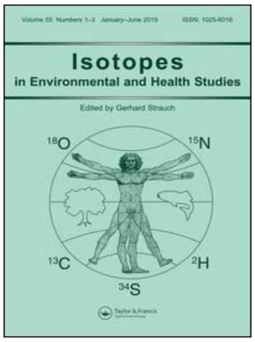

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ISOTOPES IN ENVIRONMENTAL AND HEALTH STUDIES
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Linking winter habitat use, diet and reproduction in snowy owls using satellite tracking and stable isotope analyses

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ABSTRACT
Coupling isotope values of feathers and satellite tracking of individuals have the potential to reveal multi-season linkages between wintering habitat, diet and carry-over effects on reproductive parameters in migrating birds. Snowy owls *Bubo scandiacus* have multiple wintering tactics as they can use both terrestrial and marine resources during the non-breeding season, but their nomadic behaviour complicates their study. We assessed if inter-individual variability in the diet inferred by feather isotopes could be explained by habitat use in winter as determined by satellite telemetry and examined possible carry-over effects on reproduction. Seventeen breeding female snowy owls were equipped with satellite transmitters and sampled for stable isotopes (δ^{13}C and δ^{15}N) in feathers. We found a positive relationship between the use of the coastal and marine environments in winter and the contribution of marine resources to the diet of snowy owls in the previous year based on feather analysis. The proportion of marine contribution to the winter diet was variable among individuals and showed a weak negative relationship to summer body mass but not with laying date or clutch size. Our integrated approach shows the usefulness of isotope analyses to infer habitat use and expand the temporal coverage of radio-tracking studies.

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1. Introduction

Intra-population variability in resource use is ubiquitous as different individuals or groups of individuals may specialize on various types of food or habitat at some time of the year [1,2]. Variability in resource use during the non-breeding period can have important fitness consequences in migratory animals, including carry-over effects on subsequent breeding performance [3–5]. Indeed, reproductive success may be affected by diet quality [6], food abundance [7–9] and habitat quality [10–12] during the previous non-breeding season. The different wintering tactics may thus have significant impact on fitness but few studies have been able to address those links at the individual level [13]. The complexity of tracking individuals from wintering sites to distant breeding

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grounds makes it difficult to link intra-population variability in winter resource use to subsequent breeding performance. This is especially true for nomadic species showing complex and irregular patterns of annual movements, often associated to cyclic or fluctuating resources [14,15].

The snowy owl is an Arctic top predator known for its nomadic and irruptive behaviours and for the diversity of its wintering tactics [16]. In North America, some snowy owls migrate from their tundra breeding grounds to temperate sites far inland in the Canadian Prairies and American Midwest, while others stay in the Arctic during the winter and make extensive use of the marine environment (i.e. sea ice and coasts; [17,18]). The shift to the marine environment is especially surprising for a species that strongly specializes on small mammals during the breeding season [16,19]. Owls using the marine environment are exposed to environmental conditions and food resources radically different from those encountered in terrestrial environment.

Using stable isotope analyses of two elements (N and C), we previously showed that a significant contribution of marine resources to the diet of snowy owl could be detected in feathers of individuals captured in summer, indicative that some owls were at least partly relying on marine resources during the non-breeding season [20]. Diet reconstruction models showed that the level of marine resource contribution also varied greatly among individuals [20]. In this study, we examine the hypothesis that inter-individual variability in diet during the non-breeding season, inferred using feather isotope values, is linked to individual wintering habitat use. To test this hypothesis, we related habitat use of individual female owls tracked with satellite telemetry during the non-breeding season with the contribution of marine sources in their diet. A secondary objective was to investigate potential carry-over effects of the diet and habitat use during the non-breeding season on their subsequent reproduction performance and body condition of females. Considering the large diversity of wintering tactics observed in this species, the snowy owl is a good study model to link inter-individual variability in resource use to subsequent reproduction in nomadic animals.

