



Contribution to the Theme Section 'Non-breeding distribution and movements of North Atlantic seabirds'

A two-fold increase in migration distance does not have breeding consequences in a long-distance migratory seabird with high flight costs

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ABSTRACT: Whether variation of winter migration distance among individuals within a population has consequences on their reproductive performance has rarely been assessed. Using individual global location sensor-tracking, we determined variation in migration distance, and its breeding consequences, in a Svalbard colony of the little auk *Alle alle*, a high-Arctic seabird with high flight costs. We found 2 distinct wintering quarters (north of Iceland and SW Greenland) implying a 2-fold difference in migration distance (1500 vs. 3100 km on average from the colony). This migration route from Svalbard to Greenland is among the longest recorded distances for an alcid species. Birds travelling a longer distance were more likely to be females and smaller, but more importantly, migration strategy had no apparent effect on reproductive performance (either timing or success). Our results contradict predictive studies which suggested that the establishment of migration routes to different winter destinations may be limited by the energetic constraints of flight. Our results show that a longer migration route does not necessarily have carry-over effects on subsequent reproduction.

KEY WORDS: Alcid · Little auk · *Alle alle* · Bird migration · Flight cost · Breeding success · North Atlantic · Logger

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1. INTRODUCTION

The evolution of the migration strategies of birds is predicted to be shaped by, among other factors, the energetic constraints of flight (Alerstam & Lindström 1990). Since migratory flights require time and energy (Weber & Houston 1997), this expenditure will increase with the distance covered but will also depend on the type of flight and wind conditions experienced (soaring vs. flapping species; Watanabe 2016). It has been shown in several migratory bird species that variability in wintering sites, habitats and/or migration phenology can be shaped by intra-specific competition (Croxxall et al. 2005, Phillips et

al. 2011) and may have important consequences for annual survival (Alerstam & Hedenstrom 1998, Reneerkens et al. 2020) and/or subsequent breeding performance (Alves et al. 2013) through carry-over effects (Gunnarsson et al. 2005, Norris 2005, Norris & Marra 2007, Harrison et al. 2011, Bogdanova et al. 2017). The great energetic costs during migratory flights experienced by individuals migrating over longer distances may entail fitness consequences (e.g. Hotker 2002, Bearhop et al. 2004, Bregnballe et al. 2006). However, under certain conditions, migrating farther may have no effect on reproduction (e.g. Kentie et al. 2017, Reneerkens et al. 2020) or may even be positively associated with reproduction and

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survival (e.g. Alves et al. 2013). Individuals performing long-distance migration may indeed compensate for these extra flight costs by taking advantage of optimal wintering conditions (i.e. high resource availability, low competition or predation; e.g. Alves et al. 2012, 2013, Conklin et al. 2017). The high energetic expenditure associated with a long migration distance may thus not always lead to higher fitness costs, and this relationship between energetic and fitness costs is likely to vary both at inter- and intra-species levels (Fayet et al. 2016).

In some seabird lineages like the alcids, the ability to fly has evolved under strong selective pressure toward a trade-off between flying and diving abilities. It has resulted in high flight costs (Thaxter et al. 2010, Elliott et al. 2013). In species using flapping flight, migration distance is therefore expected to be limited by the maximum physiological capabilities of a species and may also serve as a driver of individual fitness (Watanabe 2016, Fayet et al. 2017). Consequently, little variation in migration distance is expected within a given population for such species, as an increase in migration distance would lead to significant fitness costs and migrating farther would not be an adaptive strategy. While the co-existence of distant wintering grounds within the same population has been observed for this bird family (Fort et al. 2013a), the link between fitness and migration distance has rarely been assessed for alcids (but see Fayet et al. 2017). Likewise, it has never been shown in species with high flight costs, such as alcids, that wintering conditions and resource abundance may compensate for the additional flight costs that some individuals would endure (see Fort et al. 2013b).

