

## Go your own way? Reasons for divorce in a monogamous seabird

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Pair bond duration is usually associated with reproductive success in long-lived monogamous species, yet pairs sometimes divorce. Possible explanations for divorce include having access to a higher-quality partner or territory, selecting a more compatible partner, asynchronous arrival at the breeding site or displacement of one member of a pair by an intruder. Factors influencing the occurrence of divorce are still unknown for many bird species, although divorce is often associated with low reproductive success in the preceding year. The thick-billed murre, *Uria lomvia*, is a colonial long-lived seabird species that has biparental care and undergoes occasional divorce. In this study, we investigated factors influencing the occurrence of divorce as well as the impact of divorce on subsequent reproductive success using data collected over 24 years at a breeding colony on Coats Island (Nunavut, Canada). Yearly divorce rate averaged 9%. The probability of divorce decreased with breeding experience/age, nest site quality and successful fledging in the previous year. Both sexes initiated divorce. Divorced birds did not obtain a better partner or improve their nesting site quality. Divorce seemed to be triggered by low reproductive success rather than a new partner or nesting site opportunity. Finally, an initial reduction of reproductive success was found for birds that divorced. Our findings help to understand the triggers and consequences of mate changes in long-lived monogamous species.

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Many long-lived species form socially monogamous pair bonds that can last one or more consecutive breeding seasons (Black, 1996; Bried et al., 2003; Dubois et al., 1998; Kvarnemo, 2018). Staying faithful to a partner allows individuals to save time and energy that would otherwise be used to secure a new partner (Bried & Jouventin, 2002). Individuals can maximize reproductive success by adopting either compatible or similar behaviour (e.g. nest building: Griggio & Hoi, 2011; chick provisioning: Mariette & Griffith, 2015; Gabriel & Black, 2012; Spoon et al., 2006). For animals with biparental care and lasting pair bonds, selecting a mate is a crucial decision for lifetime reproductive success (Ausband, 2019; Black, 1996; Griffith, 2019; Reichard & Boesch, 2003). The fitness of both mates is jointly affected not only by the reproductive abilities of each, but also by how the mates coordinate their efforts (Wagner et al., 2019). For example, in thick-billed murres, *Uria lomvia*, 'risky' individuals that pair with 'riskless' individuals have higher recruitment than those that pair with 'risky' individuals (Elliott et al., 2010). Similarly, pair bond duration has strong potential to

enhance the reproductive performance of pair members through increased pair familiarity, coordination and cooperation within the pair (Black, 2001; Griffith, 2019; Naves et al., 2007; Sánchez-Macouzet et al., 2014; Wiley & Ridley, 2018). For example, breeding success increases with pair duration in black-legged kittiwakes, *Rissa tridactyla* (Naves et al., 2007). Despite the advantages that long-term pair bonds provide, individuals sometimes change partners (divorce) within or between breeding seasons.

Divorce occurs when (1) both partners are still alive and (2) subsequent breeding attempts (if any) of at least one bird is with a new partner (Choudhury, 1995). Mechanisms of divorce have been theorized in several studies (e.g. Lerch et al., 2022; McNamara et al., 1999; McNamara & Forslund, 1996). Divorce has been recorded in 92% of socially monogamous bird species where it has been studied, but the proportion of individuals divorcing varies considerably among species (Black, 1996; Choudhury, 1995; Culina, Radersma, et al., 2015; Jeschke & Kokko, 2008). Some bird species have a divorce rate as high as 100% between years (Dubois & Cézilly, 2002). Divorce has also been reported in monogamous species of mammals (Lardy et al., 2011; Mayer et al., 2017), fishes (Snekser & Itzkowitz, 2019; van Breukelen & Draud, 2005), crustaceans

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(Galipaud et al., 2015) and endoparasites (Beltran et al., 2009). Individuals are expected to divorce when the fitness benefits of divorce outweigh the costs, which is likely to be species specific and related to life-history traits (Choudhury, 1995). Females more often benefit from a partner change than males and commonly initiate the divorce, as male quality is typically more variable than female quality (Culina, Lachish, et al., 2015; Dhondt, 2002; García-Navas & Sanz, 2011). Nevertheless, variation in divorce rate and reasons for divorce are often unclear and vary within and between bird species.

Several nonmutually exclusive hypotheses have been proposed to explain divorce in bird (Black, 1996; Choudhury, 1995). Individuals may divorce to increase their reproductive success with a new partner that may be (1) more compatible (incompatibility hypothesis; Coulson, 1966) or (2) of higher quality (better option hypothesis; Ens et al., 1993). In these cases, divorce is often associated with recent poor reproductive performance and subsequent improvements in reproductive success (Black, 1996; Choudhury, 1995; Halimubieke et al., 2020). Indeed, two separate meta-analyses found an overall higher divorce rate in pairs with low breeding success (Culina, Radersma, et al., 2015; Dubois & Cézilly, 2002). Divorce can also be (3) a side-effect of asynchronous arrival and settlement at a pair's breeding site or territory (musical chairs hypothesis; Dhondt & Adriaensen, 1994) or (4) a result of a stochastic disturbance that separates the mates (e.g. poor environmental conditions during migration; Owen et al., 1988). Finally, divorce may not be initiated by either pair member, but instead (5) one member is displaced by the intrusion of a third individual (forced divorce hypothesis, Choudhury, 1995; Taborsky & Taborsky, 1999). Indeed, divorce in wandering albatrosses, *Diomedea exulans*, did not increase reproductive success and was related to the intrusion of an individual who outcompeted the original partner (Sun et al., 2022).

Many factors influence the incidence of divorce within populations and species. Divorce rates may be high when mortality rates are high because more unpaired but experienced mates are available (Jeschke & Kokko, 2008; Moody et al., 2005). Other factors such as poor breeding site quality (Blondel et al., 2000; Heg et al., 2003), variable environmental conditions (e.g. high temperature; Halimubieke et al., 2020; Ventura et al., 2021), low food availability (Pelletier & Guillemette, 2022) and young or inexperienced breeders (Culina, Hinde, et al., 2015) are also associated with a higher incidence of divorce.

Compared to other birds, seabirds usually have low to moderate divorce rates. For example, the divorce rate is estimated at 8% in common murre, *Uria aalge* (Moody et al., 2005), 3% in glaucous gulls, *Larus hyperboreus* (Mercier et al., 2021), and 7% in Cassin's auklet, *Ptychoramphus aleuticus* (Sydeman et al., 1996). As species with obligate biparental care and social monogamy, seabirds benefit from choosing the most adept and helpful available mate to increase their reproductive success (Bried & Jouventin, 2002). Being long-lived species, seabirds should generally maximize mate

fidelity to gain the advantage of familiarity within the pair bond, and thus divorce is expected to decrease fitness in the short term (Mercier et al., 2021; Naves et al., 2007; Pyle et al., 2001; Sánchez-Macouzet et al., 2014).

