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Local food availability and nonbreeding carry-over effects affect breeding propensity and success of a tundra-nesting predator, the Long-tailed Jaeger

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ABSTRACT

Reproduction of long-distance migrants can be affected by local conditions on the breeding grounds as well as those encountered during the nonbreeding season through carry-over effects. We show that this is true in Long-tailed Jaegers (*Stercorarius longicaudus*) because individuals that spent less time flying at sea during winter had a high breeding propensity and a reduced pre-laying interval, but breeding propensity and nesting success were also positively associated with food abundance at the breeding site. This seabird switches from a marine to a terrestrial lifestyle to breed in summer in the Arctic, where it primarily feeds on lemmings. We monitored jaeger reproduction and lemming densities on Bylot Island in the Canadian Arctic for 16 years, and we used geolocator to study annual movements. We assessed whether movement parameters (travel distance, migration duration, phenology, and number of flying bouts inferred by saltwater immersions) during the nonbreeding season affected the breeding propensity, phenology, and success of individuals. We also examined whether cyclic lemming fluctuations influenced Long-tailed Jaeger reproduction and whether nesting success affected the phenology of their outbound migration. We found that increased time spent flying during winter and early arrival at the breeding site reduced breeding propensity. Moreover, spending less time flying during winter shortened the pre-laying period, and advancing laying date increased nesting success. Birds may thus face a trade-off to minimize the relative costs associated with arriving too early and breeding too late. Local food availability had a strong effect on reproduction because breeding propensity and nesting success increased sharply with lemming abundance. Failed breeders advanced their outbound migration by 10 days on average compared to successful ones, but migration duration was similar. Therefore, the unpredictability of the highly seasonal Arctic environment, especially fluctuating food abundance, appears to be a strong driver of reproduction that can modulate the strength of carry-over effects.

Keywords: breeding propensity, carry-over effects, lemming abundance, local food resources, long-distance migration, nesting success, winter activity

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LAY SUMMARY

- Reproduction of migratory birds may be affected by both environmental conditions encountered at the breeding and wintering sites or during migration.
- We studied this question in Long-tailed Jaegers, a seabird that nests in the Arctic, where they feed on lemmings in summer, a prey that shows high-amplitude fluctuations in abundance.
- We tracked individual jaegers year-round to assess whether movement parameters during the nonbreeding season and lemming abundance in the Arctic affected their reproduction.
- We found that individuals that spent less time flying at sea during winter had a higher chance to breed and that high lemming abundance at the breeding site also increased both the chance of breeding and nesting success.
- We conclude that conditions encountered in distant ecosystems in winter can also affect the reproduction of migratory birds breeding in highly variable and unpredictable environments.

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La disponibilité locale de nourriture et les effets reportés de l'hivernage affectent la propension à la reproduction et le succès reproducteur d'un prédateur nichant dans la toundra, *Stercorarius longicaudus*

RÉSUMÉ

La reproduction des migrateurs de longue distance peut être affectée par les conditions locales sur les sites de reproduction ainsi que par celles rencontrées en dehors de la saison de reproduction par le biais d'effets reportés. Nous montrons que c'est le cas chez le labbe à longue queue (*Stercorarius longicaudus*), car les individus qui ont passé moins de temps à voler en mer au cours de l'hiver avaient une forte propension à la reproduction et un intervalle pré-ponte réduit, mais la propension à la reproduction et le succès de nidification étaient aussi positivement associés à l'abondance de la nourriture sur le site de reproduction. Cet oiseau marin passe d'un mode de vie marin à un mode de vie terrestre pour se reproduire en été dans l'Arctique, où il se nourrit principalement de lemmings. Nous avons suivi la reproduction de *S. longicaudus* et les densités de lemmings pendant 16 ans sur l'île Bylot, dans l'Arctique canadien, et nous avons utilisé des géolocalisateurs afin d'étudier les mouvements annuels chez cette espèce. Nous avons évalué si les paramètres de déplacement (distance parcourue, durée de la migration, phénologie et nombre de vols inférés à partir des immersions en eau salée) pendant l'hiver affectaient la propension à se reproduire, la phénologie de reproduction et le succès de reproduction des individus. Nous avons aussi examiné si les fluctuations cycliques des populations de lemmings influençaient la reproduction de *S. longicaudus* et si le succès de nidification affectait la phénologie de leur départ pour la migration post-reproduction. Nous avons trouvé que l'augmentation du temps de vol en hiver et une arrivée hâtive au site de reproduction réduisent la propension à se reproduire. En outre, le fait de passer moins de temps à voler pendant l'hiver raccourcit la période pré-ponte, alors que le fait de devancer la date de ponte augmente le succès de nidification. Les oiseaux peuvent donc être confrontés à un compromis pour limiter les coûts relatifs associés à une arrivée trop hâtive et à une nidification trop tardive. La disponibilité locale de la nourriture a eu un effet important sur la reproduction, car la propension à se reproduire et le succès de nidification ont fortement augmenté avec l'abondance des lemmings. Les oiseaux nicheurs qui ont échoué leur reproduction ont devancé leur départ pour la migration de 10 jours en moyenne comparativement aux oiseaux ayant eu du succès, mais la durée de la migration était similaire. Par conséquent, l'imprévisibilité de l'environnement arctique très saisonnier, particulièrement la fluctuation de l'abondance de la nourriture, semble être un puissant catalyseur de la reproduction qui peut moduler la force des effets reportés.

Mots-clés: propension à la reproduction, effets reportés, abondance de lemmings, ressources alimentaires locales, migration de longues distances, succès de nidification, activité hivernale

INTRODUCTION

Migratory animals often use resources from several distant and highly different ecosystems, such as terrestrial and marine ones. These links between ecosystems can affect population dynamics of many species (Webster et al. 2002, Bauer and Hoye 2014) and even the structure of food webs through nutrient exchanges (Gauthier et al. 2011, Zwolicki et al. 2013, Robillard et al. 2021). During their annual cycle, long-distance migrants must pass through different types of environments that change seasonally. They need to use sites when enough resources are available and which are usually predictable over time (Newton 2008, Gilg and Yoccoz 2010). Moreover, they need to arrive at breeding sites at the right time to avoid mismatches between reproduction and phenology and the abundance of their prey (Crick 2004, Both et al. 2010, Doiron et al. 2015). This creates a challenge for migrants to adjust to both local and long-distance conditions throughout their annual cycle.