2. Material and methods

2.1. Study system

Snowy owls were captured at two different sites in the eastern Canadian Arctic: Deception Bay, QC (62°02N 74°49W; Low Arctic) in 2013 and Bylot Island, NU (73°08N 80°00W; High Arctic), in 2014. Deception Bay is situated in the Nunavik region of the province of Quebec and characterized by mesic tundra and rocky terrain with lush tundra vegetation in river valleys. Nest search at Deception Bay was carried out along the road from the coastal port of Deception Bay to the Raglan mine. Bylot Island is a coastal study site composed of a mosaic of mesic (85 %) and wet (15 %) habitats (see [21] for a detailed description of the study area). Nest search was carried out in an area of ~450 km^2 on the south plain of the island. Captures of snowy owls were performed with bow-nets positioned over the nest or with a bal-chatri trap (one case) set a few metres away from their nest from 8 to 18 July 2013 at Deception Bay and 29 June to 5 July 2014 on Bylot Island. Differences in capture dates between the two sites are explained by logistic constraints that delayed our arrival at Deception Bay, and not due to differences in breeding phenology.

2.2. Capture and marking of owls

We captured 10 breeding females at Deception Bay and 8 on Bylot Island. We fitted each owl with an ARGOS satellite transmitter (Microwave telemetry, USA, PTT-100, $N = 2$; North Star Science and Technology, LLC, USA, PTT-30G, $N = 16$). The transmitter and harness weighed 40 g, which corresponds to 1.8 % (range 1.6 % to 2.1 %) of the birds' body mass. It has been shown that these transmitters do not significantly impact survival or reproductive performances of owls [22,23]. Transmitters were installed on the owls as a backpack using a harness made of Teflon strips [24].

Locations were obtained over a 4–6 h period at ~2–3 d intervals, from December to mid-June and ~5 d intervals from mid-June to November. Locations were assigned a class corresponding to their estimated precision, which followed a normal distribution with a standard deviation of <1500 m, <500 m and <250 m, respectively, for the classes we retained (i.e. 1, 2 and 3; [25]). Positions were averaged to a single mean daily coordinate to avoid non-independence of spatial data (see [18] for details).

2.3. Feather and prey sampling

Selecting feathers that grow during winter and can adequately reflect the diet at that time is challenging in snowy owl, a species with a complex, asynchronous and poorly known molt pattern [26,27]. Robillard et al. [20] examined in detail this question and recommended sampling multiple feathers from various body regions, excluding wing feathers, to investigate winter diet and habitat use of snowy owls. This approach should minimize the impact of inter-individual variability in the timing and sequence of molt on winter diet reconstruction. Following these recommendations, we collected feathers from five body regions on each captured snowy owl: head, neck, breast, flank and rump. Neck feathers were missing for 2 individuals, so analyses were performed on 4 body regions for these birds. Tissue samples collected in the field were stored frozen at −20 °C until laboratory analyses.

To reconstruct snowy owl diet, we obtained muscle and liver samples of potential prey items from different locations and environments within their known winter range in eastern Canada (Bylot Island NU, Belcher Islands NU, Deception Bay QC, Kuujjuaq QC, Twillingate NL; see Appendix 2 for details). They included: (1) marine birds collected in winter (common eider *Somateria mollissima*, thick-billed murre *Uria lomvia*, common murre *Uria aalge*, razorbill *Alca torda* and long-tailed duck *Clangula hyemalis*), (2) terrestrial birds (i.e. rock ptarmigan *Lagopus muta*), and (3) terrestrial small mammals (i.e. brown *Lemmus trimucronatus*, collared *Dicrostonyx groenlandicus* and Ungava *Dicrostonyx hudsonius* lemmings, and meadow vole *Microtus pennsylvanicus*). Seabird samples were obtained from the Tissue bank at Environment and Climate Change Canada and rock ptarmigans were given to us by Inuit hunters (Appendix 2).

2.4. Isotope analyses

Prior to stable isotope analyses, feathers were washed with a 2:1 chloroform: methanol solution, oven dried at 50 °C for 24 h, homogenized by cutting them with scissors into approximately 1–3 mm fragments, subsampled (i.e. ~0.7 mg of feathers; $N = 88$) and packed into tin capsules. Muscle and liver samples of prey were freeze-dried at −50 °C, ground to a fine powder with mortar and pestle and lipid-extracted with chloroform using a Soxtec apparatus (Tecator system 1043) before isotope analyses to reduce the risk of introducing significant biases in $\delta^{13}C$ values [28,29]. All values reported are lipid extracted values. Isotope analyses were performed at the Laboratoire d'Océanographie of Université Laval, Québec, Canada. Details on laboratory techniques and on determination of the diet–tissue discrimination factor are presented in Appendix 1.