In this study, we combined individual and pair-based analyses to study the triggers and consequences of divorce in thick-billed murre. Thick-billed murre are long-lived, colonial seabirds with low extrapair paternity (7%, Iburguchi et al., 2004). As Arctic breeders, they have a short breeding season, and this constraint should increase the cost of divorce because developing a new partnership takes time. First, we estimated divorce rate and examined how extrinsic (e.g. nesting site quality, sea ice conditions, populationwide adult survival (a metric of annual environmental conditions)), intrinsic (e.g. age, sex, breeding experience, breeding success, laying date) factors influence the probability of divorce in this species. We predicted that the probability of divorce would be inversely related to breeding experience, pair bond duration, annual adult survival rate, breeding success and nesting site quality and directly related to laying date. Second, we investigated the impact of divorce on reproductive success. We predicted that individuals that divorced would have higher reproductive success with their new partner compared to their previous partner and that divorced females would be more likely than their mates to improve reproductive success after divorce (Table 1). Third, we compared the impacts of divorce with mate change through the death of the mate (widowhood). We expected that both types of mate change would affect reproductive success but that divorced individuals would have higher reproductive success with their new partner compared to widowed individuals and that divorced individuals would pair with a more experienced new partner compared to widowed individuals (Table 1). Lastly, we hypothesized that staying faithful to a partner is advantageous, and we predicted that faithful pairs would have a higher mean reproductive success than divorced pairs (Table 1).

## METHODS

### Study Site and Population Monitoring

We collected all data at the Coats Island west murre colony (62°56'52.20"N, 82°01'03.70"W) in Hudson Bay, Nunavut (Canada) during 1991–2019, with a gap during 2011–2015. The thick-billed murre colony is situated on cliffs that host ~15 000 breeding pairs (Gaston, 2002). Demography, foraging ecology and diet have been studied at this site annually since 1981 (e.g. Elliott et al., 2010; Gaston et al., 1994, 2002). We visually identified individual site holders using band combinations and usually also metal band numbers (Elliott et al., 2009). We determined the sex of each bird via copulation position, genetics or association with a partner of known sex (Elliott et al., 2010). We monitored plots by watching murre from a blind and recorded which individuals had an egg or

**Table 1**  
Hypotheses and predictions for the influence of fidelity, divorce and widowhood on the reproductive success (RS) of thick-billed murre

Comparison	Hypothesis	Prediction
(1) Before vs after divorce	Individuals divorce to improve their RS when their current partner is suboptimal	(a) Individuals that divorce will have a higher RS with their new partner compared to their previous partner (b) Divorced females will have a higher increase in RS compared to divorced males
(2) Divorce vs widowhood	Divorce can lead to increased RS, whereas widowhood is not advantageous to either partner	(a) Divorced individuals will have higher RS with their new partner compared to widowed individuals (b) Divorced individuals will pair with a more experienced partner than their previous partner compared to widowed individuals
(3) Divorce vs fidelity	Usually, staying faithful is advantageous	(a) Faithful pairs will have an overall higher RS compared to divorced pairs

chick each day (Gaston et al., 1983). Breeding success was measured by observing each plot daily from mid-July to mid-August. We considered chicks that disappeared after 14 days as successfully fledged. We only had fledging success data for pairs from 1991 to 2010 ( $N = 321$ ). A more detailed description of population monitoring is available in Gaston (2002).

We estimated nesting site quality as the total number of fledglings divided by the number of years each nesting site was occupied and for which we had data on fledging success during the 19 years of our study (all nesting sites had at least 4 breeding attempts and 3 different pairs; Bennett et al., 2022; Kokko et al., 2004). In our data set, this method to quantify site quality was also correlated with the number of neighbours, another measure of site quality (Gilchrist & Gaston, 1997). We used the mean annual adult survival probability as calculated in Frederiksen et al. (2021). We measured breeding experience as the number of years an individual was associated with a nest. Some pairs were monitored for many years as birds returned to the same areas, and thus the proportion of experienced birds in the study population increased with time. To calculate the relative laying date for each breeding attempt, we subtracted the laying date of the pair from the average annual laying date of all marked pairs at the colony. Murres arrive at the colony as soon as enough sea ice disappears near the colony to allow foraging, and therefore, sea ice is the main determinant of timing of breeding in a given year (annual 50% spring sea ice coverage around the colony; Whelan et al., 2022). To assess the pair bond status of a bird at year  $t$ , we compared the pair bond status at year  $t + 1$ . We classified a bird as faithful if it was paired to the same partner in the successive year  $t + 1$ ; we considered a bird as a widowed if its partner the previous year was not resighted at the colony any year after year  $t$  (Dhondt & Adriaensen, 1994). Finally, we defined divorce as instances when both individuals were resighted at the colony at year  $t + 1$  but either or both were nesting with a different partner.

#### Ethical Note

Research activities on Coats Island, Nunavut, Canada, were approved by the McGill Animal Care Committee (animal use protocol 2015–7599 and precursors) and permitted by the Canadian Wildlife Service (Scientific Research Permit SC-NR-2022-NU-007 and precursors) and Nunavut government (Nunavut Wildlife Permit 2020-031 and precursors).

#### Statistical Analyses

We performed all statistical analyses using R (version 4.1.2; R Core Team, 2021). We calculated the average yearly divorce rate as the number of divorced pairs divided by the total number of reunited and divorced pairs in the data set over a 24-year period. We first tested for collinearity among all explanatory variables. Age versus breeding experience and relative versus absolute laying date were strongly correlated ( $r > 0.89$ ), so we did not include age/breeding experience and relative/absolute laying date in the same model at any time. We used breeding experience instead of age because the age of many individuals was unknown, whereas we had more reliable data on breeding experience for most individuals. To facilitate model convergence and allow better comparisons of effects across models, we standardized (centred and scaled) all variables for all models. We fitted Bayesian mixed-effect models implemented in the 'brms' package (Bürkner, 2017). We used Bayesian models because classical frequentist methods failed to converge due to the low rates of divorce, and Bayesian methods allowed us to use slightly informative priors. For all models we ran four chains of 10 000 iterations for each model, with a burn-in of 1000 iterations. We assessed model convergence

by inspecting trace plots and the output of the 'loo' function (Vehtari et al., 2017).

#### Factors Influencing Divorce Probability

We tested the influence of female and male breeding experience, laying date (relative or absolute in different models), nest site quality, pair bond duration and sea ice cover on the probability of divorce. We fitted models assuming a Bernoulli distribution and included random effects (i.e. group level effects) of year and pair identity (ID). We specified slightly informative normal priors (mean = 0; SD = 2) for the regression coefficients and normal priors (0,1) for the group level effects. We fitted 61 models containing no more than two variables and their interactions to aid model convergence (Appendix, Table A1), as a full model with all predictors led to a failed convergence because the occurrence of divorce was low. We also included the intercept in the model formulation. We used the Watanabe–Akaike information criterion (WAIC) implemented in the 'loo' package to rank models (Vehtari et al., 2017). Next, we subset the models to keep the 95% confidence set (95% of the weight of WAIC) and extracted variables appearing at least once in that subset. From these models, we computed model-averaged estimates (posterior means) and 95% credible intervals (CI) using functions in the 'brms' package (Bürkner, 2017). We used the same methods and models on a subset of 359 pairs to assess the influence of survival rate. As we only had fledging success for birds during 1991–2010, we used a subset of 321 pairs to assess the influence of this variable on the probability of divorce.