Many studies have shown that conditions encountered during migration and wintering periods (e.g., weather conditions, food abundance, competition, disturbance) can subsequently affect reproductive performance (Marra et al. 1998, Morrissette et al. 2010, Legagneux et al. 2012, Salton et al. 2015). For instance, individuals displaying high levels of activity during winter, such as more time spent flying or prospecting and less time resting, may skip a breeding season to improve body condition and ultimately their lifetime reproductive success (Kazama et al. 2013, Shoji et al. 2015). These are cases of carry-over effects, defined by O'Connor et al. (2014) as "any situation where an individual's previous history and experience explains a significant proportion of their current performance in a given situation." Carry-over effects are typically documented from the wintering period or the return migration on subsequent reproduction. However, events occurring during the breeding season can also affect processes occurring at later stages such as molting and outbound migration, and may even be carried over to the next breeding season (Kalmbach et al. 2004, Catry et al. 2013, Low et al. 2015, Shoji et al. 2015, Fayet et al. 2016).

Carry-over effects usually act in combination with conditions prevailing during the current season. Indeed, reproductive decisions such as whether to initiate breeding, and when and how much to invest in reproduction will likely be influenced both by carry-over effects and conditions encountered on breeding grounds (Morrissette et al. 2010, Legagneux et al. 2012, Buchan et al. 2021). For instance, the timing of breeding is an important determinant of reproductive success in seasonal environments (Low et al. 2015) because early breeders usually have higher reproductive success than late breeders (Perrins 1970, Lepage et al. 2000, Harms et al. 2015). The timing of breeding or clutch size can be strongly affected by local conditions, such as food availability, weather conditions, or the presence of competitors (Erikstad et al. 1998, Therrien et al. 2014). However, arrival date at breeding sites and body condition, which will often depend on events occurring during migration or the preceding wintering period, can also impact these breeding decisions (Bêty et al. 2003, Kalmbach et al. 2004, Descamps et al. 2011, Harms et al. 2015).

Migratory species nesting in environments where resources show high interannual variability face additional challenges due to the unpredictability of food resources. This is especially the case for species feeding on prey that show cyclic fluctuations of abundance, such as lemmings in the Arctic tundra that can vary 100-fold or more between peaks and lows (Gilg et al. 2006, Therrien et al. 2014, Beardsell et al. 2016). The relative importance of carry-over effects from the nonbreeding season compared to local conditions has received little attention in such systems. The Long-tailed Jaeger (*Stercorarius longicaudus*), a small seabird (body mass ~300 g), is an interesting model to study this question. Jaegers perform one of the longest avian migrations from their breeding sites in the High Arctic to wintering areas scattered throughout the southern oceans (van Bemmelen et al. 2017, Seyer et al. 2021). During their breeding season (boreal summer), jaegers switch from a marine lifestyle to an entirely terrestrial one, and their reproduction is highly dependent on cyclic lemmings (Barraquand et al. 2014, Julien et al. 2014, Therrien et al. 2014, Seyer et al. 2020). Their very long migration and ecosystem switches expose them to diverse environments throughout their annual cycle. Thus, these conditions have the potential to lead to carry-over effects across seasons and, in combination with local conditions, affect their reproduction (Webster et al. 2002, Norris and Marra 2007, Briedis and Bauer 2018).

This study aimed to test for reciprocal carry-over effects between reproduction, migration, and wintering periods in a long-distance migrant breeding in an environment where food resources are variable and unpredictable. Under such conditions, we hypothesized that reproductive success should be strongly affected by local food abundance, but weakly by carry-over effects from the nonbreeding season. We first evaluated potential carry-over effects from the wintering period (i.e., travel distance, time spent flying at wintering areas, wintering area used, and migration phenology) on subsequent reproductive parameters (breeding propensity, phenology, and success) of individuals. We expected that individuals with reduced levels of activity in winter (i.e., less time spent flying in search of food and distance travelled) or early arrival dates at breeding sites could present a higher breeding propensity and success because they might present a better body condition at arrival (Bêty et al. 2003, Shoji et al. 2015, Hennin et al. 2016). We also quantified how local conditions on the breeding ground (i.e., lemming abundance) could affect breeding propensity and success as well as breeding phenology. We expected a much higher breeding performance of individuals in years of high lemming abundance. Finally, we evaluated how reproductive success modulated outbound migration phenology.

METHODS

Study Area and Study Species

Fieldwork was conducted during the jaeger breeding seasons (mid-June to early August) on Bylot Island (Nunavut; 73.133°N, 80.000°W) in the Canadian High Arctic. The area is composed of rolling hills with gentle slopes, low-elevation plateaus, and lowlands. Mesic tundra dominates the landscape, but wetlands associated with ponds and polygons (i.e., microrelief pattern created by ice wedges in the ground that forms ridges, sometimes enclosing pools) are common in lowlands (Gauthier et al. 2011). The mesic tundra is dominated by prostrate shrubs and a sparse cover of forbs and graminoids. The Qarlikturvik Valley (35 km^2), the main study site, is situated in a large glacial valley, and the secondary site (25 km^2) is situated 30 km to the south in the center of a large Snow Goose (*Anser caerulescens*) nesting colony. Two rodent species are present at the study site, brown lemmings (*Lemmus trimucronatus*), which displays large-amplitude fluctuations of abundance every 3–4 years, and collared lemmings (*Dicrostonyx groenlandicus*), which shows weak amplitude fluctuations (Gruyer et al. 2008, Gauthier et al. 2013).

Long-tailed Jaeger nest on the tundra in open areas, mostly moist and mesic meadows on flat terrain, and to a lesser extent in mesic tundra on gentle slopes (Seyer et al. 2020, Wiley and Lee 2020). During the breeding period, jaegers feed primarily on lemmings (Seyer et al. 2020) but also on young passerines and shorebirds, arthropods, and berries (Maher 1970, Andersson 1971). Their main nest predators are Arctic foxes (*Vulpes lagopus*), Glaucous Gulls (*Larus hyperboreus*), and Common Ravens (*Corvus corax*; Wiley and Lee 2020). During the nonbreeding period, jaegers migrate mostly to austral regions and spend ~144 days at 1 of 6 identified wintering areas, all associated with major oceanic currents (van Bemmelen et al. 2017, Seyer et al. 2021). The Benguela Current is the main wintering area used by ~68% of jaegers from Bylot Island, whereas the Canary, Guinea, Agulhas, Brazil, and North Equatorial currents are used by 3–15% of the population (Seyer et al. 2021). Because data were incomplete for individuals wintering in the North Equatorial and Guinea areas, we did not consider them in our analyses.

Field Methods

Nest monitoring

From 2004 to 2019, we carried out systematic nest searches along parallel transects separated by 400 m in late June and early July throughout the main study site. Breeding jaegers are easy to detect due to their alarm call when intruders are up to 200 m from their nest (Andersson 1971, Wiley and Lee 2020). At the secondary study site, nests have been found opportunistically when conducting goose nest monitoring activities since 2015. All nests were georeferenced when found (data availability: Gauthier et al. 2020).

