rate is among the highest reported for the species (on average 14% Potti & Montalvo 1991, Canal *et al.* 2014). Unringed individuals first caught as breeders were aged (yearling vs. older) and sexed based on plumage characteristics (Karlsson *et al.* 1986, Potti & Montalvo 1991) and marked for future identification. Morphological measurements were taken from all individuals following standardized protocols.

Statistical Analyses

We used a longitudinal approach to investigate the influence of mate retention or divorce on breeding performance of males and females. We built a dataset by selecting individuals that experienced either a remating or a divorce throughout their lifespan, which requires that individuals bred at least twice. Remating cannot occur if one of the pair members dies, leading to a widowed individual, or, even if both are alive, they do not coincide in space and time. Consequently, we categorized an individual as divorced only if the following two conditions were met: 1) the mate of the previous year was recorded in the following year(s), and 2) both former mates co-occurred in space and time. To account for the spatial and temporal factors in the chances of encountering former mates, we applied a spatio-temporal filter based on the mating patterns and spatial use of the species during the breeding season (Canal *et al.* 2012, Canal *et al.* 2020). According to these patterns, we only considered individuals as divorced when their previous mate bred within 10 days before or after them and within 100 m. After applying the filters above, and because each divorced pair member mates with a new individual, we generated two separate datasets: one focused on females, including 414 breeding attempts from 174 individuals, and another focused on males, including 414 breeding attempts from 167 individuals. The consequences of divorce or remate on laying date and clutch size were analyzed using the female dataset, while the analyses on the number of fledglings were run with both the male and female datasets.

We explored the role of age and breeding dispersal to explain the patterns of divorce and remating within the population. We first used a generalized linear mixed model (GLMM) with binomial distribution to test whether the frequency of remating and divorce events varied over the study period using year as predictor. Next, we investigated whether breeding dispersal between year *t* and year *t+1* (the year when the event was recorded) differed between divorced and remated individuals, under the assumption that longer dispersal distances should result in decreased fitness due to loss of site familiarity (Greenwood & Harvey 1982, Stamps 1995, Piper 2011). Linear mixed models (LMMs, Gaussian distribution) on breeding dispersal were fitted separately for males and females using the pair status of individuals as predictor (remated or divorce) and the individual identity as random factor.

To investigate the influence of mate retention or divorce on three breeding performance parameters —laying date (only females), clutch size (only females) and number of fledglings (both males and females)—we used linear and generalized mixed models. The models on laying date (LMM, Gaussian distribution) and clutch size (GLMM, Conway-Maxwell-Poisson distribution for under-dispersed counts) had the same predictors and random-effects structure. Predictors included in these models are the following: habitat type (two-level factor: oak vs. pine forest), pair status (two-level factor: remate vs. divorce), time (two-level factor: year *t* vs. year *t+1* relative to the remating or divorcing event) and the interaction between pair status and time. Time was included in the models to test the impact of remating or divorcing on breeding performance in the year preceding/following each type of event. It is well established that age and individual experience may influence the reproductive performance of individuals (Forslund & Pärt 1995, Fowler 1995). Although individuals in our study population show variation in the age of first reproduction (1-3 years; Potti & Montalvo 1991), the individuals included in the longitudinal analyses (selected based on the criteria outlined above) showed a very high correlation between age and age of first reproduction ($r= 0.9$, $p<0.001$), preventing to disentangle the effects of age and breeding experience on breeding performance. Consequently, we included only individual age (continuous variable) as predictor in the models. Female identity and year were included as random effects in both models, except for the clutch size model, where including both year and identity caused convergence issues. We therefore excluded year from the clutch size model, after verifying that excluding it yielded similar results to excluding identity (data not shown). The models on the number of fledglings (GLMM, Conway-Maxwell-Poisson distribution for under-dispersed counts) were fitted separately for males and females, and included as predictors pair status, time and their interaction as well as habitat, laying date, and the age of the individuals (female or male in their respective models). As random effects, we included female identity, male identity, year, and nest-box identity.

Sampling intensity was limited in the years 2001 and 2003, and therefore, these years were excluded from the analyses. During the long-term monitoring of this population, we have performed several nest manipulations (e.g., clutch/nestlings cross-fostering; Potti & Canal 2011, Camacho *et al*. 2016) that might affect breeding success. Thus, data from manipulated nests were also excluded from the analyses. Similarly, data from socially polygynous matings and from replacement clutches were excluded from analyses. Lastly, it is worth noting that some individuals re-paired after a year breeding apart, and some divorced individuals were not recorded in the following year (e.g., due to early breeding failure or failure to capture). Analyses including both remating and divorce events, even when not occurring in consecutive years, yielded qualitatively similar results to those based only on consecutive years (see Table 1 in Supplementary material).