The little auk (or dovekie) *Alle alle* is a small, colonially breeding, diving seabird. Like other alcids, it is characterised by flapping flight and high wing-loading values (Sakshaug et al. 2009) imposing high flight costs (higher than in other non-alcid seabirds using flapping or soaring flight). The species is restricted to the high Arctic in summer but spends the winter in various locations in the North Atlantic Ocean (e.g. Mosbech et al. 2012, Fort et al. 2013a). Preliminary results have suggested 2 wintering areas of the Svalbard breeding populations located near Iceland and in the Labrador Sea (Isaksen & Bakken 1996, Fort et al. 2013a). Little auks that breed in Svalbard are thus good candidates to study the mechanisms leading to such different wintering destinations and their ecological and demographic consequences (Gabrielsen et al. 1991, Harding et al. 2009, Fayet et al. 2017). Using individual global location sensor (GLS) tracking data from little auks

breeding at Hornsund, one of the largest colonies in Svalbard (Isaksen & Bakken 1996, Keslinka et al. 2019), we assessed individual variation in migration distance and its potential costs for subsequent reproduction. More specifically, we tested whether individuals travelling longer distances exhibit delayed breeding phenology (later breeding) and lower reproductive performance. Late breeding is usually associated with poor breeding success and/or offspring quality in birds, especially at high latitudes (Hipfner et al. 2010, Ramírez et al. 2016), including in the little auk (Jakubas & Wojczulanis-Jakubas 2013). We tested for different environmental conditions (e.g. sea surface temperature, SST) encountered on wintering grounds that could motivate and compensate for longer travels (see Alves et al. 2013). Finally, we also investigated the role of bird body mass, body size and sex as potential drivers of the inter-individual variation in wintering destination (Croxall et al. 2005, Phillips et al. 2011, Zhao et al. 2018).

2. MATERIALS AND METHODS

2.1. Geolocator deployment

Between 2015 and 2017 (3 consecutive breeding seasons), 113 GLS loggers were deployed on 92 different adult little auks breeding in the Hornsund colony, southwest Spitsbergen (77° 00' N, 15° 22' E; 21 birds were equipped over 2 non-consecutive years). Respectively, 30, 26 and 17 birds were tagged in 2015, 2016 and 2017. Birds were captured in the nest burrow during late incubation or early chick-rearing, and all birds were ringed using a metal ring on one leg, and a geolocator (MigrateTech models C65 and F100) attached to a plastic ring was fitted on the other leg. Body feathers were collected for molecular sexing (following the protocol of Jakubas & Wojczulanis 2007).

The GLS with accompanied elements (plastic ring, wire and glue) weighed 1.8 g, which constituted ~1% of body mass. All individuals were measured (wing and head–bill length, ± 1 and ± 0.1 mm, respectively), and weighed (± 2 g) both at deployment and at GLS retrieval. We did not find a negative logger effect on bird body mass, and mass at retrieval was similar to mass at deployment. We also found no difference in body mass between logger-equipped individuals at retrieval and control individuals (i.e. individuals not burdened with any logger, captured for the purpose of another project, at a similar breeding phase as GLS-equipped

birds; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m676p117_supp.pdf).

In total, 73% of loggers ($n = 82$) were retrieved (2 loggers were retrieved 2 yr after their deployment). Of these loggers, 11% ($n = 9$) experienced technical failure and gave no (or incomplete) information on the non-breeding movement of the individual; these were excluded from the analyses. The percentage of GLS recovered varied between years: 91% in 2015/2016, 88% in 2016/2017 and 44% in 2017/2018. A total of 73 loggers (65% of all deployed) carried by 61 different individuals were included in this study (11 birds were tracked over 2 different non-breeding seasons).

2.2. Migration route and activity analysis

Light data from both types of loggers (MigrateTech C65 and F100) were decompressed and processed using the method detailed by Merkel et al. (2016), implemented in the 'prob_algorithm' function ('prob-GLS' package) with the R software v.4.0.3 (R Development Core Team 2020). Due to the high latitudinal position of the colony, and logger deployment and retrieval occurring during periods of continuous daylight, location data were only available from early September to early April (when birds are expected to arrive at Svalbard, Stempniewicz 1981). In addition, due to the equivalent day length everywhere on Earth at the autumnal and spring equinox, latitudinal positions within 15 d on each side of the 2 equinox dates could not be estimated accurately (see Phillips et al. 2004), just as the error of GLS locations is known to vary up to 200 km (Phillips et al. 2004). After computing, each computed track was visually inspected and erroneous locations, particularly around polar night and midnight sun periods, were removed.

