

## Short Communication

## High site and mate fidelity in a monogamous Arctic seabird

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In long-lived seabirds, social monogamy and mate and site fidelity are common due to the cost entailed by site change and divorce such as delayed laying or reduced reproductive success. We used 13 years of monitoring data from marked Long-tailed Jaegers *Stercorarius longicaudus* in the Canadian High Arctic to quantify the degree of mate and site fidelity, and to investigate (1) how nesting success and mate fidelity affect site fidelity and (2) how mate fidelity affects laying date and nesting success. We observed a minimum mate retention rate of 79% for males and 85% for females; the site fidelity of birds that nested successfully was higher for those faithful to their mate than for those that changed mates but we found no evidence that mate change affected laying date or nesting success. The short summer and high unpredictability of resources of the Arctic tundra probably favour high site and mate fidelity in this species.

**Keywords:** breeding, divorce, long-tailed Jaeger, mate faithfulness, monogamy, reproduction, *Stercorarius longicaudus*, tundra-nesting.

Social monogamy is widespread in birds and is the mating system of more than 90% of bird species, many of which are faithful to their mate between years (Lack 1968). This strategy may be particularly beneficial in long-lived species, as site and mate fidelity can affect reproductive success. Both familiarity with a mate and a nest-site, and divorce can have costs and benefits. On the one hand, familiarity can reduce the risks and costs associated with reproduction (Dow & Fredga 1983,

Choudhury 1995, Bried & Jouventin 2002, Sánchez-Macouzet *et al.* 2014). Breeding with a familiar mate usually increases breeding success, as it can reduce the cost related to courtship or territory acquisition (Choudhury 1995, Catry *et al.* 1997, Ismar *et al.* 2010, Jankowiak *et al.* 2018, Leach *et al.* 2020). It can also enhance coordination between mates in terms of incubation shifts, chick feeding and timing of foraging trips, thus improving reproductive performance (Bried & Jouventin 2002). On the other hand, divorce can lead to an increase in breeding success when an individual acquires a higher quality mate (Choudhury 1995, Culina *et al.* 2015, Pelletier & Guillemette 2022).

Seabird pairs usually remate at the breeding site after spending the non-breeding period separated at sea. Therefore, synchrony in arrival time may play a role in mate fidelity (Bried & Jouventin 2002). Asynchrony could cause divorce because waiting for the arrival of a mate may delay laying and lead to reduced reproductive success, thus making divorce beneficial to avoid missing a breeding opportunity (Choudhury 1995, Naves *et al.* 2006, Sánchez-Macouzet *et al.* 2014). This is especially true in highly seasonal environments where breeding early is generally advantageous (Perrins 1970, Bêty *et al.* 2003, Low *et al.* 2015). To varying degrees, previous breeding failure also triggers divorce in several species (Choudhury 1995, Naves *et al.* 2006, Ismar *et al.* 2010, Culina *et al.* 2015, Sommerfeld *et al.* 2015, Pelletier & Guillemette 2022). However, the strong association between site and mate fidelity, especially in seabirds, may act as a confounding factor, as reuniting with the same individual may be a side effect of site faithfulness (Choudhury 1995, Bried & Jouventin 1999, 2002, Jankowiak *et al.* 2018).

The Long-tailed Jaeger *Stercorarius longicaudus* (hereafter referred to as Jaeger) is a long-lived seabird (Julien *et al.* 2013) that breeds across the Arctic tundra and performs one of the longest trans-equatorial migrations annually (Seyer *et al.* 2021). During the breeding season, Jaegers switch from a marine to a terrestrial lifestyle. They hold a small inland territory, and successful breeding is highly dependent on the abundance of lemmings, which is a pulsed resource with cyclical fluctuations (Andersson 1981, Therrien *et al.* 2014). Even though these socially monogamous birds were previously assumed to be faithful to their mate and nesting territory, mate retention rate has not yet been quantified using marked individuals (Maher 1970, Andersson 1981, Seyer *et al.* 2020).

Our objectives here were to (1) quantify mate and site fidelity rates of Long-tailed Jaegers based on marked individuals, (2) investigate how site fidelity is affected by previous nesting success and mate fidelity, and (3) investigate how laying date and nesting success are affected by mate fidelity. Because of the high unpredictability and temporal variability in resource abundance in the Arctic, we expected high mate retention in

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Jaegers. Moreover, we expected delayed reproduction and reduced nesting success following a mate change.