All analyses were performed in R version 4.4.1 (R Core Team, 2022). To fit the GLMMs, we used the glmmTMB package (Brooks *et al*. 2017), version 1.1.10, while the lme4 package (Bates 2014), version 1.1.35.5, was used to fit the LMMs. During model diagnostics, we checked for residual normality and homoscedasticity with the package DHARMa (Hartig 2018), as well as for multicollinearity issues using the VIF function of car package (Fox & Weisberg 2019). Model diagnostics showed no deviations from model assumptions.

Results

Overall, we observed 69 events of pair retention in consecutive years over the study period, representing 3.52 % of all breeding events (including divorces and widowing cases). Only 5 of the remating pairs continued breeding a third breeding season but not any longer. The number of divorces was 525, representing 26.8% of all breeding events. After applying the spatio-temporal filter to consider only those divorces occurring despite previous mates co-occurring in space and time, the number of divorces was 92 cases (4.7% of all breeding events).

The frequency of remating events and divorces did not change over the study period (GLMM; p = 0.230; Fig. 1). Breeding dispersal distance between year *t* and year *t+1* was lower for remated than for divorced individuals (LMM; p < 0.001 for females and males). Among divorced individuals, females showed greater breeding dispersal distances than males (Fig. 2).

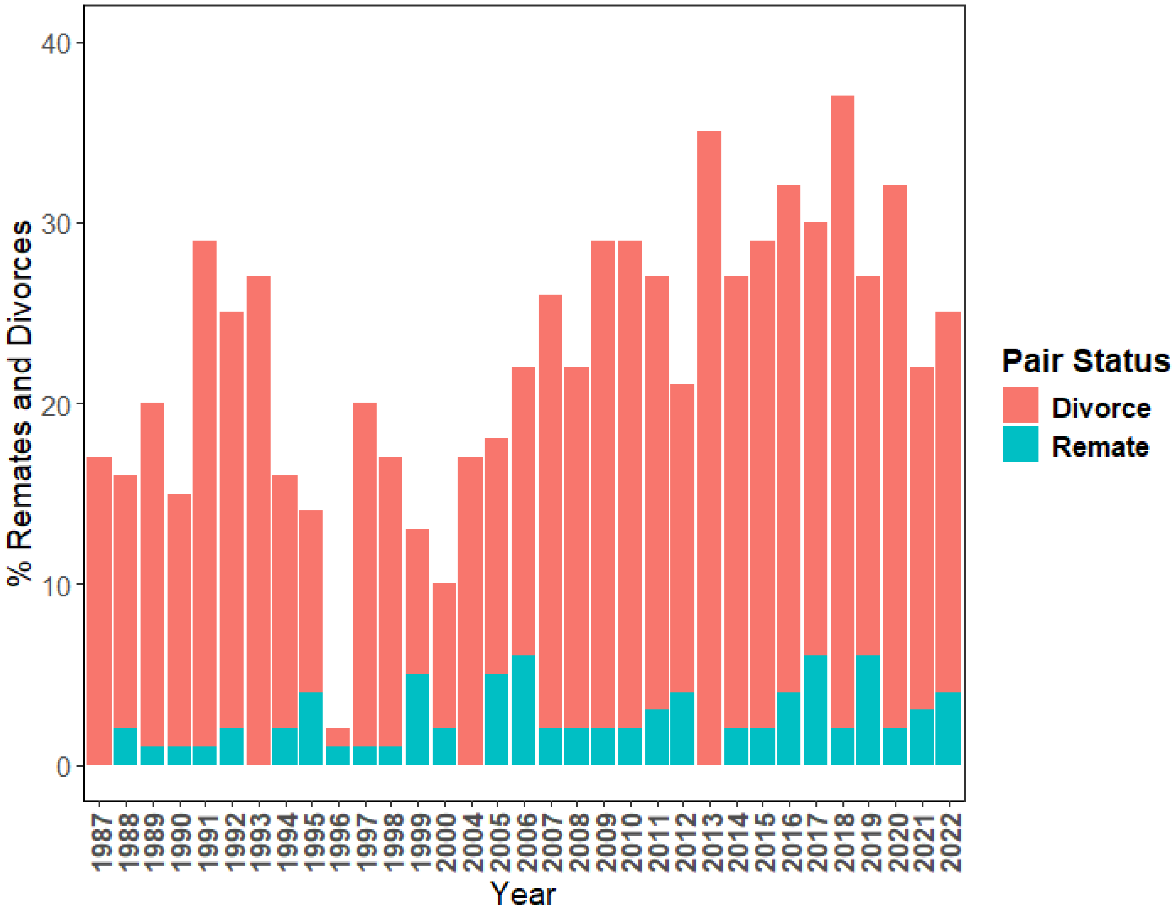

Figure 1. Frequency of remates and divorces over the study period. Data from 2023 (last study year) are excluded, as assessing divorces and remating events required information form subsequent years. Data are unavailable for 1987 (the first study year), 2001-2003 (due to limited fieldwork), and 2004 (first study year after the 2001-2003 break). See main text for further details.