The maximum distance from the colony was then calculated as the great-circle distance between the colony and the farthest recorded position of the bird (Hijmans et al. 2015). We estimated the total distance covered during migration by summing the great-circle distances from averaged positions per 10 d period between 15 September and 9 April (outside the period of continuous daylight), thus excluding the distance between the colony and the moulting area.

We illustrated the different wintering and post-breeding locations of Hornsund birds using GLS positions of birds and the kernel density function of the ArcGIS software (ArcGIS Desktop 10.6, ESRI). Density values were then obtained for each location point and ranked (only in the case of wintering) into 3 classes of densities (25, 50 and 75%).

2.3. Environmental conditions on wintering grounds

To test whether environmental conditions, being a proxy for resource availability (see Fort et al. 2012) on the wintering grounds, differ between migration strategies, we extracted SST ($^{\circ}\text{C}$) values (mean, minimum and maximum) from polygons defined by individual locations (convex hull) in December and January. We extracted the average SST from 2002–2017 from the NASA OceanColor data (<https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MYD28M>). Gaps occurring in the raster files were filled using the kriging method in ArcGIS software. These monthly averaged SST values were then averaged into 1 wintering SST value for each individual. We chose SST, rather than a proxy for food availability such as primary productivity (i.e. chlorophyll *a* concentration), because it was the most complete at these latitudes during the winter months. Moreover, it has been shown that the distribution of prey (e.g. copepods) of little auks is temperature dependent, with more energetic prey (richer in lipids) frequenting colder waters and preferentially fed upon by little auks (Karnovsky et al. 2010, Jakubas et al. 2011, Grémillet et al. 2012), and that SST is a good proxy explaining copepod distribution (Fort et al. 2012). We therefore used SST as an indicator of food availability and/or productivity in the different wintering areas.

2.4. Breeding parameters

Due to the difficulty of direct observation in focal nests, breeding parameters (of the post-winter breeding season) could not be collected for all individuals. Hatching success (little auks lay only 1 egg) was recorded for 68 tracked individuals (93% of all tracked). To test the putative effect of wintering destination on hatching date, we calculated the relative number of days between the individual hatching date and the median hatching date for the colony ('relative hatching date' hereafter). Hatching date, corresponding to the first date on which a chick was recorded (nests were checked every 2–3 d), was recorded for the nests of 59 tracked individuals (81% of all tracked). For each breeding season, the median hatching date was calculated for a group of control nests ($N = 104$ in 2016, 50 in 2017 and 65 in 2018), varying between 7 and 13 July. Hatching dates are used as

a proxy of the breeding phenology and are expected to reflect the laying dates, since the incubation duration is virtually constant among individuals (mean \pm SD = of 29 ± 0.8 d, based on 332 nests monitored in another project and for which both laying and hatching dates were available; K. Wojczulanis-Jakubas unpubl.). Finally, chick survival (present/absent, i.e. alive/dead), expected to be a good proxy for parental performance (see Stempniewicz 2001), was recorded during the last nest control performed when chicks were up to 15 d old. Since it is unlikely not to find living chicks, chicks that were not found during this last check were considered dead.

2.5. Statistical analyses

To assess the variation in migration distance, we used a hierarchical cluster analysis (using the functions 'hclust' in R) on the winter location farthest from the breeding colony of each tracked individual (R Development Core Team 2020). Based on the higher relative loss of inertia criteria, we found that no more than 2 areas were used by migrating little auks (Iceland and Greenland wintering grounds, Fig. 1).

To assess little auk structural body size, we used the first principal component (PC1) of a principal component analysis (PCA), reducing the 2 body measurements (wing length and head-bill length) to a body size index (BSI; Freeman & Jackson 1990, Wojczulanis-Jakubas et al. 2011). PC1 extracted from the 2 variables accounted for 71.2% of the variability, with high BSI values indicating larger birds with a larger head and longer wings.