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 laying of the two eggs (maximum clutch size; Maher 1970), we considered laying date as the day before that visit. If a nest was found after laying, we used flotation to estimate the incubation stage. Eggs were placed in a receptacle with warm water, and we noted their exact position, which changed from horizontal at the bottom for freshly laid eggs to upright with the blunt end breaking the water surface near hatching because egg density decreased during incubation (Furness and Furness 1981, Liebezeit et al. 2007). Egg position was related to the incubation stage in a sample of nests with known laying date. Finally, if a nest was visited 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. Because jaeger chicks leave the nest within 2 days after hatching and are hard to find on the tundra, 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. Success could be confirmed only for nests located at the main study site due to field constraints.

Bird capture

We captured breeding jaegers at the nest during incubation from 2007 to 2019 using a bownet trap, or in the nest vicinity using a noose carpet, a netgun, or a bal-chatri trap (Bloom et al. 2007). All captured birds were marked with a metal band and a coded plastic band that could be read at distance. Fifty-seven individuals were also equipped with a geolocator (light-level loggers; Intigeo-C65, Migrate Technology, Cambridge, UK) attached to the plastic band (see Seyer et al. 2021 for more details; data availability: Seyer et al. 2022). Geolocators measured 14 × 8 × 6 mm and weighed 1 g, representing ~0.7% (geolocator with band) of the body mass (female: 318 g, male: 286 g; Seyer et al. 2019). Because jaegers are faithful to their nesting territory (Seyer et al. 2023), all nesting territories of jaegers marked with geolocators were thoroughly searched in subsequent years to find their nest and recapture individuals. This sample was also used to estimate breeding propensity, defined as the probability to initiate a breeding attempt at the study site. A marked bird was considered to have skipped breeding if (1) it was resighted on/near its breeding territory, but no nest was found or (2) it was not resighted in that year but was resighted in the following year on/near its breeding territory.

Monitoring of lemmings

We live-trapped lemmings annually from 2004 to 2019 in 2 permanent 11-ha grids in the center of the main study site, 1 in wet tundra habitat and 1 in mesic habitat (see Fauteux et al. 2015 for details on methods). Three-day trapping sessions were conducted twice (mid-June and mid-July), and all captured lemmings were identified to species, marked, and released. Lemming densities were estimated with spatially explicit capture–recapture models for each trapping period and grid (details in Fauteux et al. 2015). We averaged June and July lemming densities to avoid an underestimation of the early summer lemming density (hereafter lemming density) in late snowmelt years. Finally, we averaged densities between grids, and we summed densities of each species.

Movement Analysis

We deployed 65 geolocators from 2014 to 2018, and we recovered 40 of them from 2015 to 2019, which yielded 41 tracks from 32 different individuals ($n = 8$ individuals received 2 geolocators). Among these, we had 23 complete migrations including the return date to the breeding ground after a full year. Geolocators sampled light intensity each minute and recorded its maximum value every 5 min. Wet-immersion sensors recorded values on an arbitrary scale from 0 to 127 every 30 s, a good indication of whether the bird was in contact with saltwater (values > 63 indicated immersion in saltwater and those < 63 immersion in freshwater; Fox 2013). During the nonbreeding period, saltwater immersions were associated with resting and/or foraging bouts, while non-immersions were associated with flying bouts (either travel or vagrant flight; Seyer et al. 2021). We estimated locations of individuals with light intensity data twice daily throughout the annual cycle with the threshold method (Ekstrom 2004, Lisovski and Hahn 2012) using a Bayesian approach implemented in the *SGAT* package (Wotherspoon et al. 2013) in R (other packages mentioned below are also in R).

We used a changepoint analysis with the *cpt.meanvar* function from the package *changepoint* (Killick and Eckley 2014) to identify sudden changes in daily number of immersions when jaegers finished breeding and switched to a marine lifestyle to migrate, and conversely when they arrived to breed in the subsequent year. We summed daily number of immersions and calculated a 3-day running mean. A visual inspection of changepoint plots allowed us to select transitions corresponding to the beginning of outbound and the end of return migrations.

To define the wintering period, we used a 3-step approach based on the "Migratory Analytical Time Change Easy Detection" method (Chen et al. 2016, Doko et al. 2016). First, we performed a changepoint analysis to identify sudden changes in an ordered sequence of data for 3 parameters: latitude, longitude, and net-squared displacement (NSD), which corresponds to the straight-line distance between the starting location, the breeding site, and any other subsequent location. During the wintering period, we expected the 3 parameters to present flat and stable lines because birds should be staying in the same region. Second, a visual inspection of these parameters (latitude, longitude, NSD) plotted together with the migratory path helped identify the beginning and end of the wintering period. Finally, we validated dates with those estimated from stationary periods revealed by the *ChangeLight* function from the package *GeoLight* (Lisovski and Hahn 2012) for the same time period (i.e., winter; see Seyer et al. 2021 for more details).

Analyses of geolocator data yielded several variables: departure and arrival dates at the breeding site and at wintering areas, duration of outbound and return migrations, the wintering area used and time spent there, distance travelled, travel speed, and daily number of immersions (see Seyer et al. 2021 for details and Seyer 2022 for individual data). We used daily number of non-immersions (2,880 minus daily number of immersions) as a proxy of the time spent in flight (hereafter flying bouts), the rest being either foraging or resting at sea (Seyer et al. 2021). As suspected, several of these variables were correlated (Supplementary Material Table S1). For analyses, we selected variables that were the most biologically meaningful in relation to our question of interest (i.e., best proxies of winter activity levels and phenology) and showed a low correlation (≤0.51) between them. To test the influence of the nonbreeding period on reproductive parameters, we selected daily number of flying bouts and distance travelled at wintering areas, return migration duration, and arrival date at the breeding site as predictor variables. To test the influence of reproductive success on outbound migration, we selected the departure date from the breeding site and duration of outbound migration as response variables.

Statistical Analyses

Conducting a global analysis with all our predictor variables was not possible because missing values for several individuals would have forced us to discard many of them, thus leaving us with too small sample size. We preferred to run multiple analyses using simpler models with only one or two predictor variables to maximize sample size in each analysis (see Discussion for limitations of the data). We used a generalized linear model (GLM) to assess the influence of daily number of flying bouts and distance travelled at wintering areas and return migration duration (predictor variables) on arrival date at the breeding site (response variable) for jaegers marked with geolocators. We used two different GLMs to assess the influence of (1) daily number of flying bouts at wintering areas and (2) distance travelled at their wintering areas and arrival date at the breeding site on either breeding propensity (binomial distribution in this case) or laying date. We also used a GLM to assess the influence of daily number of flying bouts at wintering areas on the prelaying interval (delay between arrival date at the breeding site and laying date) in an a posteriori analysis.