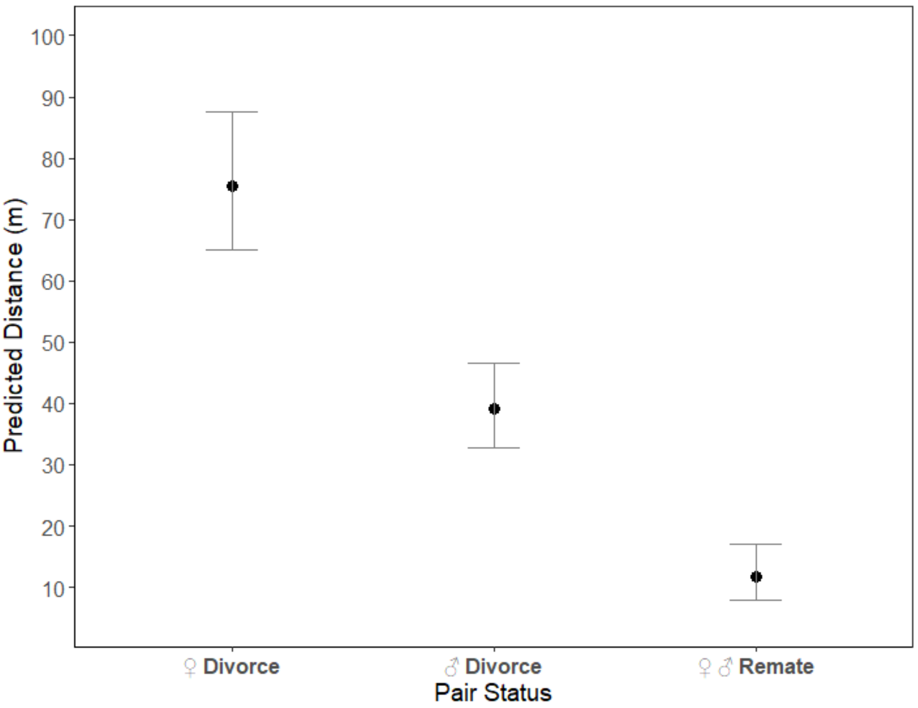

Figure 2. Breeding distance (mean ± standard error) between year *t* and year *t+1* for divorced females (left), divorced males (center) and remating pairs (right).

We found no significant effect of pair status (remating vs. divorcing) neither of its interaction with time (year *t* vs. year *t+1*) on laying date (Table 1a) nor on clutch size (Table 1b). Instead, laying date was influenced by age, with individuals breeding earlier as their age increased, while clutch size was negatively related to laying date and differed between habitats (oak>pine). However, in the models on the number of fledglings, we found an interactive effect between pair status and time (Table 1c-d) in both males and females. This effect was driven by a positive impact of mate switching on the number of fledglings in the year following divorce, whereas individuals retaining the same mate tended to produce fewer fledglings (Fig. 1). The number of fledglings was also influenced by laying date and habitat (oak >pine) in both sexes.

Table 1. Results of the models analyzing the influence of pair status (mate retention or divorce) on laying date (LMM), clutch size and number of fledglings (both GLMM). The table presents estimated coefficients (β) and standard errors (SE) derived from the model. P-values were calculated via ANOVA type II due to the presence of interaction terms.

a) Laying date			N = 322
Random effects	**σ^2**	**SD**	
Female identity	9.925	3.150	

Year	11.190	3.345		
Fixed effects	**β**	**SE**	**Wald X^2**	**P value**
Intercept	21.479	1.142		
Pair status (remate)	-0.019	0.833	0.073	0.787
Habitat (pine)	0.976	0.710	1.894	0.169
Time (*t+1*)	-1.106	0.700	2.812	0.094
Age	-1.153	0.287	16.120	**0.001**
Pair status (remate) *Time (*t+1*)	0.370	0.988	0.140	0.708

b) Clutch size				N = 322
Random effects	**σ^2**	**SD**		
Female identity	0.004	0.061		
Fixed effects	**β**	**SE**	**Wald X^2**	**P value**
Intercept	1.810	0.031		
Laying date	-0.007	0.001	37.678	**0.001**
Pair status (remate)	0.032	0.018	1.806	0.179
Habitat (pine)	-0.041	0.014	8.253	**0.004**
Time (*t+1)*	0.027	0.015	1.732	0.188
Age	0.008	0.006	1.593	0.207
Pair status (remate) *Time (*t+1*)	-0.026	0.022	1.352	0.245

c) Number of fledglings (females)				N = 317
Random effects	**σ^2**	**SD**		
Year	0.002	0.048		
Female identity	0.006	0.074		
Male identity	0.001	0.001		
Nestbox identity	0.004	0.066		
Fixed effects	**β**	**SE**	**Wald X^2**	**P value**

Intercept	1.711	0.079		
Laying date	-0.008	0.003	8.992	**0.003**
Pair status (remate)	0.059	0.041	0.009	0.926
Habitat (pine)	-0.114	0.032	13.050	**0.001**
Time (*t+1*)	0.074	0.038	0.619	0.431
Age female	-0.002	0.013	0.026	0.871
Age male	0.002	0.012	0.023	0.879
Pair status (remate) *Time (*t+1*)	-0.119	0.054	4.812	**0.028**

d) Number of fledglings (males) N = 320

Random effects	**σ^2**	**SD**
Year	0.005	0.069
Female identity	0.001	0.001
Male identity	0.001	0.023
Nestbox identity	0.001	0.001