We used generalised linear and linear models ('lme4' package, Bates et al. 2014) to test the effect of the wintering grounds (Greenland vs. Iceland) on relative hatching date (using a Gaussian distribution), as well as on hatching success and chick survival in the following breeding season (using binomial distributions). Visual inspection of model residuals indicated a normal and homoscedastic distribution. To test whether the effect of the

wintering grounds differs among sexes, we included the interaction between sex and wintering grounds in our models. We also included year as a fixed effect in the models with hatching success and chick survival as variables to be explained, to take into account the inter-annual variation in breeding performance. Statistical significance was assessed with likelihood ratio tests comparing full and null models.

To test the effects of sex, body condition and body size as drivers of winter distributions, we fit a generalised linear model (GLM) with wintering destination as the dependent binary variable (coded as 0: Greenland, 1: Iceland) and BSI, body mass and sex as fixed effects. To deal with the collinearity detected between the explanatory variables (see Fig. S2) and to

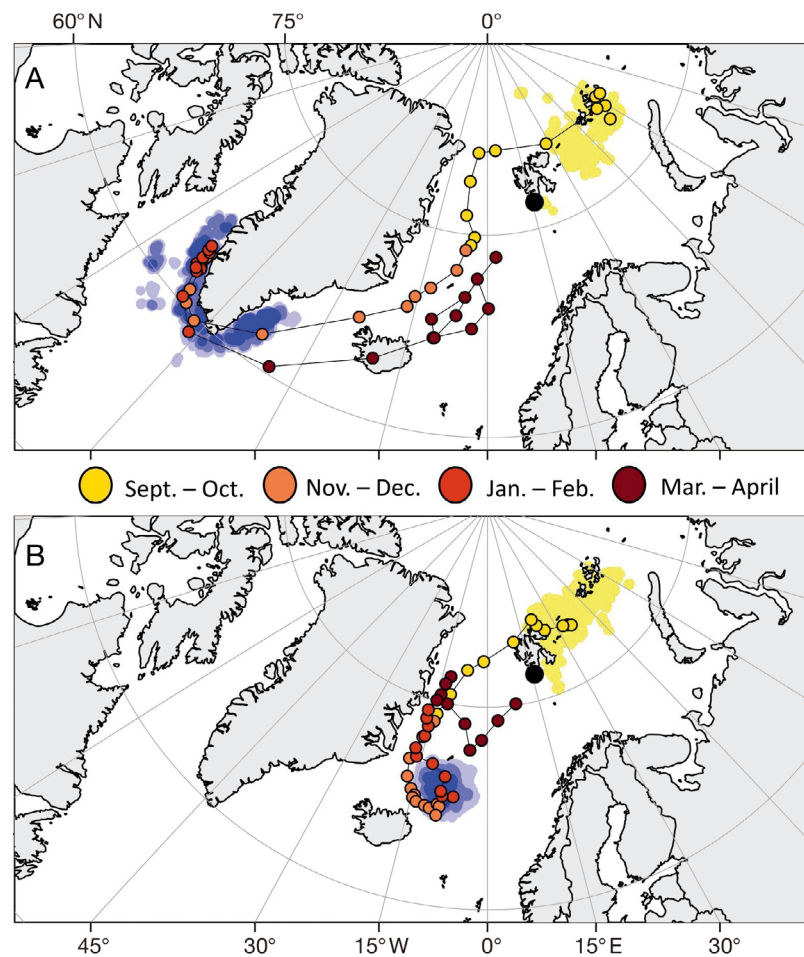


Fig. 1. Winter tracks of 2 global location sensor-equipped little auks breeding at the Hornsund colony (marked with a black dot) migrating to (A) Greenlandic waters (GRE) or (B) Icelandic waters (ICE). Each coloured point is a 5 d average position, and each colour represents a different period. Kernel density estimation of wintering areas for all birds of each wintering ground (N = 22 in GRE for 19 individuals and N = 51 in ICE for 45 individuals) are indicated in blue (see Section 2.2); yellow areas indicate putative moulting areas of staging positions during September and October

disentangle the effect of each variable, we considered in our model the residuals of the BSI adjusted for sex and body mass, and the residuals of the body mass adjusted for sex and BSI. Even if some individuals had been tracked for several years, using mixed models (generalised linear mixed models) with bird identity as a random effect or GLM (without this random effect) led to the exact same results and we have thus decided to only present results from the GLM. The amount of deviance explained by the model was calculated with the function 'Dsquared' (Barbosa et al. 2014).