#### Outcome of Divorce

To investigate the outcome of divorce, we tested divorced birds ( $N = 60$ ) for effects of age, breeding experience and sex (i.e. regression coefficient) on a change in (1) mates' age and breeding experience, (2) nest site quality, (3) laying date and (4) fledging success. We categorized fledging success with the new mate as 1 if fledging success was higher and as 0 if fledging success was lower or the same. We fitted eight models assuming a normal distribution and included a group level effect for year (Appendix, Table A3). We specified slightly informative normal priors of (0,5) for regression coefficients and normal priors (0,1) for the group level effects. We did not include individual identity as a group level effect when we computed models based on individuals because most individuals were only recorded once. For the difference in fledging success, we fitted models assuming a Bernoulli distribution and used slightly informative normal priors (0, 2) for regression coefficients. We used the Pareto smoothed importance sampling (PSIS) leave-one-out cross-validation (LOO) implemented in the 'loo' package (Vehtari et al., 2017) to rank models for each of the four response variables. We followed the same methodology as earlier to assess the posterior estimate and 95% CI. We also tested whether age, breeding experience or sex influence the probability of moving between nest sites following a divorce. We fitted models assuming a Bernoulli distribution and included a group level effect for year. We specified slightly informative normal priors (0,2) for regression coefficients and normal priors (0,1) for group level effects.

#### Comparison Between Divorced and Widowed Birds

To evaluate the impacts of partner change, we compared changes in divorced ( $N = 60$ ) and widowed ( $N = 64$ ) birds (1) mates' age and breeding experience, (2) laying date and (3) fledging success (only birds from 1991 to 2010;  $N = 52$ ). We fitted five models for each variable (i.e. difference in age, breeding experience,

laying date) assuming a normal distribution and included group level effects for year and site (Appendix, Table A5), with the same priors as above. For the difference in fledging success, we fitted models assuming a Bernoulli distribution and the same priors as above. We used the same methodology that we used for testing the outcome of divorce to access posterior estimates and 95% CIs. We also tested whether individuals' sex or status (divorced versus widowed) influenced the probability of moving between nest sites following a mate change using models assuming a Bernoulli distribution as above.

#### Advantages of Remaining Faithful

To evaluate the advantages of remaining faithful over an entire pair bond, we compared average fledging success and average laying date (average laying date during all breeding attempts of a pair) between pairs that ended in a divorce (divorced:  $N = 21$ ) and pairs that ended because one individual disappeared (faithful:  $N = 101$ ). The fledging success was over all breeding attempts of a pair from 1991 to 2010 as we only had fledging success data for these individuals (average of fledging success during all breeding attempts of a pair). For the average fledging success, we fitted eight models assuming a Bernoulli distribution and included group level

effects for first year of breeding and nesting site (Appendix, Table A7), with the same priors as before for these types of models. For average laying date, we fitted eight models assuming a normal distribution and included group level effects for year and site (Appendix, Table A7). We specified slightly informative normal priors (0,5) for the regression coefficients and normal priors (0,1) for the group level effects.

## RESULTS

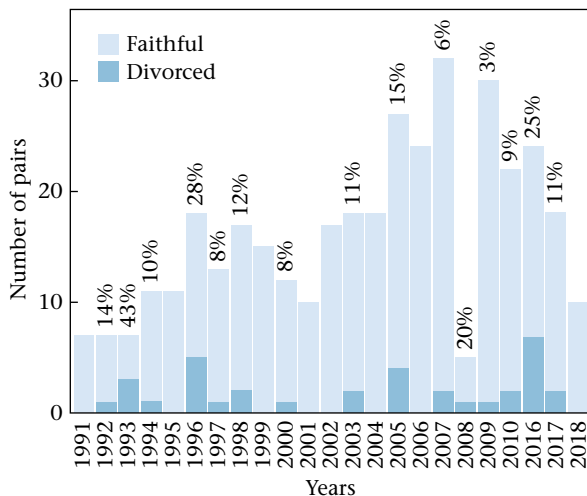
### Factors Influencing Divorce Probability

The final data set included 372 thick-billed murre breeding attempts and 145 unique breeding pairs. Divorce occurred in 34 thick-billed murre pairs, giving an average divorce rate of 9%, with a median of 8% (Fig. 1). Divorce rate decreased with increased breeding experience (and age, given that they were highly correlated) and nest site quality (Table 2, Figs 2 and 3). Laying date, relative laying date, pair bond duration and sea ice cover had no significant effect on the probability of divorce (Table 2, Fig. 2). We did not find an effect of populationwide survival rate on the probability of divorce (Appendix, Table A2). However, we did observe a lower divorce probability following a successful fledging (Fig. 3, Appendix, Table A2).

### Outcomes of Divorce

Changes in the age and breeding experience of a mate or in nest site quality following a divorce were not associated with a bird's sex, age or breeding experience (Appendix, Table A4). We found a negative intercept between new laying date and previous laying date (Appendix, Table A4), which indicates that birds laid earlier with their new mate compared to their previous mate following a divorce (Fig. 4a).

We did not find an effect of age, sex or breeding experience on the probability of moving to a new nesting site following a divorce (Appendix, Table A4). Both sexes were equally likely to remain on site after divorce (female = 48%; male = 52%). For birds that moved after a divorce, we did not find any difference in the nest site quality between the initial site and the new site (Appendix, Table A4). Divorced birds were more likely to have a lower fledging success with their new mate compared to their previous mate the season following divorce (24% probability of increased fledging success; Fig. 4b, Appendix, Table A4). We found no difference between the sexes in reproductive success following a divorce (female = 32% (7 of 22); male = 28% (7 of 25)) and no effect of age or breeding experience (Appendix, Table A4).