Fixed effects	**β**	**SE**	**Wald χ^2**	**P value**
Intercept	1.684	0.078		
Laying date	-0.007	0.003	7.394	**0.007**
Pair status (remate)	0.057	0.042	0.063	0.802
Habitat (pine)	-0.120	0.029	16.711	**0.001**
Time (*t+1*)	0.078	0.038	0.738	0.390
Age female	0.001	0.012	0.009	0.924
Age male	0.007	0.012	0.325	0.569
Pair status (remate) *Time (*t+1*)	-0.126	0.057	4.832	**0.028**

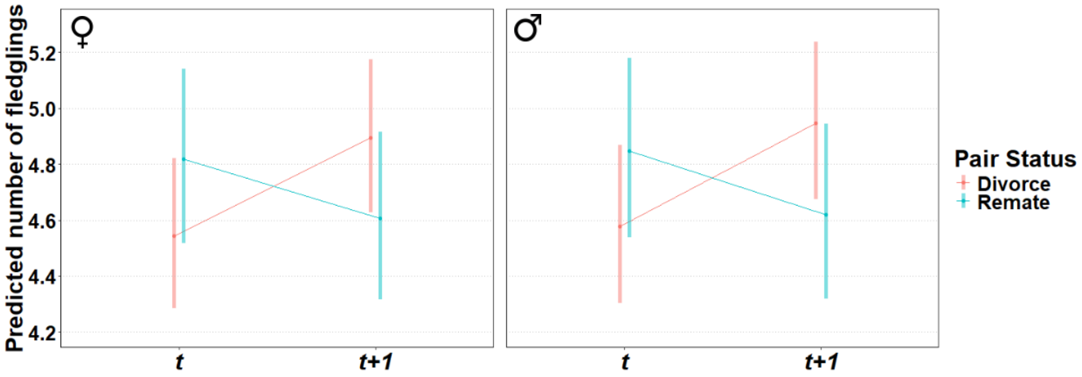

Figure 3. Number of fledglings (mean ± standard error) produced by females (left panel) and males (right panel) in relation to the pair status (remating or divorce) and time (year t vs t+1).

Discussion

Using a long-term and individual-based dataset spanning four decades, we analyzed the reproductive consequences of remating and divorce in pied flycatchers (*Ficedula hypoleuca*), a long-distance migratory and short-lived passerine, while controlling for confounding factors such as habitat type, breeding dispersal or individual age. We showed that pair status (remating vs. divorce) had no effect on laying date or clutch size but found a positive impact of mate switching on fledgling numbers in the year following divorce in both males and females.

Most research examining the consequences of pair retention and divorce has concentrated on long-lived species, resulting in limited understanding of these processes in short-lived and migratory species (Choudhury 1995, Culina *et al*. 2015, Botero-Delgadillo *et al*. 2024, but see Dumas *et al*. 2024). We found a positive influence of divorce on the number of fledglings, which increased in the year following divorce compared to remated pairs for both females and males. The observed improvement in reproductive success after divorcing aligns with findings from a previous metanalysis (Culina *et al.* 2015), suggesting that the benefits of mate switching might outweigh the potential costs, such as the energy and time needed to find a new mate or the risk of missing a breeding attempt. Although comprehensively testing these costs are out of the scope of this study, some characteristics of the study population, including high breeding synchrony and density (i.e., several potential mates may be available at short distances; Canal *et al.* 2020, Morales-Mata 2022), as well as a low probability of skipping breeding seasons (over 95% individuals breed continuously until death once they enter the breeding pool), likely minimize the cost associated with finding new mates. The positive effects of divorce on reproductive performance may stem from increased compatibility with the new mate or the acquisition of a breeding site or mate of higher quality (Montalvo & Potti 1992, Blondel *et al*. 2000, Cézilly *et al*. 2000, García-Navas & Sanz 2011). In relation to the latter idea, an interesting possibility is that the observed reproductive patterns related to breeding status may be (partially) driven by assortative mating. High-quality individuals, more likely to pair together, may have lower divorce rates due to limited opportunities to improve mate quality, whereas low-quality pairs may experience higher rates of mate switching, with one or both partners seeking improvement. This is supported by the fact that, in year *t*, reproductive success (number of fledglings) was higher for pairs that subsequently remained together compared to those that divorced in the following year. Overall, regardless of the underlying drivers, our results suggest that divorce may represent an adaptive strategy, potentially improving reproductive success after separation (Linden 1991, Dhondt & Adriaensen 1994, García-Navas & Sanz 2011, Culina *et al*. 2015). Future research evaluating the long-term fitness consequences of divorce or remating, such as survival prospects and offspring quality (e.g., offspring's lifetime reproductive success), are necessary steps to clarify the adaptive potential of these alternative strategies.