## METHODS

### Study area

Fieldwork was conducted during the Jaeger breeding season (mid-June to early August) on Bylot Island, Nunavut (73°08'N, 80°00'W) in the Canadian High Arctic. The Qarlikturvik Valley (35 km<sup>2</sup>), the main study site, was situated in a large glacial valley, and the secondary site (25 km<sup>2</sup>) was situated 30 km to the south at the centre of a large Snow Goose *Anser caerulescens* nesting colony (see Seyer *et al.* 2020 for additional details on the study area).

### Field methods

We carried out systematic nest searches along parallel transects separated by 400 m in late June and early July throughout the main study site, from 2007 to 2019. Breeding Jaegers are easy to detect in the flat tundra due to their alarm call when intruders are up to 200 m from their nest (Andersson 1971, Wiley & Lee 2020). At the secondary study site, nests have been found opportunistically when conducting other fieldwork since 2015. All nests were georeferenced when found. We captured breeding Jaegers at the nest during the incubation period using a bownet trap, or in the nest vicinity using a noose carpet, a net gun or a baited Bal-chatri trap. All captured birds were marked with a metal ring and a coded plastic ring that could be read at a distance (~50 m). A few body feathers were plucked from the breast to sex birds by DNA analysis (see Seyer *et al.* 2019 for details). Jaegers encountered during nest searches or nest visits were checked for the presence of plastic rings, either with binoculars or on high-resolution photos, identified and their position recorded with a GPS.

Active nests were monitored every 1–2 weeks until hatching. The laying date was defined as the date the first egg was laid. If a nest was found between the laying of the two eggs (maximum clutch size; Maher 1970), we considered the laying date as the day before that visit. If a nest was found after laying, eggs were floated to estimate the incubation stage (Furness & Furness 1981, Liebezeit *et al.* 2007). If a nest was found at hatching, we estimated the laying date by subtracting the mean incubation length (24 days; Maher 1970) from the hatching date. A nest was considered successful if at least one chick left the nest. As Jaeger chicks are hard to find on the tundra after hatching, we considered a nest successful based on the presence of (1) chicks or aggressive adults in the nest vicinity, or (2) small shell fragments in nests visited soon

after hatching. A mate change occurred when a marked individual was observed with a new mate in a subsequent year, which could be due to a divorce or a death. We considered individuals to be divorced when both members of a pair were confirmed to be still alive and at least one was observed breeding with another mate (Choudhury 1995). Mate fidelity was calculated as the number of individuals, either males or females, breeding with the same mate, divided by the total number of breeding males or females that were re-observed. As Jaegers defend a radius of ~200–300 m around their nest (Andersson 1971), we considered site fidelity as the propensity for an individual to breed in this same area between years.

### Statistical analyses

For all analyses, we used generalized linear models using breeding pair as the sampling unit. First, we tested the relationship between nest displacement distance between years  $t-1$  and  $t$  (response variable), and mate fidelity between years  $t-1$  and  $t$  as an interaction with nesting success on year  $t-1$ . [Correction added on 18 October 2022, after first online publication: In the above sentence, the first occurrence of the term ' $t-1$ ' has been corrected in this version]. Second, we examined the relationship between nesting success in year  $t$  (response variable) and nest displacement distance between year  $t-1$  and  $t$ , either alone or with mate fidelity as an interaction, using a binomial distribution (response variable here is success or failure). Finally, we assessed the influence of mate fidelity on laying date and nesting success (at least one chick hatched). We used laying date relative to the annual mean (relative laying date = individual date minus annual mean) to correct for interannual environmental variability. All analyses were done using the software R (R Core Team 2021). Means are presented with standard errors throughout the results and slope parameters ( $\beta$ ) with their 95% confidence intervals.