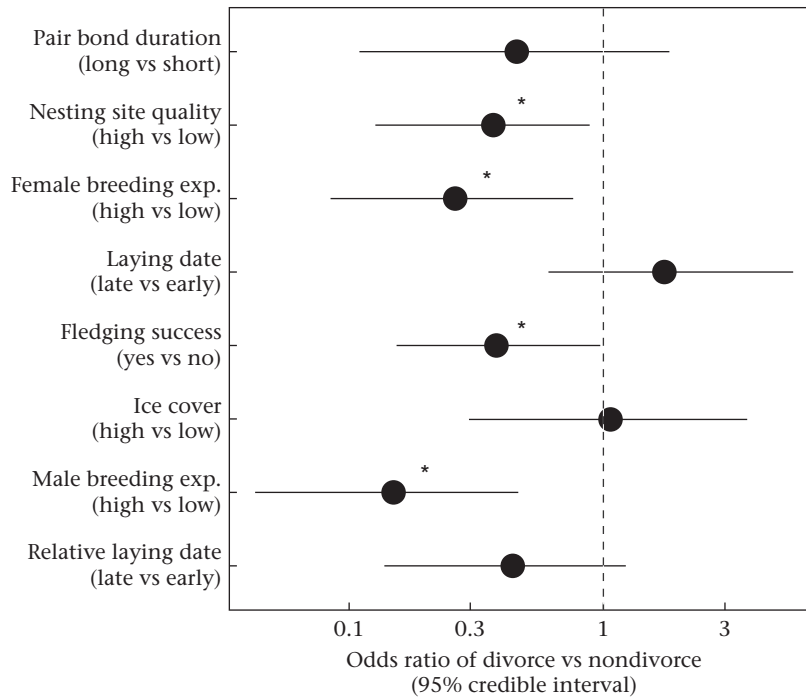


**Figure 1.** Number of faithful and divorced thick-billed murre pairs at the Coats Island colony (Nunavut) per year during 1991–2018 (with a gap during 2011–2015; data were collected in 2013 and 2015 but did not allow estimation of divorce rate). The percentages above the bars represent the yearly divorce rate.

**Table 2**  
Modelling results for the effect of different variables on the probability of divorce ( $N = 372$ )

Variable	Estimate	Estimate error	95% CI	
Intercept	-3.152	0.470	-4.194	-2.354
Male experience	<b>-1.902</b>	<b>0.609</b>	<b>-3.144</b>	<b>-0.774</b>
Female experience	<b>-1.331</b>	<b>0.560</b>	<b>-2.467</b>	<b>-0.276</b>
Nesting site quality	<b>-0.996</b>	<b>0.484</b>	<b>-2.053</b>	<b>-0.131</b>
Laying date	0.557	0.563	-0.501	1.717
Male experience <sup>2</sup>	-1.331	1.265	-3.837	1.086
Pair bond duration	-0.788	0.700	-2.207	0.589
Relative laying date	-0.817	0.552	-1.980	0.200
Year	-0.166	0.631	-1.436	1.084
50% Sea ice cover	0.067	0.639	-1.222	1.296
Fledging success: Male experience	1.496	1.204	-0.780	3.952
Male experience: Female experience	1.352	1.135	-0.847	3.646
Site quality: Male experience	-0.353	1.040	-2.335	1.697
Laying date: Male experience	-1.169	1.137	-3.461	0.996

Model-averaged estimates (posterior means) and 95% credible intervals (CI) are presented. The CIs of variables in bold did not overlap zero. All variables were standardized.



**Figure 2.** Odds ratio (95% credible interval) of divorce versus nondivorce in thick-billed murre pairs for variables included in the Bayesian mixed model. An asterisk denotes a statistically significant effect ( $P < 0.05$ ) on divorce probability.

#### Comparison Between Divorced and Widowed Birds

Widowed birds tended to remate with birds that were younger and less experienced than their previous partners as compared to divorced birds (Fig. 4c, Appendix, Table A6) and laid later with their new mate relative to divorced birds (Fig. 4c, Appendix, Table A6). Furthermore, the probability of moving to a new nesting site was much higher after divorce (53% of all divorced birds moved) than after widowhood (16% of all widowed birds moved; Fig. 4d, Appendix, Table A6). We did not find any difference in fledging success between widowed and divorced birds (Fig. 4d, Appendix, Table A6).

#### Advantages of Remaining Faithful

Fledging success was higher for faithful pairs than for divorced pairs (Fig. 5), and divorce had no effect on the average laying date (Appendix, Table A8).

## DISCUSSION

We investigated the triggers and consequences of divorce in thick-billed murre pairs. Divorce occurred primarily in pairs with inexperienced/young individuals and in pairs with low-quality nest sites, and the probability of divorce tended to be higher in pairs that failed to rear a chick in the previous year. However, divorced individuals did not gain more experienced partners or a better-quality site following a divorce. Individuals had a lower fledging success with their new mate in the year following the divorce, and this applied to both sexes. We found no evidence that environmental conditions (i.e. sea ice cover) influenced divorce probability.

#### Divorce Rate

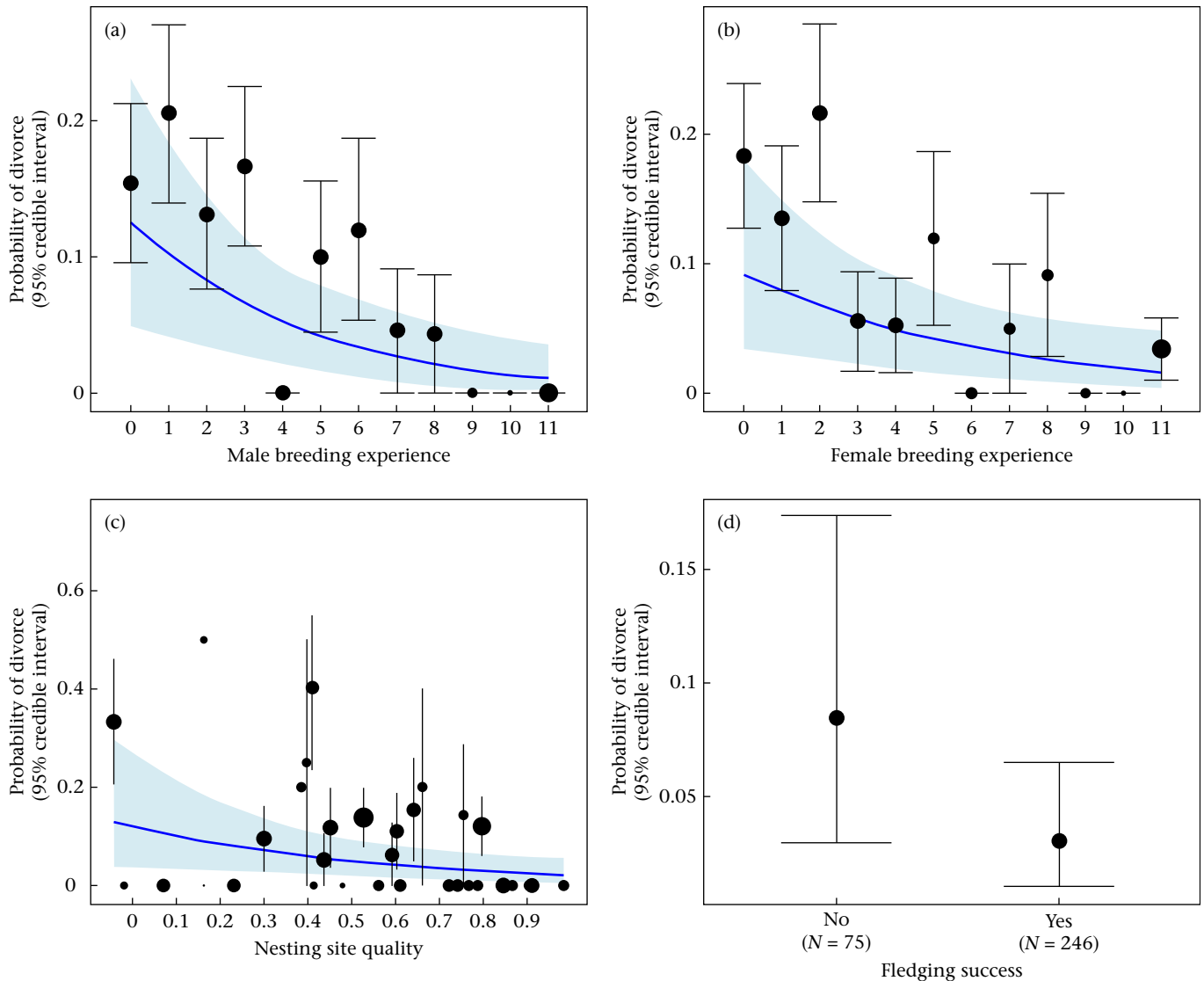
Divorce rates are often related to intrinsic factors such as low breeding success and mate/site availability (i.e. declining versus