Because jaegers are known to be faithful to their wintering areas (van Bemmelen et al. 2017, Seyer 2022), we considered that individuals equipped with a geolocator always wintered at the same site every year, even though that site was determined in a single year for most individuals. Thus, we included all breeding attempts of these individuals either to assess the influence of wintering areas used on breeding propensity or laying date using generalized linear mixed models (GLMM; *lme4* package; Bates et al. 2015). We also used a GLM to assess the influence of wintering areas used and lemming density at the breeding site (predictor variables) on nesting success (response variable). For analyses using individuals marked with geolocators, we used GLMMs with year as a random factor when the sample size was sufficient to account for interannual variability in lemming density at the breeding site. We calculated marginal R^2_m (for fixed effects) and conditional R^2_c (for fixed and random effects) based on Nakagawa and Schielzeth (2013).

We used a GLM with a binomial distribution to assess the influence of lemming density on breeding propensity of marked individuals. We used two GLMs to assess the influence of lemming density on laying date (expressed as the day of the year to compare across years) and clutch size (with a binomial distribution in the latter case) using all nests monitored during the study period. We considered clutch size as a binary variable because jaegers lay 1 or 2 eggs. With two different models, we also tested whether nesting success (response variable) was affected by either lemming density or laying date (predictor variables). We repeated the same analysis by expressing laying date as a deviation of the annual mean to control for annual variation in nesting phenology. Nesting success was analyzed as a daily survival rate (DSR) of nests using a binary response variable (success or failed hatched) modeled with the logistic-exposure method (Shaffer 2004). Nesting success was estimated as $(DSR)^{24}$, where 24 is the duration of the incubation period from laying of the first egg to hatching (Maher 1970). Finally, we used GLMs to examine whether the phenology of outbound migration (i.e., departure date from the breeding site and duration of the outbound migration; response variables) differed between successful and failed breeders (predictor variable).

Daily number of flying bouts, distance travelled, and duration of migration data were scaled and centered by subtracting the mean and dividing by the standard deviation in all analyses. All analyses were done using the software R v.4.1.0 (R Core Team 2021). Means are presented with standard errors (SE) throughout the results and slope parameters (β) with their 95% confidence intervals (CIs).

RESULTS

Influence of the Nonbreeding Season on Reproductive Success

Arrival date on Bylot Island of jaegers marked with geolocators (June 3 ± 0.9 days, $n = 23$) was apparently not associated with either duration of the return migration ($\beta = -0.04$ [−0.11, 0.03]), daily number of flying bouts ($\beta = -0.98$ [−2.90, 0.94]) or distance travelled at their wintering areas ($\beta = -1.62$ [−3.74, 0.50], $R^2 = 0.22$, $n = 22$; Figure 1). However, if we exclude the outlier (latest arrival date), the relationship with the number of flying bouts was significant ($\beta = -2.41$ [−3.75, −1.07], $R^2 = 0.49$, $n = 21$).

Breeding propensity of jaegers was negatively related to daily number of flying bouts at their wintering areas and positively related to arrival dates at their breeding site (Table 1; Figure 2). On average, a 10% increase in the number of flying bouts reduced breeding propensity by 5%, and each day of delay in arrival after May 26 increased it by 4%. However, breeding propensity was not associated with the wintering area used or distance travelled in winter. Similarly, laying date was not associated with the wintering area used, daily number of flying bouts and distance travelled in winter, or arrival date at the breeding site (Table 1). However, an increase in daily number of flying bouts at wintering areas

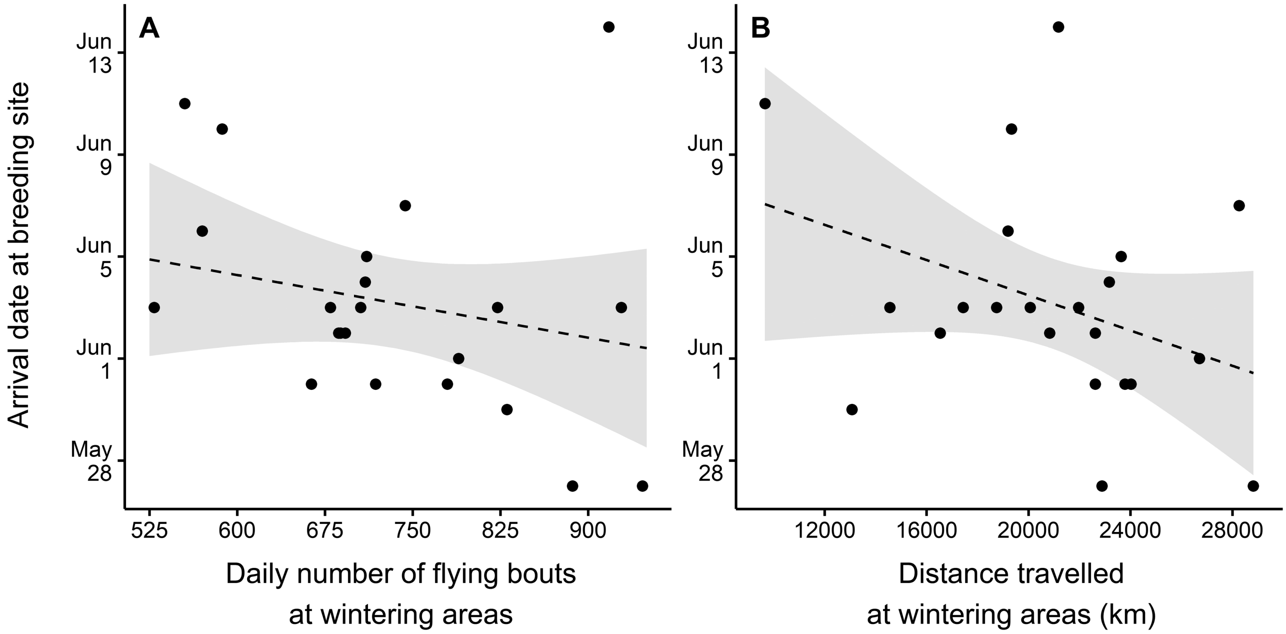

FIGURE 1. Arrival date of Long-tailed Jaegers at the breeding site on Bylot Island, Nunavut, Canada, in relation to (**A**) daily number of flying bouts at wintering areas or (**B**) distance travelled at wintering areas ($n = 22$), 2014–2019. Dashed lines represent non-significant relationships. Gray-shaded area represents the 95% CI.

TABLE 1. Slope parameters (β) and their 95% CIs in models examining links between parameters of the wintering and return migration periods and subsequent breeding parameters of Long-tailed Jaegers equipped with geolocators at their breeding site, Bylot Island, Nunavut, Canada, 2014–2019.