## RESULTS

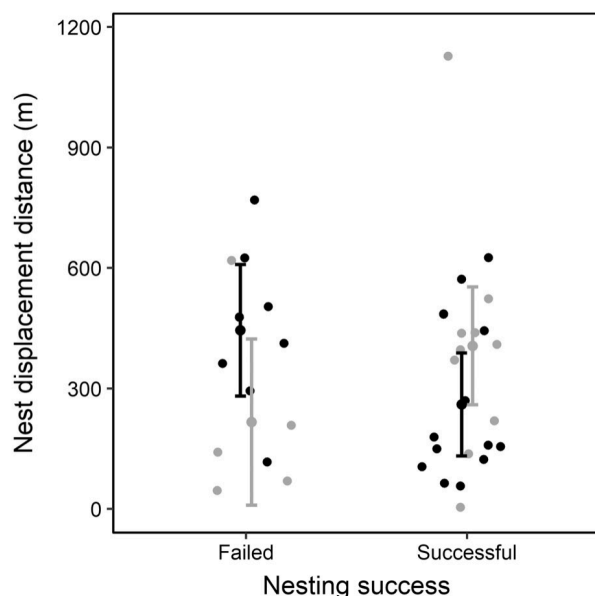
From 2007 to 2019, we observed 69 breeding pairs of marked individuals during 8 years of reproduction (Jaegers skip breeding when lemmings are scarce). These pairs were composed of 65 different ringed individuals (30 females, 29 males, six unknown) and were sighted on average during 1.8 years (range: 1–5 years).

Nesting sites of Jaegers that returned to breed at the study sites were separated by  $386 \pm 56$  m (range: 4–2266 m,  $n = 50$  nests) in different years. We found that nest-site fidelity was influenced by an interaction between nesting success (at least one chick hatched) in the previous year and mate fidelity ( $\beta = 374.1$  m (46.5 to 701.6),  $n = 36$  nests). Following successful nesting in year  $t-1$ , faithful mates moved a smaller distance the

subsequent year compared with those that remated (Fig. 1), whereas failed nesters that were faithful to their mate moved further in the subsequent breeding season compared with those that switched mates. We found no evidence that nesting success in year  $t$  was affected by nest displacement distance between year  $t-1$  and  $t$ , either alone ( $\beta = 0.001$  ( $-0.006$  to  $0.004$ )) or with mate fidelity as an interaction ( $\beta = 0.003$  ( $-0.004$  to  $0.009$ ),  $n = 35$  nests).

Overall, 72% of the males ( $n = 32$ ) retained their mate, whereas 28% were seen nesting in a subsequent year with a new mate. Among these, if we exclude females presumed to be dead (due to deployment of satellite transmitters; Seyer *et al.* 2021), then minimum mate retention was 79% ( $n = 29$ ) in males. For females, 85% retained their mate ( $n = 27$ ) and 15% switched mates. Considering an annual survival rate of 91% in Long-tailed Jaegers (Julien *et al.* 2013), we estimated that potentially 12% of males and 6% of females divorced annually, and that the remaining 9% were widowed. However, among all individuals that changed mates, we confirmed only one female breeding with a new mate at a new nest-site when her former mate was known to be alive because the latter was resighted nesting with a new female.

Nesting success of individuals that retained their mate was  $0.57 \pm 0.11$  ( $n = 21$ ), compared with  $0.80 \pm 0.11$  ( $n = 15$ ) for individuals that remated. However,



**Figure 1.** Annual nest displacement of Long-tailed Jaeger breeding pairs ( $n = 35$ ) on Bylot Island, Nunavut, based on nesting success (at least one chick hatched) in the previous year and mate fidelity (black: mate retained; grey: new mate). Error bars represent the 95% confidence intervals.

this difference was not statistically significant ( $\beta = 1.10$  ( $-0.36$  to  $2.78$ ),  $n = 36$ ), nor did we find a significant difference in relative laying date between these two groups ( $\beta = 1.04$  days ( $-0.38$  to  $2.45$ ),  $n = 32$ ).

## DISCUSSION

Our results provide the first evidence of relatively high nest and mate fidelity in Long-tailed Jaegers based on marked individuals, confirming assumptions in previous demographic models (Barraquand *et al.* 2014). Site fidelity was affected by both previous nesting success (success to hatch at least one chick) and mate retention. Birds whose nesting attempts have been unsuccessful often move further to breed in the following year compared with those that are successful (Dow & Fredga 1983, Switzer 1993, Hakkarainen *et al.* 2001, Sommerfeld *et al.* 2015). Breeding failure may serve as an index of site quality, and this may encourage individuals to look for a higher quality site in the same territory or move to another territory to nest. Curiously, the pattern was reversed in Long-tailed Jaegers that changed mates. Perhaps this is because the challenge of finding a new mate outweighs the potential effects of previous breeding success or because individuals evaluate the performance of their mate and attribute the failure to a poor territory, thus deciding to move further. Moreover, when mating with a new individual, site selection may be affected by the previous success of both pair members, one of which is unknown in this case. Thus, our results confirm the strong association between nest and mate fidelity as previously described for other species (Choudhury 1995, Bried & Jouventin 1999, 2002, Jan-kowiak *et al.* 2018).