The potential reproductive benefits of pair-bond strength may be confounded by factors such as age, habitat quality or familiarity. Age is widely recognized as a crucial predictor of reproductive success, as long-term survival is itself an indicator of intrinsic individual quality, with older individuals typically possessing better territories and having superior foraging skills (Fowler 1995, Pärt 1995, Hatch & Westneat 2007). Further, early breeding, which is primarily age-dependent in migratory birds (e.g., Smith & Moore 2005, Stewart *et al*. 2002, Canal *et al*. 2020), is commonly associated with reproductive success in this and other temperate-region migratory birds (Newton 2008, Pitera *et al*. 2020). In line with these ideas, we found significant effects of age and/or laying date in most models, highlighting their importance in the reproductive success of individuals. Regarding habitat familiarity, divorced individuals dispersed farther between seasons (*t* vs *t*+1: on average of 76 m and 39 m in divorced females and males, respectively) compared to remating individuals (17 m), yet showed higher reproductive success in the year following divorce (*t*+1). Although dispersal distances were relatively small and habitat conditions likely did not change markedly between consecutive years, breeding dispersal itself entails additional energetic and time costs, such as locating and defending suitable nesting, foraging sites and repelling aggressions from prior residents. Thus, that fitness increased among divorced individuals despite the potential costs of dispersing longer distances point to an independent effect of pair status on the reproductive performance of individuals. It is also worth noting that divorce or, alternatively absence of remating, may simply result from asynchronous arrival at the breeding grounds or long-distance breeding dispersal, rather than being a reproductive strategy of at least one pair member. To address this confounding effect, and unlike most previous studies, we applied a spatiotemporal filter based on the species' behavior, to exclude cases where both pair members survived but did not coincide in space or time in the subsequent season, making remating virtually impossible (Gilsenan *et al*. 2017). Overall, the fact that fitness consequences of divorce/remating were detected after accounting for these confounding factors further support the direct influence of pairing status (divorced or remated) on breeding performance.

The apparent reproductive advantages associated with divorce compared to pairs remating raise the question of why remating persists, even at low frequency, in the population. In long-lived or non-migratory species, pair retention offers clear benefits, such as reduced mate-searching costs and increased cooperation (Bradley *et al*. 1990, Griggio & Hoi 2011, Gabriel & Black 2013, Sánchez- Macouzet *et al*. 2014, Culina *et al*. 2020, D'amelio *et al*. 2024). However, in short-lived, long-distant migratory species such as the pied flycatcher, the probability that both pair members survive to the next breeding season may be low. Consequently, selection may not favor mate retention, as the time and energy costs of waiting for a mate that might not return are high (Choudhury 1995). However, the persistence of remating in the study population could be explained by benefits beyond the immediate reproductive parameters analyzed here (e.g., survival or offspring quality, rather than quantity), which could lead to weak selection pressure for divorcing over remating, thus allowing both strategies to coexist. Alternatively, given the low breeding dispersal distance observed in the population, particularly in remated pairs (17m with several pairs breeding in the same nest), remating could simply result from site fidelity or from stochastic processes, such as local encounter rates with the previous mate, rather than being an adaptive behavior (Montalvo & Potti 1992). Indeed, the relatively low and stable frequency of remating in the population over the study period, despite these short breeding dispersal distances, could suggest some level of avoidance of former partners, though further research is needed to evaluate this possibility.

Conclusions

Using an individual-based dataset from a short-lived, long-distant migratory passerine, we found evidence that divorce improved reproductive success (number of fledglings) in the year following separation relative to individuals retaining the same pair between breeding seasons, which performed better in their initial breeding compared to divorced individuals. These findings underscore the complex dynamics of mate relationships in short-lived migratory birds and highlight key areas for investigation: i) Behavioural observations to investigate the mechanisms underlying divorce (e.g., whether it is initiated by a pair member or forced by a third party) and its reproductive consequences (e.g., acquisition of a better territory or mate); ii) experimental approaches to manipulate costs and benefits of each breeding strategy, and iii) studies of their long-term consequences (e.g., offspring performance) as well as iv) studies of the genetic bases of divorce and remating and its evolutionary potential are promising avenues of research.

Acknowledgments

We would like to thank all the people who helped us in the field over the four decades of study. Permission for working in protected areas was granted by the Consejerías de Medio Ambiente de la Comunidad de Madrid and Comunidad de Castilla-La Mancha. Over the years, this research received support from projects CGL2006-07481/BOS (to J.C. Senar), CGL2009-10652 (to J.C. Senar), CGL2011-29694 (to J. Potti), CGL2014-55969-P (to F. Valera) and PID2019-104835GB-I00 (to J. Martinez-Padilla) from the Spanish Ministry of Science. More recently, this work has been supported by the Autonomous Community of Madrid (CAM), Spain (project: 2022-T1_AMB-24025 to David Canal) and the MCIN/AEI/10.13039/501100011033 (projects: PID2022-141763NA-I00 to David Canal and PID2022-138133NB-I00 to J. Martinez-Padilla). D.R was supported within the project PID2022-141763NA-I00 and the grant JAE intro (JAEINT_23_00500), both funded by MCIN/AEI. I.R was supported within the project 2022-T1_AMB-24025 funded by CAM. J. CC was supported by the grant ref. RYC2021-033977-I funded by MCIN/AEI and the European Union NextGenerationEU/PRTR. D.C. received support from a CAM Talent Attraction grant associated with project 2022-T1_AMB-24025 and the project PID2022-141763NA-I00 funded by MCIN/AEI.