Response variable	Predictor variable	*k*	β	95% CI	R^2_m	R^2_c	*n*
Breeding propensity [a]	Wintering area: Agulhas c.	5	1.45	[−0.61, 4.15]	0.02	0.74	87
	Wintering area: Brazil c.		0.54	[−1.77, 3.41]			
	Wintering area: Canary c.		1.26	[−0.53, 3.65]			
	Daily number of flying bouts at wintering areas	2	−1.23	[−2.41, −0.37]	0.22	–	37
	Distance travelled at wintering areas	3	0.34	[−0.71, 1.56]	0.17	–	23
	Arrival date at breeding site		0.26	[0.01, 0.62]			
Laying date [b]	Wintering area: Agulhas c.	5	0.02	[−2.64, 2.75]	0.03	0.28	48
	Wintering area: Brazil c.		−1.22	[−4.17, 1.79]			
	Wintering area: Canary c.		1.17	[−1.16, 3.50]			
	Daily number of flying bouts at wintering areas	3	0.36	[−1.03, 1.75]	0.02	–	15
	Distance travelled at wintering areas	4	1.26	[−3.06, 5.58]	0.20	–	13
	Arrival date at breeding site		0.68	[−0.20, 1.55]			
Nesting success [c]	Wintering area: Agulhas c.	5	−0.10	[−1.37, 1.16]	–	–	61
	Wintering area: Brazil c.		0.28	[−0.97, 1.54]			
	Wintering area: Canary c.		−0.61	[−1.78, 0.55]			
	Lemming density		0.62	[0.16, 1.08]			

R^2_m is the marginal *R*-squared for fixed effects (GLMMs) or *R*-squared (GLMs). R^2_c is the conditional *R*-squared for fixed and random effects. *n* is sample size. *k* is number of parameters. Reference levels were set as "not nesting" for breeding propensity, "failed breeding" for nesting success, and "Benguela current" for wintering areas. Dates were converted to day of the year for statistical analyses.

[a] Dataset includes jaegers monitored at least once with a geolocator for all years they nested between 2015 and 2019. Year was used as a random factor when possible.

[b] Dataset includes jaegers monitored at least once with a geolocator for all years they nested between 2008 and 2019. Year was used as a random factor when possible.

[c] Dataset includes jaegers monitored at least once with a geolocator for all years they nested between 2008 and 2019.

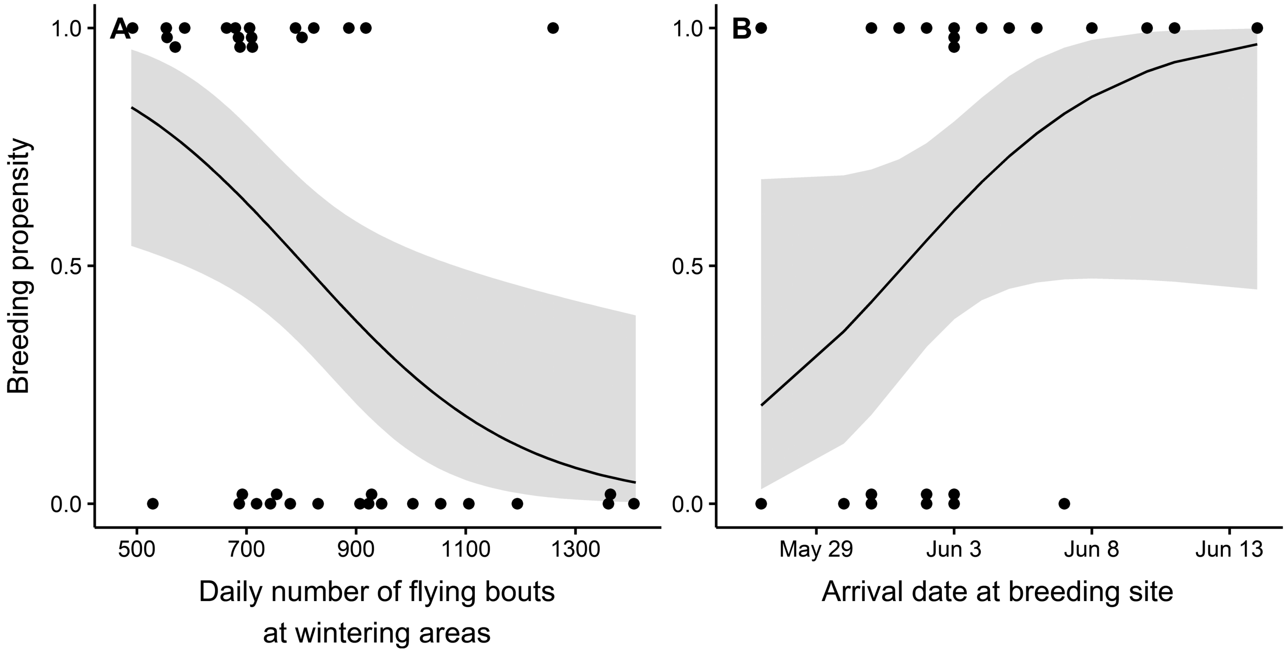

FIGURE 2. Breeding propensity of Long-tailed Jaegers on Bylot Island, Nunavut, Canada, in relation to (**A**) daily number of flying bouts at wintering areas and (**B**) arrival date at breeding sites (*n* = 37 and 23, respectively), 2014–2019. Solid lines represent significant relationships. Gray-shaded area represents the 95% CI.

was associated with a lengthening of the pre-laying interval (β = 3.67 [0.86, 6.48], $R^2 = 0.37$, *n* = 13; Figure 3; β = 4.00 [−1.65, 9.66], $R^2 = 0.16$, *n* = 12 if the right-most value is excluded). Nesting success did not vary according to the wintering area used (Table 1).

Local Determinants of Reproductive Success

We monitored a total of 406 Long-tailed Jaeger nests and 279 of them had a known outcome. Breeding propensity of jaegers increased with lemming density (β = 2.36 [1.33, 4.68], $R^2 = 0.43$, *n* = 94; Figure 4); on average, an increase from 1

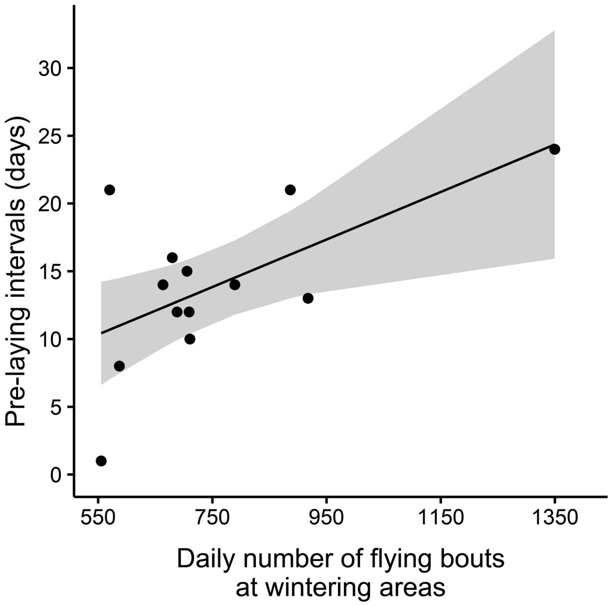

FIGURE 3. Pre-laying interval (in days) of Long-tailed Jaeger nesting on Bylot Island, Nunavut, Canada, in relation to daily number of flying bouts at wintering areas (*n* = 13), 2014–2019. Solid line represents a significant relationship. Gray-shaded area represents the 95% CI.