increasing populations), and thus and may be specific to each colony. In our case, the thick-billed murre divorce rate on Coats Island was higher than observed in a Svalbard thick-billed murre colony (Kongsfjorden colony; average divorce rate of 1.9%, Mercier et al., 2021). The average yearly divorce rate of 9% among Coats Island murre pairs is similar to the yearly average divorce rates for the closely related common murre on Great Island (Newfoundland, Canada: 8%; Moody et al., 2005) and on Isle of May (Scotland: 10%; Jeschke et al., 2007). This rate is near the median divorce rate for seabirds (13.8%;  $N = 123$  studies; Mercier et al., 2021).

#### Factors Influencing Divorce Probability

Divorce in thick-billed murre pairs in our system seemed to be linked to low breeding success in the previous year rather than opportunities for a more experienced mate or a higher-quality nesting site. Individuals that had unsuccessful breeding attempts (no fledging success) had a higher probability of divorce than pairs that successfully bred, whereas we did not find an effect of annual survival rate. Changing partners may be a way to increase reproductive success in the long term, consistent with the 'incompatibility hypothesis' (Choudhury, 1995). Our results are also consistent with two meta-analyses that found that divorce is triggered by low breeding success (Culina, Radersma, et al., 2015; Dubois & Cézilly, 2002). A higher chance of divorce following a breeding failure also occurs in other seabird species like black-browed albatrosses, *Thalassarche melanophris* (Ventura et al., 2021), short-tailed shearwaters, *Puffinus tenuirostris* (Bradley et al., 1990), and yellow-eyed penguins, *Megadyptes antipodes* (Setiawan et al., 2005). In our system, considerable variation in breeding success is likely linked to factors only partially related to mate 'quality' (e.g. predation, egg loss and other factors associated with 'poor luck') and thus measuring quality by average reproductive success may be less precise than in other seabird species.

While divorce appeared to be associated with prior breeding failure, its benefits for future breeding success were modest. Indeed, for most divorced birds, the fledging success with the new



**Figure 3.** Predicted probabilities of divorce in thick-billed murres in relation to (a) male breeding experience, (b) female breeding experience, (c) nesting site quality and (d) fledging success. For (a)–(c), the size of dot represents the sample size (1–49) for each category.

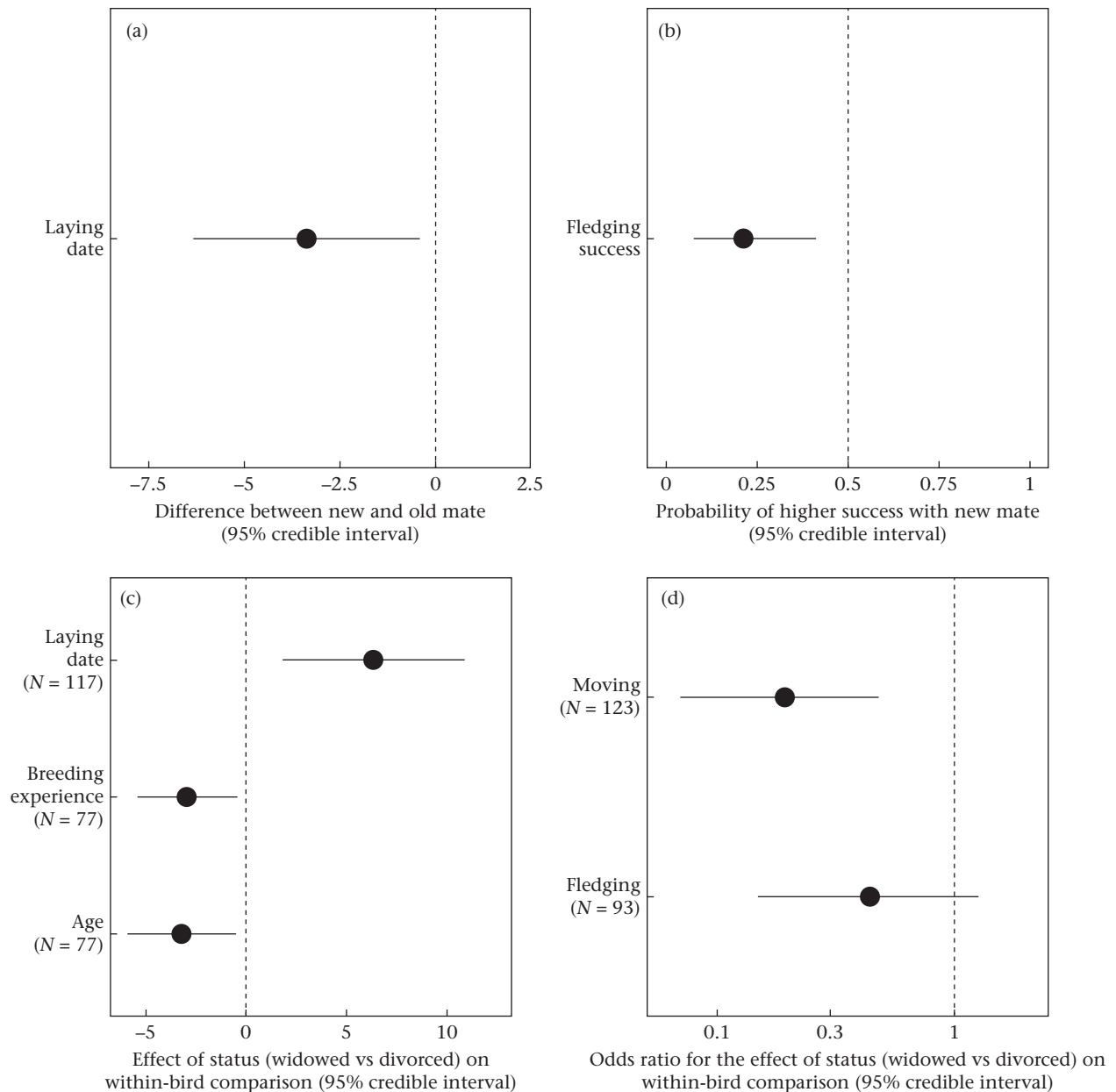
mate was lower the first year after divorce compared with the previous mate.