3. RESULTS

Little auks breeding at Hornsund spent the non-breeding season either in marine areas located between Iceland and Spitsbergen, south of Jan Mayen (hereafter 'ICE') or in the Labrador Sea, southwest of Greenland, which they reach through the Denmark Strait (hereafter 'GRE'; Fig. 1). These 2 wintering areas were used by 70 and 30% of study birds, respectively, and this proportion remained relatively similar over years (varying respectively between 65 and 72% and between 28 and 35% in the period 2015–2018). We found that birds usually adopted the same migration strategy in consecutive years (8 out of 11 birds tracked over 2 yr followed the same routes; see Fig. S3). The categorisation into 2 wintering groups is well illustrated by the non-overlapping distances from the breeding colony when birds reached the farthest positions in December and January (Fig. 2A): GRE and ICE wintering birds reached on average 3145 ± 245 km (SD) and 1516 ± 273 km from the colony, respectively.

The total distance travelled over winter differed between the individuals wintering in the 2 distinct grounds (t -test: $t = -8.66$, $df = 71$, $p < 0.001$), with ICE birds covering considerably less distance (6347 ± 1265 km) than GRE birds (9569 ± 1930 km; see also

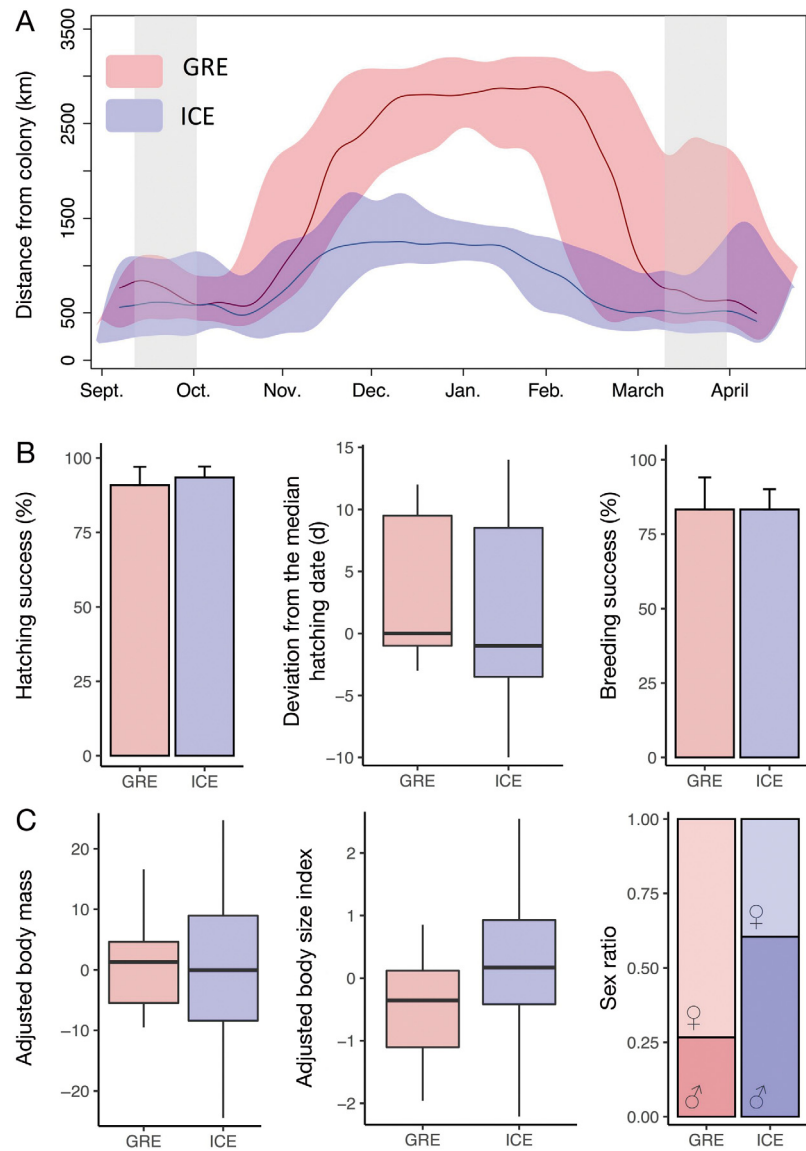


Fig. 2. (A) Estimated distance from the breeding colony in Hornsund for global location sensor-equipped little auks spending winter around Greenland (GRE, $N = 22$) and Iceland (ICE, $N = 51$). The solid line represents the median of each category. Upper and lower limits indicate 5 and 95% percentiles. Grey shaded areas in September and March indicate equinox periods. (B) Breeding parameters (hatching success [mean \pm SD], hatching date, and breeding success [mean \pm SD]) as a function of winter destination. None of these comparisons was significant. (C) Morphometric measurements and sex ratio as a function of winter destination. Adjusted body size index (BSI) and body mass represent the residuals of these variables (see Section 2.5). Boxplots show the median (band inside the box), the first (25%) and third (75%) quartile (box) and the lowest and the highest values within $1.5 \times$ the interquartile range (whiskers)