For stable isotope mixing models, sources were pooled in two groups: marine ($N = 5$ species) and terrestrial sources ($N = 5$ species), given equal weight to each species within group. We also assumed that prey isotope ratios did not vary significantly from year to year, based on the high winter site fidelity of some prey species (e.g. [30–32]) or small and overlapping home ranges of others (e.g. [33–35]), which suggest that these prey feed on similar resources inter-annually. However, even if this assumption was not entirely met, annual variation in isotope values within prey species is likely to be small compared to the large differences between the terrestrial and marine prey (See Results) and thus should have little impact on our results. Another issue arose because one individual wintered in the Prairies (see Results) where it had access to prey that could have different isotope values than those encountered in the Arctic. For instance, deer mice (*Peromyscus maniculatus*) in Saskatchewan have isotope values ($\delta^{15}N$: 7.6 ± 1.6 ‰, $\delta^{13}C$: −23.4 ± 1.0; [36]) slightly higher than terrestrial prey in the Arctic (Appendix 2). Therefore, for the individual that wintered in the Prairies, we repeated the stable isotopes mixing models using deer mice as a third prey source besides terrestrial and marine arctic prey.

2.5. Habitat use data

We used locations of snowy owls provided by the transmitters to characterize habitat use. First, we measured the distance to the coast for each location with the nearest-neighbor interpolation method of NASA available in the Movebank Env-Data system [37]. Distances (d) to the coast were signed (positive values on land, negative values at sea) and were averaged to a mean daily distance. Each location was then assigned to a habitat class: marine ($d < -5$ km), terrestrial ($d > 5$ km) or coastal (i.e. marine coasts only; $5 \text{ km} > d > -5$ km). The width of the coastal habitat (i.e. 10 km) was chosen based on the mean daily distance covered by individuals in this study (i.e. 7.3 ± 2.8 km, $N = 1949$ locations for 11 individuals) during the winter (i.e. January–February–March), which was less than the width of our coastal strip. Nonetheless, we ran sensitivity analyses by using a coastal width of 15 and 20 km. We obtained very similar results (not shown) and thus presented only analyses based on the 10 km width. Proportions of locations at sea (i.e. number of locations at sea/total number of locations) and proportions of locations at sea or in the coastal area (i.e. [number of locations at sea + number of locations along the coast]/total number of locations) as well as mean wintering latitude were calculated.

2.6. Statistical analyses

To infer the contribution of marine prey to the isotope ratios of each individual, we used stable isotopes mixing models (R, package SIAR; Parnell and Jackson 2013). We determined the marine contribution to each feather in each individual using the function siarsolomcmcv4 in R, which is based on a Markov chain Monte Carlo (MCMC) procedure. Models were ran using the following parameters: iterations = 500,000, burnin = 50,000 and flat priors [38,39]. Diet–tissue discrimination factors estimated for snowy owl feathers (δ^{13}C: 1.88 ± 0.04 ‰; δ^{15}N: 4.12 ± 0.26 ‰; see Appendix 1) were used as trophic enrichment factors in the models.

We analysed the link between the inferred marine proportion in the diet and wintering habitat use variables at different periods of the year using linear models. In a previous analysis, we found large intra- and inter-individual variability in marine proportion among body feathers [20]. To account for that, we used two response variables in our analyses: mean marine proportion across all feathers ($N = 5$ per individual) and mean marine proportion in the two feathers with the most marine signal on each individual, i.e. with the highest δ^{13}C and δ^{15}N values regardless of their origin (hereafter called most marine feathers). This category allowed us to target feathers that most likely grew during the previous winter when owls potentially fed on marine prey [18,20,40]. All marine proportions were log-transformed in subsequent analyses to meet normality requirements.