Bibliography

Bates, D. (2014) Fitting linear mixed-effects models using lme4. *arXiv preprint*, arXiv:1406.5823.

Bennett, P.M. & Owens, I.P. (2002) *Evolutionary ecology of birds: life histories, mating systems, and extinction*. Oxford University Press.

Black, J.M. (Ed.) (1996) *Partnerships in birds: the study of monogamy*. Oxford University Press, UK.

Blondel, J., Perret, P. & Galan, M.J. (2000) High divorce rates in Corsican blue tits: how to choose a better option in a harsh environment. *Oikos*, 89, 451–460.

Botero-Delgadillo, E., Vásquez, R.A. & Kempenaers, B. (2024) Assessing the reproductive consequences of mate retention and pair bond duration in Thorn-tailed Rayadito (*Aphrastura spinicauda*), a short-lived, socially monogamous neotropical bird. *Ibis*, 166, 396–410.

Bradley, J.S., Wooller, R.D., Skira, I.J. & Serventy, D.L. (1990) The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *Journal of Animal Ecology*, 59, 487–496.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. & Bolker, B.M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Camacho, C., Canal, D. & Potti, J. (2013) Nonrandom dispersal drives phenotypic divergence within a bird population. *Ecology and Evolution*, 3, 4841–4848.

Camacho, C., Canal, D. & Potti, J. (2016) Natal habitat imprinting counteracts the diversifying effects of phenotype-dependent dispersal in a spatially structured population. *BMC Evolutionary Biology*, 16, 123.

Camacho, C., Pérez-Rodríguez, L., Abril-Colón, I., Canal, D. & Potti, J. (2018) Plumage colour predicts dispersal propensity in male pied flycatchers. *Behavioral Ecology and Sociobiology*, 72, 2.

Canal, D., Jovani, R. & Potti, J. (2012) Multiple mating opportunities boost protandry in a pied flycatcher population. *Behavioral Ecology and Sociobiology*, 66, 67–76.

Canal, D., Serrano, D. & Potti, J. (2014) Exploring heterozygosity-survival correlations in a wild songbird population: contrasting effects between juvenile and adult stages. *PLoS One*, 9, e105020.

Canal, D., Schlicht, L., Manzano, J., Camacho, C. & Potti, J. (2020) Socio-ecological factors shape the opportunity for polygyny in a migratory songbird. *Behavioral Ecology*, 31, 598–609.

Cézilly, F., Dubois, F. & Pagel, M. (2000) Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiforms. *Animal Behaviour*, 59, 1143–1152.

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

Covas, R. & Griesser, M. (2007) Life history and the evolution of family living in birds. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1349–1357.

Culina, A., Radersma, R. & Sheldon, B.C. (2015) Trading up: the fitness consequences of divorce in monogamous birds. *Biological Reviews*, 90, 1015–1034.

Culina, A., Firth, J.A. & 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, 20201554.

D'amelio, P.B., Covas, R., Ferreira, A.C., Fortuna, R., Silva, L.R., Theron, F. et al. & Doutrelant, C. (2024) Benefits of Pair-Bond Duration on Reproduction in a Lifelong Monogamous Cooperative Passerine. *The American Naturalist*, 203, 576–589.

Desrochers, A., & Magrath, R. D. (1993) Environmental predictability and remating in European blackbirds. *Behavioral Ecology*, 4(3), 271–272.

Dhondt, A. A., & Adriaensen, F. (1994) Causes and effects of divorce in the blue tit *Parus caeruleus*. *Journal of Animal Ecology*, 979–987.

Dubois, F., & Cézilly, F. (2002) Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*, 52, 357–364.

Dumas, M.N., Meier, C.M., Bize, P., & Martin, J.G.A. (2024) Who Keeps the House after Divorcing? Partner and Nest Fidelity in the Long-Lived Alpine Swift. *The American Naturalist*, in press; https://doi.org/10.1086/733307.

Forslund, P., & Pärt, T. (1995) Age and reproduction in birds—hypotheses and tests. *Trends in Ecology & Evolution*, 10(9), 374–378.

Fowler, G. S. (1995) Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist*, 35(4), 318–328.

Fox, J., & Weisberg, S. (2019) Using car functions in other functions. CRAN R.

Friedman, S. L., Brasso, R. L., & Condon, A. M. (2008) An improved, simple nest-box trap. *Journal of Field Ornithology*, 79(1), 99–101.