to 2.5 lemmings per ha increased the breeding propensity from 0.04 to 0.66. The mean laying date of jaegers was June 18 ± 0.3 days (Figure 5) and was not associated with lemming density (β = −0.21 [−0.54, 0.13], *n* = 218). Mean proportion of 2-egg clutches was high in most years (0.88 ± 0.03; *n* = 11 years; Figure 5) although this proportion tended to increase with lemming density (β = 0.14 [−0.04, 0.34], *n* = 361). Mean annual nesting success was 0.44 ± 0.10 and was highly variable among years (range: 0 – 0.95; *n* = 13 years; Figure 5). Nesting success increased with lemming density (β = 0.43 [0.31, 0.56], *n* = 279); on average, an increase of 1 lemming per ha increased the probability of successful breeding by 11%. In contrast, the probability of successful breeding decreased by 4% on average with each day of delay in laying (β = −0.15 [−0.21, −0.09], *n* = 169; Figure 6; results did not change when laying date was expressed as deviations of mean annual laying date).

Influence of Reproductive Success on Outbound Migration

Compared to failed breeders, jaegers that bred successfully departed about 10 days later from the breeding site on average (successful breeders: August 17 ± 1.2 days, *n* = 15 vs. failed: August 7 ± 2.8 days, *n* = 12; β = 9.53 [3.95, 15.12]). However, the duration of the outbound migration did not differ between successful and failed breeders (61.7 ± 4.6 days, *n* = 14 vs. 58.4 ± 3.3 days, *n* = 10; β = 3.27 [−8.68, 15.23]).

DISCUSSION

We showed that the reproduction of a long-distance Arctic migrant relying on variable and unpredictable resources is strongly driven by food availability at the breeding site but also by carry-over effects from the nonbreeding season spent in southern marine ecosystems. The negative relationship between breeding propensity and the number of flying bouts in winter suggests that increased time spent flying in winter could have a negative effect on the subsequent reproduction. Yet, the unpredictability of the highly seasonal Arctic environment, especially fluctuating food abundance, appears to be a strong driver of reproduction that could modulate the strength of carry-over effects.

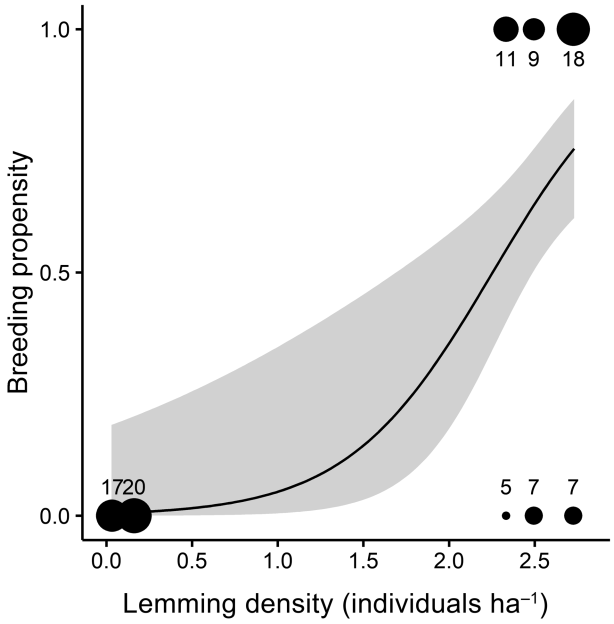

FIGURE 4. Breeding propensity of Long-tailed Jaegers (*n* = 94) in relation to lemming density on Bylot Island, Nunavut, Canada, 2015–2019. Numbers above or below each data point represent annual sample size, and size of the dots is proportional to it. Solid line represents a significant relationship. Gray-shaded area represents the 95% CI.

Effects of the Winter and Return Migration on Reproductive Success

Arrival date at the breeding site was not associated with the duration of the return migration even though individuals wintering close to the breeding site left more than 45 days later, spent less time in migration, and travelled faster than those spending the winter 7,500 km further away (Seyer et al. 2021). Leaving earlier for return migration at the most distant sites may be a strategy to compensate for the additional cost of a longer migration without delaying arrival date at the breeding site (Oppel and Powell 2009). While individuals wintering closer to the breeding site may sometimes arrive earlier to breed (Hötker 2003, Bregnballe et al. 2006), the costs of wintering further could be offset by the quality of the wintering areas used (e.g., Alves et al. 2012).

A high proportion of time spent in flight during winter may indicate that individuals were spending less time foraging or resting at sea and more time traveling in search of good foraging areas. Therefore, these birds may have been in lower body condition, which could explain the carry-over effect of the number of flying bouts recorded in winter on the breeding propensity that we observed. Seabirds displaying a high level of activity during winter (i.e., more time spent flying, more prospecting for good foraging sites, less resting) occasionally skip a reproduction event, presumably to improve their lifetime reproductive performance (Kazama et al. 2013, Shoji et al. 2015). Therefore, jaegers that spent more time foraging