Fig. S4). Despite this, birds spending the winter in both areas showed a similar general migration pattern in that they left the expected moulting areas (between Spitsbergen and Franz Josef Land) at the end of September to reach their wintering area in

November. In addition, for each wintering group, we found no difference in phenology and migration routes between the sexes after the breeding period and during the winter season (Fig. S3); we only found a significant sex difference for individuals spending winter in Greenland quarters during the first days of April (between 1 and 9 April), with females located farther from the colony compared to males (Student's *t*-test: $t = 2.66$, $df = 25$, $p = 0.01$; Fig. S3).

Winter SST differed significantly between the 2 wintering areas, with GRE birds spending winter in colder waters (mean \pm SE = $3.73 \pm 0.26^\circ\text{C}$) than ICE birds ($4.50 \pm 0.11^\circ\text{C}$) (Fig. 3). The difference was greatest for minimal temperatures (difference of 1.07°C ; *t*-test: $t = 4.90$, $df = 67$, $p < 0.001$; Fig. 3), followed by maximal values (1.01°C ; *t*-test: $t = 3.91$, $df = 67$, $p < 0.001$) and by mean values (0.76°C on average for GRE birds; *t*-test: $t = 3.55$, $df = 67$, $p < 0.001$).

Birds migrating to ICE and GRE exhibited similar breeding phenology (likelihood ratio test, LRT, $p = 0.63$), hatching success (LRT, $p = 0.53$) and chick survival (LRT, $p = 0.89$; see Fig. 2B) in the subsequent season.

Migration routes were independent of body mass but dependent on BSI (Table 1; see Fig. 2C), with large birds (high BSI) spending the winter more

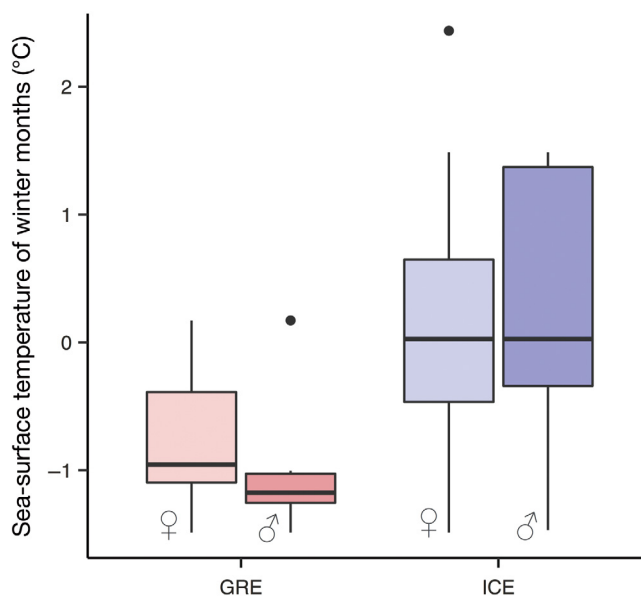


Fig. 3. Winter conditions encountered by little auks according to adopted wintering strategy (GRE: Greenland wintering area, ICE: Iceland wintering area) and sexes (♀: female, ♂: male). Sea surface temperatures (here minimal values) are for December and January. Boxplots show the median (band inside the box), the first (25%) and third (75%) quartile (box), the lowest and the highest values within 1.5× the interquartile range (whiskers) and outliers (dots)