The influence of adult annual survival rate on the probability of divorce appears to differ between thick-billed murres and common murres; divorce in common murres appeared to be opportunistic and correlated with annual average mortality rates over 6 years (Moody et al., 2005). In our system, over a much longer period, we found no effect of annual average survival rate on the probability of divorce in a given year. However, 54% of the divorces in our system happened after a breeding success, which is similar to what Mercier et al. (2021) found for thick-billed murres in Svalbard (two of three divorces occurred after successful breeding). Nonadaptive mechanisms could potentially explain the many divorces that occurred after successful breeding attempts. At the Isle of May common murre colony, observations best supported the ‘forced-divorced hypothesis’ (Jeschke et al., 2007). At Coats Island, divorce was associated with reproductive failure for some pairs. However, divorces could happen for multiple reasons (Ens et al., 1993; Heg et al., 2003), and we cannot dismiss that divorces were opportunistic, accidental or forced in some

situations. Investigating the behavioural sequences that lead to a divorce and identifying which individuals initiate divorce are important next steps to determine whether forced divorce is common in this system.

Divorces also were related to low-quality partners and nesting sites, similar to common murres (Jeschke et al., 2007). As predicted, individuals at low-quality nest sites had a higher probability of divorce (Heg et al., 2003) and were more likely to improve breeding success by changing partners or nest sites. Surprisingly, thick-billed murres that moved following a divorce did not gain higher-quality nest sites.

Birds with lower breeding experience, which were also younger birds, divorced more often, likely because inexperienced thick-billed murre pairs on Coats Island are not as successful as older, experienced pairs (de Forest & Gaston, 1996). For inexperienced birds, the possibility of improvement with a new partner is higher than for experienced birds (Ens et al., 1993). An error in mate choice or evidence of incompatibility should happen more often in less experienced birds (Choudhury, 1995). A negative relationship between divorce probability and breeding experience has also been

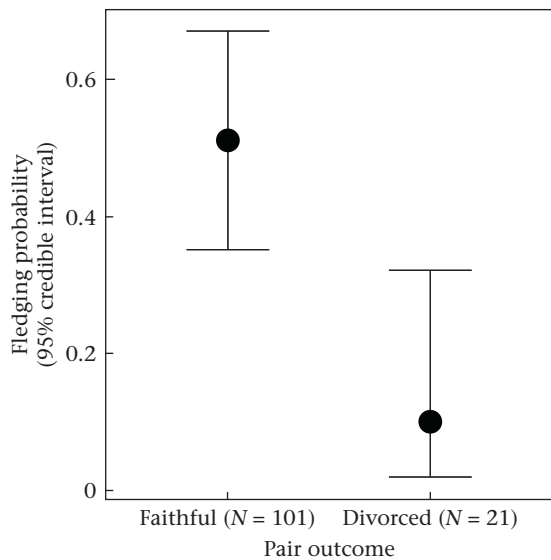


**Figure 4.** Estimate and 95% credible interval of (a) the difference in laying date between a new mate and a previous mate following divorce, (b) the probability of higher fledging success with a new mate following divorce (1 = higher fledging success with a new mate, 0 = lower or same fledging success with new mate) and (c) the effect of status (widowed versus divorced) on continuous response variables for within-bird comparisons between a new mate and a previous mate. (d) Odds ratio (95% credible interval) of widowed versus divorced birds for the effect of status on the probability of moving to a new nesting site and on fledging success with a new mate.

found in other seabird species, including Cassin's auklets, *Ptychoramphus aleuticus* (Sydeman et al., 1996), white-chinned petrels, *Procellaria aequinoctialis* (Bried & Jouventin, 1999), and red-billed gulls, *Larus novaehollandiae* (Mills et al., 1996). In our study, male breeding experience had a stronger effect on the probability of divorce, thus male experience may be key to mate retention. Indeed, in some other seabird species, there is a significantly stronger relationship between age and mate fidelity in males than in females (Pyle et al., 2001). Older males may be better able to retain or select high-quality mates than younger males, further improving their reproductive output (Pyle et al., 2001).

We also did not find any effect of sea ice cover on the probability of divorce, although there was a nonsignificant tendency for birds to have more divorce in years when populationwide median lay date

was earlier. Sea ice cover is likely the most important environmental factor in our system as an indicator of a regime shift in the marine ecosystem associated with laying date and chick mass at fledging (Gaston et al., 2003, 2005; Sauve et al., 2023; Whelan et al., 2022). The effect of environment on the prevalence of divorce was found in a study on black-browed albatross (Ventura et al., 2021). Warm sea surface temperature anomalies increased the probability of divorce in this system (Ventura et al., 2021). In our system, sea surface temperature is highly correlated with sea ice cover concentration (Whelan et al., 2022) and so may not independently affect the probability of divorce. Nevertheless, variation in sea ice distribution at a subpixel level (i.e. invisible from the satellite data we used) during prelaying may be more important in determining social conditions during prelaying than average sea ice concentration, and



**Figure 5.** Estimates and 95% credible intervals of fledging success probability for faithful pairs and divorced pairs.

such variation may affect divorce rate. Indeed, the nonsignificant tendency for birds to divorce more often in early years suggests that other environmental conditions that impact timing of laying could be important and worth investigating with a larger data set with more statistical power.

#### Outcomes of Divorce

New partners of divorced thick-billed murres were similar in age and breeding experience to previous partners, as was nest site quality. Consequently, our results do not support the 'better option hypothesis', a result also found for common terns, *Sterna hirundo* (González-Solís et al., 1999). In alpine marmots, *Marmota marmota*, individuals also gained no benefits from mate switching (Lardy et al., 2011). Also, less than a third of re-pairings resulted in a fledged chick in the first year after divorce. The immediate decrease in breeding success in newly formed pairs is referred to as 'the syndrome of the first-year bond' (Naves et al., 2007). Culina, Radersma, et al. (2015) showed in a meta-analysis that species laying one-egg clutches suffer more from divorce than those laying larger clutches, as the fledging success of their offspring is reduced more. While we only looked at fledging success during the first breeding season following divorce, it would be interesting to examine longer-term outcomes to test how many years divorced birds need to be paired to achieve the same reproductive success as faithful pairs.