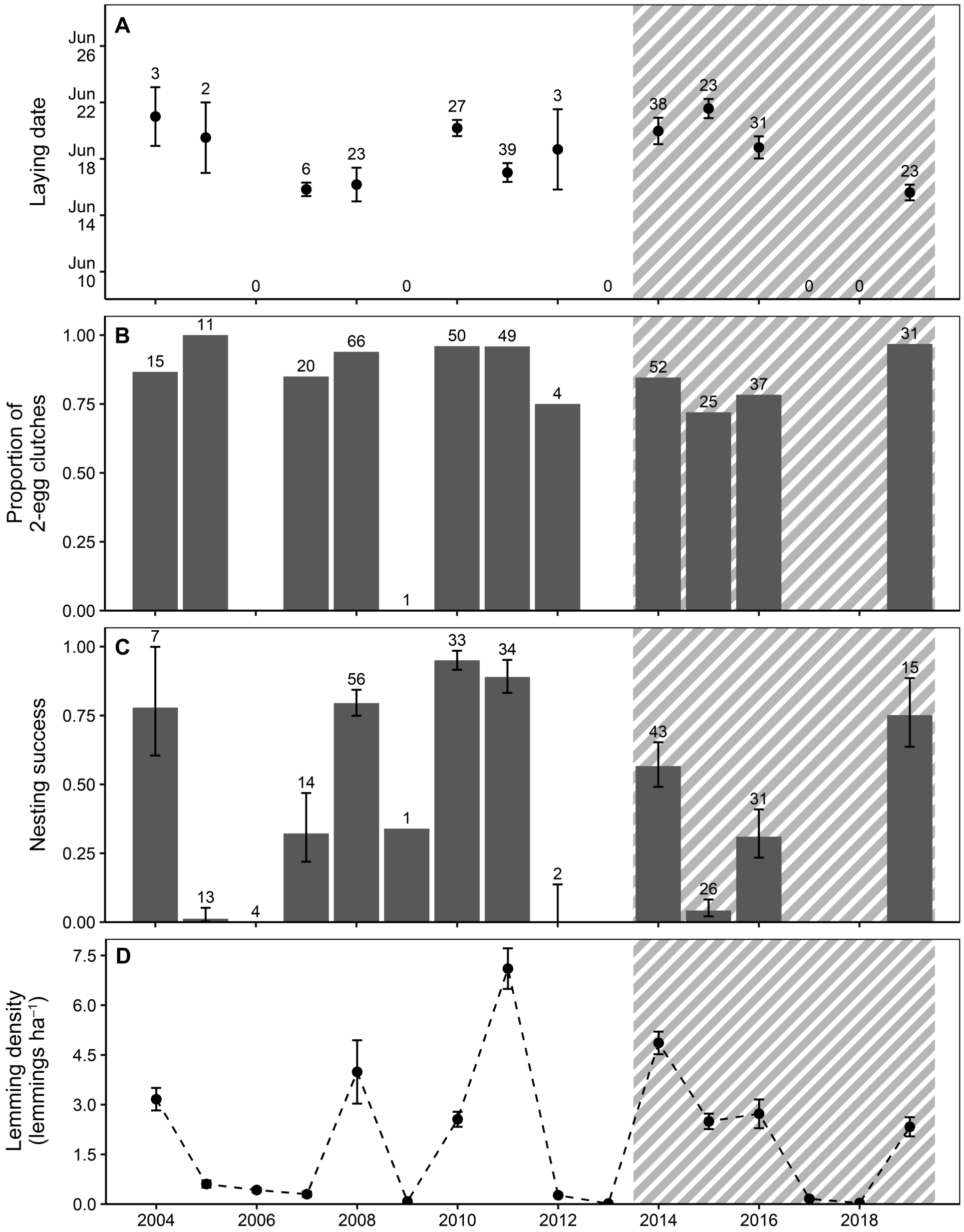

FIGURE 5. (**A**) Laying date (mean ± SE), (**B**) proportion of 2-egg clutches, and (**C**) nesting success (mean ± SE) of Long-tailed Jaegers estimated from the daily nest survival modeled with the logistic-exposure method, and (**D**) lemming density (mean ± SE) on Bylot Island, Nunavut, Canada, 2004–2019. Numbers above each column or data point represent annual sample size. Gray-striped area represents years when geolocator data were collected.

and/or resting during the winter could have reached a better pre-migration body condition, which would be carried over their long-distance migration and increase their chances of breeding.

Jaegers arriving early at the breeding site had a reduced probability of breeding and a longer pre-laying interval, a period during which they likely attempted to improve their body condition and acquire resources needed to produce eggs (Rowe et al. 1994, Bêty et al. 2003, Lamarre et al. 2017). It is possible that the earliest arriving birds faced more challenging environmental conditions and had more difficulty acquiring food resources during the pre-laying period. Indeed, the presence of snow cover in early spring in some years may limit access to terrestrial food resources such as lemmings, while ice cover at sea prevents access to marine prey (Seyer et al. 2021). As suggested for other long-lived species, arriving too early in the Arctic may entail some costs and compromise breeding attempts of some individuals (e.g., Snow Goose: Bêty et al. 2004; Common Eider [*Somateria mollissima*], Legagneux et al. 2016, Jean-Gagnon et al. 2018), as we found in jaegers. Nevertheless, there was a clear advantage for jaegers to initiate nesting early as shown by the strong seasonal decline in nesting success, with a 50% reduction in success with a 2-week delay in laying dates, a common pattern in birds (Perrins 1970, Lepage et al. 2000, Harms et al. 2015). Hence, as reported for Snow Geese (Bêty et al. 2004), our results indicate that jaegers may face opposing selection pressures because delaying arrival may increase the probability of breeding, but at the cost of reduced nesting success if they nest late.

Use of different wintering areas can influence subsequent breeding parameters in migrants (e.g., Pied Avocets