Table 1. Results of the generalised linear model (with a binomial distribution where 0: Greenland, 1: Iceland) testing the effect of sex, body condition and morphometry as drivers of winter distribution. Adjusted body size index (BSI) and body mass represent the residuals of these variables (see Section 2.5). Significant variables (at $p < 0.05$) are indicated in **bold**

Variables (fixed)	Estimate	SE	z	p
Intercept	0.48	0.41	1.17	0.242
Adjusted BSI	0.69	0.34	2.01	0.045
Adjusted body mass	0.00	0.03	0.11	0.911
Sex (male)	1.57	0.70	2.24	0.025

frequently in ICE. Similarly, the sex ratio differed among the 2 wintering destinations, being female-biased in GRE and male-biased in ICE (Table 1; GRE: 70.5% females, ICE: 40.9% females). We found that 14.7% of deviance was explained by the model.

4. DISCUSSION

Our study shows that little auks breeding in Hornsund, Svalbard, have 2 distinct winter destinations, and these locations are consistent with previous findings from another colony in Svalbard (Kongsfjorden, Fort et al. 2013a). The co-existence of distinct wintering destinations within the same population has also been observed in other alcids (e.g. Brünnich's guillemots *Uria lomvia*, Frederiksen et al. 2016; Atlantic puffins *Fratercula arctica*, Fayet et al. 2017) and in other seabirds in general (e.g. Kopp et al. 2011, Rayner et al. 2011). However, the dichotomy of migration routes observed in little auk breeding in Hornsund is remarkable. In fact, the estimated distance travelled from Hornsund to southwest Greenland (ca. 10 000 km) is among the longest recorded distances to date for an alcid species (McFarlane Tranquilla et al. 2013, Frederiksen et al. 2016, Fayet et al. 2017), and is comparable to soaring species (e.g. northern fulmar *Fulmarus glacialis*, Hatch et al. 2010; great skua *Catharacta skua*, Magnúsdóttir et al. 2012).

In several bird species, travelling longer distances during the non-breeding period entails costs in the following breeding season through carry-over effects (see Bearhop et al. 2004, Bregnballe et al. 2006). However, our results show that even in seabirds with high flight costs, such as alcids (Elliott et al. 2013), migration distance may not have any apparent carry-over effect on subsequent reproductive performance. Little auks that overwintered in Greenland travelled twice as far as those wintering in Iceland; nevertheless, we did not detect any apparent differences in

breeding parameters in the following season between these 2 groups. Our results are consistent with those found in several species of shorebirds (Conklin et al. 2017, Kentie et al. 2017, Reneerkens et al. 2020), which show no effect of long migration distance on reproduction. Although these 2 wintering distances may in theory be associated with different survival rates (see Reneerkens et al. 2020), our study does not support the hypothesis that migrating farther leads to reduced breeding performance in little auks. However, this does not mean that migrating farther has no fitness cost. This study focusses on the potential costs on subsequent reproduction, but migrating farther may also entail costs to long-term survival and lifetime reproductive performance of individuals (Frederiksen et al. 2016). This lack of effect likely indicates that increased travel costs are compensated for by potentially higher energetic benefits at the wintering grounds (Lundberg 1988, Grémillet et al. 2012, Fort et al. 2013b), such that these higher energetic costs do not translate into breeding costs. In support of this, we found that winter SST differed significantly between the 2 wintering areas, with Greenland birds spending winter in colder waters than Iceland birds. Even if colder waters increase the energetic expenditure of the birds (Fort et al. 2009), the differences in SST observed between wintering areas could indicate that birds in these areas access a different composition or abundance of prey (Fort et al. 2012), since more energetic prey (richer in lipids) may occupy colder waters (Karnovsky et al. 2010, Grémillet et al. 2012). While we currently lack empirical support confirming this mechanism, such a trade-off between prey availability/profitability and distance to the wintering grounds could explain why Hornsund birds have the same reproductive output regardless of different wintering grounds. Further research on the winter diet and energy intake of little auks would be needed, but this result still suggests that even for a species with high flight costs, a migratory journey of several thousand kilometers could be compensated for by finding more energetic resources at the wintering sites.