We failed to identify which member of a pair initiated the divorce, and thus, failed to detect whether one individual benefited more than another from a divorce (higher reproductive success postdivorce). In other systems, divorce has different consequences for breeding success depending on whether an individual chooses to initiate divorce or is the 'victim' (Ens et al., 1993; Moody et al., 2005), perhaps because choosers may change partners for an older or more experienced mate. Among other bird species, females often initiate divorce by moving to another territory (e.g. Blondel et al., 2000; Cézilly et al., 2000; Ens et al., 1993) and typically benefit more from a divorce than do males in terms of increased reproductive success (Culina, Radersma, et al., 2015). In our study, males and females had similar probabilities of moving to a new site after a divorce, which is consistent with other murre studies

(Kokko et al., 2004; Moody et al., 2005). However, given our small sample size, we cannot rule out some sex-related bias. Yet, the absence of sex differences in breeding outcomes following a divorce suggests that in thick-billed murres, divorce may be initiated by either sex.

#### Comparison Between Divorced and Widowed Birds

As in other species (e.g. common tern; González-Solís et al., 1999), divorced thick-billed murres tended to re-pair with individuals of the same age. In contrast, apparently widowed birds paired with younger, less experienced partners and laid eggs later. Later laying dates among widowed birds have been observed in other seabird species (Ens et al., 1993; Mills et al., 1996). Divorce, if initiated at the start of the season or even in the previous season among unsuccessful pairs, may provide the divorcing birds with a broad pool of available mates. By contrast, widowed birds may lose time waiting for their previous mate to return to the colony (Mills, 1973) and then have access to a smaller pool, consisting of young, less experienced birds that typically lay late (de Forest & Gaston, 1996).

Widowed thick-billed murres were less likely to change nest sites than divorced birds. In common murres and Eurasian oystercatchers, *Haematopus ostralegus*, widowed individuals also often stayed at the same nest site (Ens et al., 1993; Moody et al., 2005). Divorced birds may move to another site to join a new partner or be forced to change sites by their previous partner, while widowed birds return to defend the same nest site but without their previous partner. Widowed birds may only move to another site if they are unable to defend the site from an intruding pair.

Reproductive success was similar for divorced and widowed birds with a new mate, a result also obtained by Culina, Radersma, et al. (2015). Birds that are victims of a divorce (the noninitiator) are similar to widowed birds in facing a forced, rather than voluntary, mate change.

#### Advantages of Remaining Faithful

Faithful pairs had a higher probability of fledging success than pairs that divorced. Nevertheless, the average laying dates of divorced and faithful pairs were similar. Pairs formed from at least one divorced individual also had a shorter pair bond duration than pairs that stayed together. Faithful thick-billed murres may be better at cooperation and coordination (e.g. for foraging trips and nest and chick defence), thus increasing their chances of successful breeding compared to birds that divorce. Other studies have found an advantage to staying faithful: in the blue-footed booby, *Sula nebouxii*, pairs that remain together longer produce more fledglings, independent of their age and reproductive experience (Sánchez-Macouzet et al., 2014). Higher fledging success in faithful pairs has also been observed in Cassin's auklets (Sydeman et al., 1996) and Australasian gannets, *Morus serrator* (Ismar et al., 2010).

#### Conclusion

At 9%, the rate of divorce among thick-billed murres at Coats Island was typical for seabirds. It was influenced by breeding experience/age, nest site quality and fledging success. After a divorce, individuals did not necessarily gain access to better-quality partners or nest sites. In this population, divorce seemed to be associated with low reproductive success prior to the event, but divorced individuals also had lower fledging success than non-divorcing pairs in the first year after the mate change. More research is needed to investigate whether divorce is advantageous in the long term. Understanding divorce is important as it



influences lifetime fitness and pairing decisions (Heg et al., 2003; Ismar et al., 2010; Leach et al., 2020; Streif & Rasa, 2001) as well as population dynamics and genetic structure (Bai & Severinghaus, 2012; Bercé & Boukal, 2004; Culina, Lachish, et al., 2015; Martin et al., 2014). Our findings help to understand the mechanisms and costs of mate changes in monogamous seabirds as we had access to a long-term data set.

### Author Contributions

**M. Gousy-Leblanc:** Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing review & editing. **T. Merklig:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing review & editing. **S. Whelan:** Investigation, Resources, Writing review & editing. **A. J. Gaston:** Investigation, Methodology, Resources, Writing review & editing. **V. L. Friesen:** Supervision, Writing review & editing. **K. H. Elliott:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing review & editing.

### Data Availability

Data set is available on figshare: <https://figshare.com/s/709b01132ce56a0294b>.

### Declaration of Interest

We declare that we have no conflict of interest.

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Appendix

**Table A1**  
Models tested for the variables affecting the probability of divorce

Models
ProbDiv ~ 0 + Intercept + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdYear + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge + stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge + stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge + stdPairBond + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge + stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdExpMale + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdLaying + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty + stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond + stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdLaying + stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond + stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond + stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty + stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdExpMale + stdExpMaleSq + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdExpFemale + stdExpFemaleSq + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty + stdQtySq + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond + stdPairBondSq + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdLaying + stdLayingSq + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge × stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge × stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge × stdPairBond + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdFledge × stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdExpMale × stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty × stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond × stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdLaying × stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty × stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond × stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdLaying × stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond × stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdPairBond × stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdQty × stdLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying + stdFledge + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying + stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying + stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying + stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying + stdPairBond + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying × stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying × stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying × stdQty + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdRLaying × stdPairBond + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_doy + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_doy × stdFledge + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_past + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_past × stdExpMale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_past × stdExpFemale + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_doy + stdRLaying + (1 Year) + (1 PairID)
ProbDiv ~ 0 + Intercept + stdiceOut_doy × stdLaying + (1 Year) + (1 PairID)

All variables were standardized (centred and scaled). ExpFemale = breeding experience of female; PairID = pair identity; ExpMale = breeding experience of male; PairBond = number of years pair bred together; Fledge = fledging success (1 = yes, 0 = no); Qty = nesting site quality; Laying = absolute laying date; iceOut\_doy = 50% sea ice cover the year of the breeding attempt; iceOut\_past = 50% sea ice cover the year before the breeding attempt.