After correcting our raw estimates of mate change for mortality rate (i.e. widowed birds), we estimated that only 12% of males and 6% of females divorced annually. A low divorce rate overall was further confirmed by a single observation of a divorced pair where both pair members returned to the study sites and mated with a different individual in subsequent years. Although we lack precision in our estimated divorce rates due to small sample size and acknowledge potential biases such as movement of birds outside the study area, our estimated values are lower than the median divorce rate (14%) for seabirds (see review in Mercier *et al.* 2021). Compared with other Stercorariidae, our estimates are comparable to divorce rates of Great Skuas *Stercorarius skua* (6%; Catry *et al.* 1997), Parasitic Jaegers *Stercorarius parasiticus* (7%; Phillips 1995) and Brown Skuas *Stercorarius antarcticus* (8%; Pich & Catry 2022), but higher than South Polar Skuas *Stercorarius maccormicki* (0%; Mercier *et al.* 2021).

Laying date was not influenced by mate fidelity, contrary to results for other species (González-Solís

*et al.* 1999, Sánchez-Macouzet *et al.* 2014, Lv *et al.* 2016). This suggests that when the previous mate does not return to the breeding site early in the season, individuals may start searching for a new one shortly after arrival to avoid missing or delaying breeding. Indeed, as breeding late in the season often reduces success (Perrins 1970, Bêty *et al.* 2003), including in Jaegers (Phillips *et al.* 1998, Seyer 2022), the benefits of remating quickly may exceed the costs of waiting in those situations (Sánchez-Macouzet *et al.* 2014).

Previous studies in this population showed an average delay of 14 days between the mean arrival and laying dates of Jaegers and a synchronous arrival of previous pair members (5 days apart on average; Seyer *et al.* 2021). Though courtship behaviour of Jaegers remains unknown (Wiley & Lee 2020), Furness (1987) reported that even faithful pairs take a few days before remating after they re-encounter each other on the nesting territory. Considering that seabirds generally do not remain together during the non-breeding period (Bried & Jouventin 2002, Seyer *et al.* 2021) and the short pre-laying period upon arrival, there is a strong pressure for synchronous arrival at the breeding site. Accordingly, the formation of a new pair is believed to be based on temporal assortative mating, allowing synchronicity in arrival in subsequent years (Furness 1987). Otherwise, asynchronous arrival may quickly lead to a divorce due to time constraints (González-Solís *et al.* 1999, Naves *et al.* 2006). This strategy probably reduces costs associated with the loss of a mate and could explain why laying date was not affected by mate retention.

As reported by Jeschke *et al.* (2007) and Ismar *et al.* (2010) in other seabirds, but contrary to Culina *et al.* (2015) and Sommerfeld *et al.* (2015), newly formed pairs did not suffer from lower nesting success compared with remated pairs. This suggests that when individuals remate without losing an opportunity to reproduce, the effect on reproductive performance is negligible. Nevertheless, finding a new mate and territory may involve time and energy costs associated with prospecting and fighting, which risks the breeding attempt being missed (Choudhury 1995, González-Solís *et al.* 1999, Jankowiak *et al.* 2018). This risk is especially severe for species breeding in an environment such as the Arctic where the reproductive season is very short (Mercier *et al.* 2021) and where interannual variability in resources is high (Seyer *et al.* 2020). However, the similarities in roles and investment in reproduction between mates (Furness 1987, Wiley & Lee 2020), and acquisition of food in a small inland territory (Andersson 1971), may reduce the cost of remating. This may help to reduce any inefficiencies associated with breeding with a new mate, which is often encountered in seabirds that need to synchronize incubation and chick-rearing duties (Choudhury 1995, van Rooij &

Griffith 2013, Pelletier & Guillemette 2022). Further work is needed to understand whether divorce in species such as Jaegers living in a variable environment is an adaptive strategy to increase breeding performance (see Choudhury 1995, Culina *et al.* 2015) or a random event in an otherwise highly faithful species.

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## AUTHOR CONTRIBUTIONS

**Yannick Seyer:** Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Gilles Gauthier:** Conceptualization (equal); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (equal); supervision (lead); visualization (supporting); writing – original draft (equal); writing – review and editing (equal). **Jean-François Therrien:** Conceptualization (equal); investigation (equal); methodology (equal); writing – review and editing (supporting).

## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## ETHICAL NOTE

None.

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## Data Availability Statement

Nesting data are available online (Gauthier *et al.* 2020).

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