Gabriel, P. O., & Black, J. M. (2013) Correlates and consequences of the pair bond in Steller's Jays. *Ethology*, 119(2), 178–187.

García-Navas, V., & Sanz, J. J. (2011) Females call the shots: breeding dispersal and divorce in blue tits. *Behavioral Ecology*, 22(5), 932–939.

Gilsenan, C., Valcu, M., & Kempenaers, B. (2017) Difference in arrival date at the breeding site between former pair members predicts divorce in blue tits. *Animal Behaviour*, 133, 57–72.

González-Solís, J., Becker, P. H., & Wendeln, H. (1999) Divorce and asynchronous arrival in common terns, *Sterna hirundo*. *Animal Behaviour*, 58(5), 1123–1129.

Greenwood, P. J., & Harvey, P. H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, 13, 1–21.

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(6), 1329–1335.

Hartig, F. (2018) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 020.

Hatch, M. I., & Westneat, D. F. (2007) Age-related patterns of reproductive success in house sparrows *Passer domesticus*. *Journal of Avian Biology*, 38(5), 603–611.

Huang, A. (2017) Mean-parametrized Conway–Maxwell–Poisson regression models for dispersed counts. *Statistical Modelling*, 17(6), 359–380.

Karlsson, L., Persson, K., & Walinder, G. (1986) Ageing and sexing in pied flycatchers, *Ficedula hypoleuca*. *Vår Fågelvärld*, 45, 131–146.

Kikkawa, J., & Wilson, J. M. (1983) Breeding and dominance among the Heron Island Silvereyes *Zosterops lateralis chlorocephala*. *Emu-Austral Ornithology*, 83(3), 181–198.

Kvarnemo, C. (2018) Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy. *Biological Reviews*, 93(4), 1795–1812.

Lack, D. (1968) *Ecological adaptations for breeding in birds* (Vol. 33). Methuen and Company, London.

Liker, A., Freckleton, R. P., & Székely, T. (2014) Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology*, 24(8), 880–884.

Linden, M. (1991). Divorce in great tits, chance or choice? An experimental approach. *The American Naturalist*, 138(4), 1039–1048.

Llambías, P. E., Wrege, P., & Winkler, D. W. (2008). Effects of site fidelity and breeding performance on mate retention in a short-lived passerine, the tree swallow *Thachycineta bicolor*. *Journal of Avian Biology*, 39(5), 493–499.

Lundberg, A., & Alatalo, R. V. (1992). *The pied flycatcher*. Poyser, London.

Lv, L., Komdeur, J., Li, J., Scheiber, I. B., & Zhang, Z. (2016). Breeding experience, but not mate retention, determines the breeding performance in a passerine bird. *Behavioral Ecology*, 27(4), 1255–1262.

Montalvo, S., & Potti, J. (1992). Breeding dispersal in Spanish pied flycatchers *Ficedula hypoleuca*. *Ornis Scandinavica*, 491–498.

Morales-Mata, J. I., Potti, J., Camacho, C., Martínez-Padilla, J., & Canal, D. (2022). Phenotypic selection on an ornamental trait is not modulated by breeding density in a pied flycatcher population. *Journal of Evolutionary Biology*, 35(4), 610–620.

Møller, A. P. (1986). Mating systems among European passerines: a review. *Ibis*, 128(2), 234–250.

Morrison, C. A., Alves, J. A., Gunnarsson, T. G., Þórisson, B., & Gill, J. A. (2019). Why do earlier-arriving migratory birds have better breeding success? *Ecology and Evolution*, 9(15), 8856–8864.

Naves, L. C., Cam, E., & Monnat, J. Y. (2007). Pair duration, breeding success and divorce in a long-lived seabird: benefits of mate familiarity? *Animal Behaviour*, 73(3), 433–444.

Newton, I. (2008). *The ecology of bird migration*. Academic Press, London.

Pampus, M., Schmidt, K. H., & Wiltschko, W. (2005). Pair bond and breeding success in blue tits *Parus caeruleus* and great tits *Parus major*. *Ibis*, 147(1), 92–108.

Pärt, T. (1995). Does breeding experience explain increased reproductive success with age? An experiment. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 260(1357), 113–117.

Piper, W. H. (2011). Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology*, 65, 1329–1351.

Potti, J., & Montalvo, S. (1991). Male arrival and female mate choice in pied flycatchers *Ficedula hypoleuca* in central Spain. *Ornis Scandinavica*, 45–54.

Potti, J., & Canal, D. (2011). Heritability and genetic correlation between the sexes in a songbird sexual ornament. *Heredity*, 106(6), 945–954.

Potti, J., Canal, D., & Serrano, D. (2013). Lifetime fitness and age-related female ornament signalling: evidence for survival and fecundity selection in the pied flycatcher. *Journal of Evolutionary Biology*, 26(7), 1445–1457.

Potti, J., Canal, D., & Camacho, C. (2014). Ontogenetic variation in the plumage colour of female European Pied Flycatchers *Ficedula hypoleuca*. *Ibis*, 156(4), 879–884.