**Table A2**

Modelling results for the effect of different variables on the probability of divorce from a subset of pairs with known yearly adult survival rate ( $N = 359$ ) and a subset of pairs with known fledging success during 1991–2010 ( $N = 321$ )

Variable	Estimate	Estimate error	95% CI	
<b>Pairs with known yearly adult survival (<math>N = 359</math>)</b>				
Intercept	-3.140	0.490	-4.246	-2.310
Breeding experience Female	<b>-1.533</b>	<b>0.576</b>	<b>-2.708</b>	<b>-0.458</b>
Breeding experience male	<b>-2.093</b>	<b>0.633</b>	<b>-3.406</b>	<b>-0.912</b>
Laying date	0.490	0.605	-0.665	1.715
Year	-0.396	0.698	-1.813	0.958
Nesting site quality	<b>-1.111</b>	<b>0.548</b>	<b>-2.334</b>	<b>-0.161</b>
Pair bond duration	-0.809	0.741	-2.247	0.696
Survival rate	-0.051	0.678	-1.410	1.295
<b>Pairs with known fledging success during 1991–2010 (<math>N = 321</math>)</b>				
Intercept	-3.292	0.449	-4.278	-2.529
Breeding experience male	<b>-2.101</b>	<b>0.665</b>	<b>-3.468</b>	<b>-0.863</b>
Fledging success	<b>-0.969</b>	<b>0.467</b>	<b>-1.875</b>	<b>-0.033</b>
Breeding experience female	<b>-1.443</b>	<b>0.593</b>	<b>-2.677</b>	<b>-0.345</b>
Nesting site quality	<b>-1.020</b>	<b>0.453</b>	<b>-1.913</b>	<b>-0.130</b>

Model-averaged estimates (posterior means) and 95% credible intervals (CI) are presented. The CIs of variables in bold did not overlap zero. All variables were standardized.

**Table A3**

Models tested for each response variable of a focal bird following divorce

Response variables	Models tested
Age difference	~ 0 + Intercept + stdSex × stdAge + (1 Year)
Breeding experience difference	~ 0 + Intercept + stdSex × stdExp + (1 Year)
Laying date difference	~ 0 + Intercept + stdSex + stdAge + (1 Year)
Nesting site quality difference	~ 0 + Intercept + stdSex + stdExp + (1 Year)
Probability of moving	~ 0 + Intercept + stdSex + (1 Year)
Fledging success difference	~ 0 + Intercept + stdAge + (1 Year)
	~ 0 + Intercept + stdExp + (1 Year)
	~ 0 + Intercept + (1 Year)

**Table A4**

Modelling results for the effect of differences in age, breeding experience, fledging success, laying date, nesting site quality and probability of moving for new mates and previous mates following a divorce

Variable	Estimate	Estimate error	95% CI	
<b>Age difference</b>				
Intercept	0.684	0.803	-0.882	2.260
<b>Breeding experience difference</b>				
Intercept	0.442	0.663	-0.878	1.772
<b>Fledging success difference</b>				
Intercept	<b>-1.306</b>	<b>0.539</b>	<b>-2.499</b>	<b>-0.352</b>
<b>Laying date difference</b>				
Intercept	<b>-3.376</b>	<b>1.517</b>	<b>-6.321</b>	<b>-0.405</b>
<b>Nesting site quality difference</b>				
Intercept	0.076	0.086	-0.099	0.241
<b>Probability of moving</b>				
Intercept	-0.182	0.308	-0.791	0.401
Breeding experience difference	0.953	0.574	-0.132	2.123

Model-averaged estimates (posterior means) and 95% credible intervals (CI) are presented. The CIs of variables in bold did not overlap zero. All variables were standardized.

**Table A5**

Models tested for each response variable to evaluate the difference between a new mate and a previous mate

Response variables	Models tested
Age difference	~ 0 + Intercept + stdSex × stdStatus + (1 Year) + (1 Site)
Breeding experience difference	~ 0 + Intercept + stdSex + stdStatus + (1 Year) + (1 Site)
Laying date difference	~ 0 + Intercept + stdSex + (1 Year) + (1 Site)
Nesting site quality difference	~ 0 + Intercept + stdStatus + (1 Year) + (1 Site)
Probability of moving	~ 0 + Intercept + (1 Year) + (1 Site)
Fledging success difference	~ 0 + Intercept + (1 Year) + (1 Site)

'Status' refers to divorced versus widowed birds.

**Table A6**Modelling results comparing differences between divorced ( $N = 60$ ) and widowed ( $N = 64$ ) birds in age of new mate versus previous mate, breeding experience of new mate versus previous mate, fledging success, laying date, nesting site quality and probability of moving

Variable	Estimate	Estimate error	95% CI	
<b>Age</b>				
Intercept	-0.879	0.684	-2.254	0.461
Status	<b>-3.400</b>	<b>1.330</b>	<b>-5.983</b>	<b>-0.691</b>
<b>Breeding experience</b>				
Intercept	-0.844	0.684	-2.198	0.501
Status	<b>-2.998</b>	<b>1.304</b>	<b>-5.564</b>	<b>-0.433</b>
<b>Fledging success</b>				
Intercept 1	-1.851	0.447	-2.822	-1.068
Intercept 2	1.673	0.401	0.935	2.527
Status	-0.522	0.510	-1.541	0.466
<b>Laying date</b>				
Intercept	-0.155	1.373	-2.872	2.561
Status	<b>5.318</b>	<b>2.217</b>	<b>1.001</b>	<b>9.670</b>
<b>Nesting site quality</b>				
Intercept	-0.111	0.064	-0.016	0.235
<b>Probability of moving</b>				
Intercept	<b>-0.952</b>	<b>0.259</b>	<b>-1.483</b>	<b>-0.464</b>
Status	<b>-1.546</b>	<b>0.462</b>	<b>-2.496</b>	<b>-0.690</b>

Model-averaged estimates (posterior means) and 95% credible intervals (CI) are presented. The CIs of variables in bold did not overlap zero. All variables were standardized.

**Table A8**Modelling results comparing differences between divorced ( $N = 21$ ) and faithful ( $N = 101$ ) pairs in average fledging success and average laying date over an entire pair bond

Variable	Estimate	Estimate error	95% CI	
<b>Average fledging success</b>				
Intercept	-0.082	0.289	-0.630	0.507
Outcome	<b>-1.207</b>	<b>0.612</b>	<b>-2.461</b>	<b>-0.059</b>
<b>Average laying date</b>				
Intercept	30.781	1.078	28.585	32.840
Age male	-0.780	0.994	-2.722	1.155
Outcome	-2.411	1.432	-5.196	0.439
Age male: Outcome	-4.904	2.702	-10.172	0.406

Model-averaged estimates (posterior means) and 95% credible intervals (CI) are presented. The CIs of variables in bold did not overlap zero. All variables were standardized.

**Table A7**

Models tested for each response variable to evaluate the difference between divorced pairs and faithful pairs over an entire pair bond (i.e. outcome)

Response variable	Models tested
Average fledging success	~ 0 + Intercept + stdAgeFemale1 × stdOutcome + (1 FirstYear) + (1 Site)
Average laying date	~ 0 + Intercept + stdAgeMale1 × stdOutcome + (1 FirstYear) + (1 Site)
	~ 0 + Intercept + stdAgeMale1 + stdOutcome + (1 FirstYear) + (1 Site)
	~ 0 + Intercept + stdAgeFemale1 + stdOutcome + (1 FirstYear) + (1 Site)
	~ 0 + Intercept + stdAgeFemale1 + (1 FirstYear) + (1 Site)
	~ 0 + Intercept + stdAgeMale1 + (1 FirstYear) + (1 Site)
	~ 0 + Intercept + stdOutcome + (1 FirstYear) + (1 Site)
	~ 0 + Intercept + (1 FirstYear) + (1 Site)