Our results also indicate that more females winter around Greenland than males while the opposite is true for Iceland. This suggests a partial spatial sex segregation during winter. Sex segregation has been observed in several migratory seabirds, and in migratory birds in general (Marra & Holmes 2001, Croxall et al. 2005, Ruckstuhl 2007). However, previous studies demonstrating sex segregation in seabirds have found that males and females segregate for the entire non-breeding season and occupy dif-

ferent ecological niches (Phillips et al. 2011). In little auks, a possible explanation for sex differences could come from the fact that females end their breeding season before chick fledging (Konarzewski et al. 1993), may leave the colony before males and have more time to reach a more distant destination. However, here we found sex segregation only in the wintering areas, whereas there were no apparent sex differences in bird locations prior to reaching their wintering destinations, when they are migrating and potentially moulting between Spitsbergen and Franz Josef Land (see Mosbech et al. 2012).

Another hypothesis for this sexual segregation could come from sex-specific requirements (see Phillips et al. 2011), since females may need to replenish after the breeding season. Indeed, they spend a lot of energy to produce their egg. While the production cost is unknown (see Williams 2005), it is assumed to be high given the size of the egg (~20% of the female body mass; Stempniewicz 2001). We also found that individuals wintering in Greenlandic waters have a smaller body size (independent of sex), suggesting that intra-specific competition may cause smaller and potentially less competitive individuals to migrate farther (Marra & Holmes 2001). On the other hand, it has also been shown that smaller birds are more likely to travel long distances (Zhao et al. 2018) and with relatively low flight costs (Alerstam & Lindström 1990, Watanabe 2016), which is consistent with this result. Collectively, these results indicate that differential migration may exist in little auks (see Cristol et al. 1999), but the reasons behind such winter spatial segregation remain unclear. Competition for food mediated by sex or body size (Ruckstuhl 2007) could drive such a segregation. Even if there is no indication for sex partitioning in the winter diet of little auk (Rosing-Asvid et al. 2013), food intake may still be different between sexes, but information on little auk winter diet is thus far very limited.

An alternative potential explanation is based on the observation of a body size gradient in little auks between the west and east of their distribution range (Wojczulanis-Jakubas et al. 2011), with birds getting larger from west to east. This suggests that smaller individuals from Svalbard may be more closely related to Greenland birds and may have retained their overwintering habits in Greenlandic waters, assuming imprinted migration and wintering choices. Since major glacial events have probably shaped the little auk distribution many times, it is possible that the locations of the wintering areas observed today are the result of a post-glacial recolonisation pathway of the species. This hypothesis

remains speculative for now and should be tested with a tailored phylogeographic approach. In addition, since we observed a few individuals that changed their wintering destination among the birds followed over 2 wintering seasons, we may assume that wintering quarters and migration routes are not completely imprinted and that individuals are flexible in their migration strategies. It would be interesting to track both parents of a pair. This would allow testing if the choices of one parent, and/or the change in wintering destination, have consequences on the following breeding season (see Fayet et al. 2017), as well as testing if reproductive success has an effect on the wintering destination of the parents (see Bogdanova et al. 2011). It would also be interesting to track the wintering destinations of the juvenile birds (Péron & Grémillet 2013) to test whether the orientation of a juvenile depends on that of the male, which accompanies the juvenile when it leaves the colony (Bradstreet 1982). If the juvenile accompanies the male during its first winter, it can be assumed that the male leads the juvenile to overwintering areas near the colony (to avoid a long and difficult trip). Such a constraint would then be invalid in the case of failed breeding.

To conclude, this study, based on one of the longest journeys to the wintering area recorded among alcid species, suggests that migration distance may not be tightly related to individual fitness, and travel cost may be compensated for by resource benefits, even in species with high flight costs. This study also invites an examination of the consequences that these migratory choices have on survival and breeding performance in the long term. Such results may have important implications for understanding how little auks will be able to adapt their migration strategies in response to the rapid environmental changes they are facing at their wintering grounds (see Amélineau et al. 2019, Clairbaux et al. 2019).

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