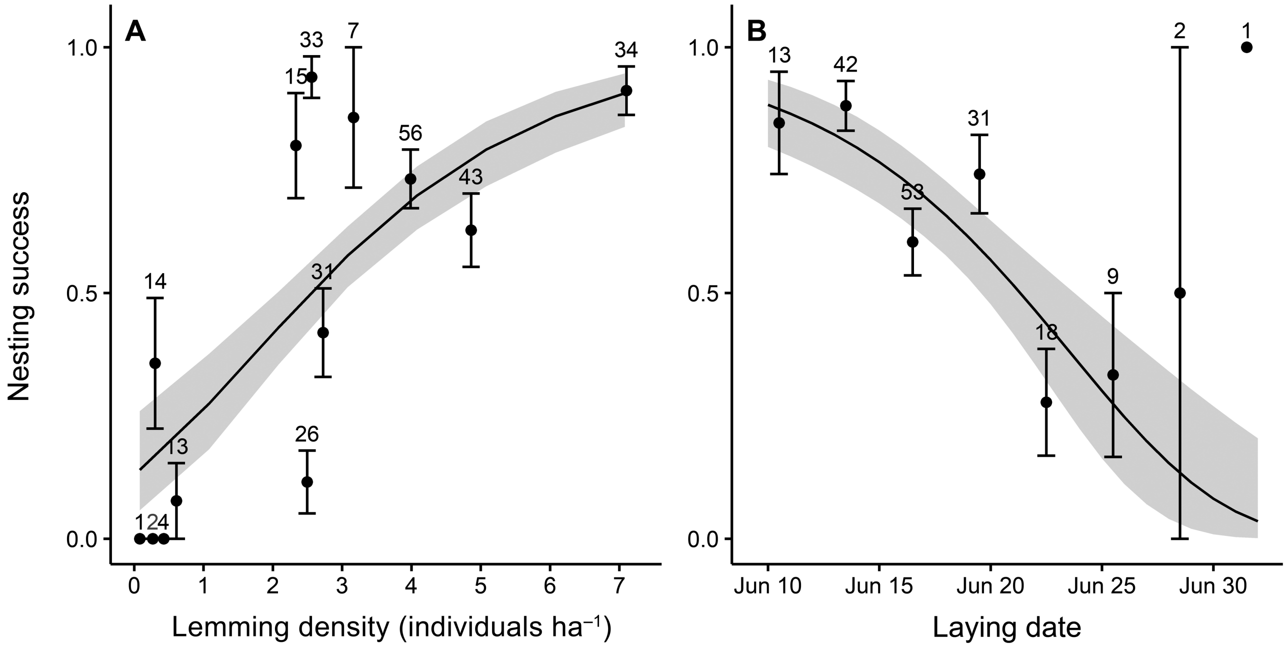

FIGURE 6. Nesting success of Long-tailed Jaegers on Bylot Island, Nunavut, Canada, in relation to (**A**) lemming density or (**B**) laying date (*n* = 279 and 169, respectively), 2004–2019. Even though analyses were performed on individual data points, for the sake of clarity, we present mean nesting success by year (**A**) or by 3-day bin classes (**B**) with standard errors. Numbers above each data point represent the sample size of each class. Solid lines represent significant relationships. Gray-shaded area represents the 95% CI.

[*Recurvirostra avosetta*], Hötker 2003; Great Cormorants [*Phalacrocorax carbo*], Bregnballe et al. 2006; American Kestrel [*Falco sparverius*], Anderson et al. 2016). Although wintering areas of jaegers were spread over a latitudinal range of 7,500 km, we found no effect of the area used on reproduction. This suggests that environmental conditions encountered at each wintering area could be relatively similar for jaegers (Seyer et al. 2021). Alternatively, the higher energetic costs to reach a more distant wintering area may be compensated by some benefits, such as richness and predictability of food resources at the selected area or lower competition levels. It is also possible that the additional energetic cost of migration may be too low to affect subsequent reproduction in a species that uses gliding as a primary flight mode (Pennycuick 2008).

Local Determinants of Reproductive Success

Previous studies documented a close relationship between breeding effort of tundra-nesting predators and lemming density, their main food resources (Barraquand et al. 2014, Therrien et al. 2014, Seyer et al. 2020). They also pointed out that a minimal lemming density can be required to initiate breeding. Although jaegers may arrive with a body condition sufficient to lay eggs, a low lemming abundance during the crash phase may not provide enough resources to raise chicks. Our analysis conducted at the individual level confirmed that most jaegers skip breeding when lemming density is below ~2 lemmings ha^{-1}, which is expected in a long-lived species facing poor environmental conditions during the breeding period (Erikstad et al. 1998, Descamps et al. 2011, Barraquand et al. 2014). Interestingly, when lemming density is sufficient to allow jaegers to breed, food resources apparently have little effect on the timing of breeding or clutch size (>85% of breeding individuals produced 2 eggs).

Even though lemming abundance had little influence on the reproductive investment of breeding birds (i.e., clutch size), it had a strong positive effect on nesting success. This is probably due to a higher predation rate on jaeger eggs by foxes and gulls in years of low lemming abundance (Gauthier et al. 2015, Bowler et al. 2020, Duchesne et al. 2021, Beardsell et al. 2022). Although abandoned nests are rarely found, it is also possible that reduced nest attentiveness by jaegers in years of low food abundance increases vulnerability of eggs to predation as foxes increase their activity and travel a longer distance in those years (Beardsell et al. 2022). Similarly, the strong seasonal decline in nesting success that we observed could be due to a temporal decrease in resource availability, primarily lemmings (Gilg 2002, Fauteux et al. 2015), but also to a temporal increase in predation pressure, which could reduce the nesting success of late breeders.

Effects of Reproductive Success on Outbound Migration

Post-breeding departure from the breeding site occurred over a long-time span (5 weeks) and this was partly due to the early departure of failed breeders, as is commonly observed in seabirds (Bogdanova et al. 2011, Catry et al. 2013, Fayet et al. 2016). In late summer, feeding conditions may be better at sea than on land because lemming density often decreases during the season (Gilg 2002, Fauteux et al. 2015), and competition for resources with other lemming predators increases (Gilg et al. 2006, Seyer et al. 2020). Failed breeders may thus leave the terrestrial environment earlier to quickly return to the marine environment, a primary and likely safer foraging habitat for nonbreeding jaegers. Because jaegers start molting their flight feathers on their wintering areas (van Bemmelen et al. 2018) and because the length of outbound migration is similar among all individuals, failed breeders may thus start molting earlier and get benefits from an early arrival at wintering areas (Seyer et al. 2021).

Limitation of the Data

Working on a species breeding sporadically and at low density in the remote Arctic tundra has consequences for our ability to collect large sample sizes despite considerable field effort over several years. Therefore, the statistical power of our analyses is sometimes low, and some conclusions must be interpreted with caution. The greatest limitation in the present study was our inability to assess the influence of local food abundance and carry-over effects on several breeding parameters in a joint analysis due to low sample size. Nonetheless, our separate analyses were still able to uncover the presence of carry-over effects on some key breeding parameters such as breeding propensity, a difficult parameter to study in birds. Nevertheless, this study can guide future research on carry-over effects in long-distant migrants by highlighting important breeding parameters to consider and suggesting mechanisms that could explain these carry-over effects.

Conclusions

Our results show that carry-over effects linked to individual movement parameters during the nonbreeding season are likely playing a role in tandem with local conditions at the breeding site in modulating reproduction of a tundra-nesting avian predator. First, activity levels at wintering areas have a strong effect on breeding probability in the following season, likely through an effect on individual body condition (Rowe et al. 1994). However, local conditions, and in particular the highly variable lemming abundance, also have a strong impact on individual decisions to breed and have the potential to override carry-over effects, as previously suggested in other migrants (Legagneux et al. 2012, Buchan et al. 2021). Furthermore, because carry-over effects were detected at the individual level and not related to the wintering area used, it may be more a matter of individual ability to exploit a specific wintering area and to reach a good body condition than a matter of how good conditions encountered are at wintering areas. Our study adds to growing evidence (Holdo et al. 2011, Bauer and Hoye 2014, Furey et al. 2018, Moisan et al. 2023) showing that events occurring in distant ecosystems can affect the tundra food web via carry-over effects mediated by long-distance migrations even in a system characterized by highly variable and unpredictable food resources.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

All protocols were approved by the Animal Care Committee of Université Laval in accordance with the guidelines of the Canadian Council on Animal Care.

Conflict of interest statement

The authors have no conflict of interest to declare.

Author contributions

Y.S., G.G., and J.F.T. conceived the study; Y.S., N.L., and J.F.T. collected data in the field. Y.S. analyzed the data and wrote the manuscript with the assistance of G.G. All contributed to the interpretation of the data and revision of the manuscript.

Data availability

Analyses reported in this article can be reproduced using the data provided in Gauthier et al. (2020) and Seyer et al. (2022).

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