Potti, J., Camacho, C., Canal, D., & Martinez-Padilla, J. (2018). Long-term occupancy of nest boxes as a measure of territory quality for Pied Flycatchers. *Journal of Field Ornithology*, 89(4), 337–347. https://doi.org/10.1111/jofo.12266

Potti, J., Camacho, C., Canal, D., & Martínez-Padilla, J. (2021). Three decades of crimes and misdemeanours in the nest box life of European pied flycatchers *Ficedula hypoleuca*. *Ardeola*, 68(2), 315–333. https://doi.org/10.13157/arla.68.2.2021.ra1

Reichard, U. H., & Boesch, C. (Eds.). (2003). *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press.

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(1786), 20132843.

Slagsvold, T., Lifjeld, J. T., Stenmark, G., & Breiehagen, T. (1988). On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Animal Behaviour*, 36(2), 433–442.

Slagsvold, T., & Dale, S. (1991). Mate choice models: can cost of searching and cost of courtship explain mating patterns of female pied flycatchers? *Ornis Scandinavica*, 319–326.

Smith, R. J., & Moore, F. R. (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology*, 57, 231–239.

Stamps, J. (1995). Motor learning and the value of familiar space. *The American Naturalist*, 146(1), 41–58.

Stewart, R. L., Francis, C. M., & Massey, C. (2002). Age-related differential timing of spring migration within sexes in passerines. *The Wilson Bulletin*, 114(2), 264–271.

Tarwater, C. E., & Arcese, P. (2017). Age and years to death disparately influence reproductive allocation in a short-lived bird. *Ecology*, 98, 2248–2254.

Supplementary Material.

Table 1. Results of the models analyzing the influence of pair status (mate retention or divorce) on laying date (LMM), clutch size and number of fledglings (both GLMM) including remating (n=81) and divorces (n=152) events that did not occur in consecutive years (e.g., because some individuals re-paired after one or more years breeding apart or because some divorced individuals were not recorded in the following year). The table presents estimated coefficients (β) and standard errors (SE) derived from the model. P-values were calculated via ANOVA type II due to the presence of interaction terms.

a) Laying date			N = 461
Random effects	**σ^2**	**SD**	

Female identity	10.04	3.168		
Year	14.30	3.781		
Fixed effects	**β**	**SE**	**Wald χ^2**	**P value**
Intercept	20.510	1.029		
Pair status (remate)	-0.724	0.685	0.394	0.530
Habitat (pine)	1.969	0.528	11.169	**0.001**
Time (*t+1*)	-1.398	0.589	6.486	**0.011**
Age	-0.864	0.230	14.126	**0.001**
Pair status (remate) *Time (*t+1*)	0.7460	0.822	0.824	0.364

b) Clutch size N = 461

Random effects	**σ^2**	**SD**		
Female identity	0.002	0.047		
Year	0.001	0.014		
Fixed effects	**β**	**SE**	**Wald χ^2**	**P value**
Intercept	1.824	0.027		
Laying date	-0.007	0.001	47.768	**0.001**
Pair status (remate)	0.022	0.017	1.768	0.184
Habitat (pine)	-0.034	0.007	7.207	**0.007**
Time (*t+1)*	0.015	0.014	0.981	0.322
Age	0.005	0.005	1.120	0.290
Pair status (remate) *Time (*t+1*)	-0.010	0.022	0.209	0.647

c) Number of fledglings (females) N = 456

Random effects	**σ^2**	**SD**
Year	0.002	0.049
Female identity	0.013	0.113
Male identity	0.001	0.001
Nest-boxes	0.001	0.016

Fixed effects	**β**	**SE**	**Wald χ^2**	**P value**
Intercept	1.698	0.066		
Laying date	-0.008	0.002	14.578	**0.001**
Pair status (remate)	0.054	0.036	0.145	0.703
Habitat (pine)	-0.082	0.028	8.777	**0.003**
Time (*t+1*)	0.061	0.029	1.716	0.190
Age female	-0.013	0.011	1.267	0.260
Age male	0.012	0.010	1.479	0.224
Pair status (remate) *Time (*t+1*)	-0.085	0.046	3.382	0.066

d) Number of fledglings (males) N = 461

Random effects	**σ^2**	**SD**
Year	0.003	0.054
Female identity	0.006	0.078
Male identity	0.001	0.001
Nest-boxes	0.001	0.001

Fixed effects	**β**	**SE**	**Wald χ^2**	**P value**
Intercept	1.606	0.068		
Laying date	-0.006	0.002	6.444	**0.011**
Pair status (remate)	0.056	0.037	0.207	0.649
Habitat (pine)	-0.066	0.026	6.385	**0.012**
Time (*t+1*)	0.061	0.031	1.358	0.244
Age female	0.007	0.011	0.464	0.496
Age male	0.005	0.010	0.240	0.624
Pair status (remate) *Time (*t+1*)	-0.089	0.051	2.991	0.083