To examine inter-individual variability in the marine contribution to feather isotope values, we ran linear models using four explanatory variables: (1) proportion of all locations at sea, (2) proportion of all locations at sea and along the coast, (3) mean distance to the nearest coast (km) and (4) latitude, as conditions experienced by birds wintering in the Arctic are different than those at more southern latitudes. Each explanatory variable was tested in separate models to avoid over-parametrization and because most of them were highly correlated. We examined these relationships over three periods of the annual cycle: (1) autumn (1 Sep–31 Dec), (2) winter (1 Jan–31 Mar) and (3) all year (starting at capture date and including all locations until the next breeding season). To ensure enough temporal coverage of each period used in the analyses (autumn, winter and entire year), we selected individuals that were tracked during more than half of the period for the autumn and winter periods (autumn: $N = 17$; winter: $N = 12$ individuals), and individuals that were tracked from summer (capture date) to 1 May or later for the entire year period ($N = 11$ individuals). For all models, collection year was also entered as a fixed effect because this variable affected both δ^{13}C and δ^{15}N values of snowy owl feathers from which the diet was inferred [20]. Models with year as a fixed variable always performed better than models without it in terms of AICc. Statistical analyses were performed using R 3.2.0 software [41]. Results are presented as means ± SD, unless otherwise stated.

A limitation of our study is that movements of snowy owls and the marine contribution to their diet could not be estimated over the same time period. Indeed, feathers collected during the summer reflect the diet of owls at the time when feathers were grown in the previous year (i.e. prior to capture) whereas tracking of individuals took place after capture (Figure 1). A previous radio-tracking study revealed that most individuals (76 %; $N = 21$; [18]) were consistent in their use of marine/coastal and inland environments over successive winters although fidelity was not absolute. To further address this issue, we ran repeatability analyses of our explanatory variables for individual owls that were tracked for two consecutive years or more [18]. Repeatability analyses were performed with the *rpt* function of the rptR package in R [42] using a logit link for proportion data and a Gaussian distribution for other variables, and bird id as a random effect. These

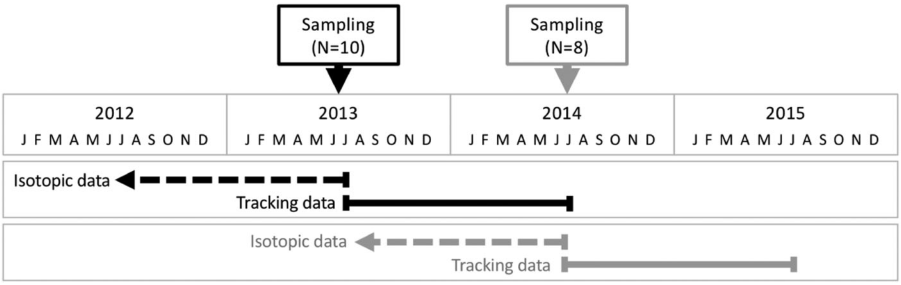

Figure 1. Schematic timeline depicting the sampling of snowy owl tissues in Deception Bay, QC, 2013 (black box) and on Bylot Island, NU, 2014 (gray box) along with the potential period (months of the year, indicated by uppercase letters) from which isotope data may origin (dashed arrows) and the period when owls were tracked by satellite telemetry (solid lines).

analyses revealed that our explanatory variables were highly repeatable between consecutive winters of tracking (R ± SE: proportion of locations at sea = 0.72 ± 0.12, proportion of locations at sea and along the coast = 0.72 ± 0.08, distance to the nearest coast = 0.73 ± 0.12, absolute distance to the nearest coast = 0.82 ± 0.09 and latitude = 0.97 ± 0.02; all $N = 20$; $P < 0.001$). Hence, we assumed that birds were consistent in their pattern of habitat use from one year to the next. Consequences of failure of this assumption on our results are addressed in the Discussion.

3. Results

3.1. Habitat use

Among the 18 marked owls, 17 females were tracked for extended time periods, ranging between 132 and 714 days (mean = 411 ± 222 days), which allowed the recording of 18 to 256 daily locations (mean = 154 ± 87 locations) after location-class filtering. One transmitter emitted for only 2 weeks, and hence this individual was excluded from analyses.

Owls tracked during our study period exploited different areas throughout the years. We successfully tracked 12 of the 17 individuals throughout the winter, of which 10 stayed in the Arctic (e.g. Hudson Bay and Hudson and Davis straits) while one travelled to the southern Canadian Prairies and one to the coast of Newfoundland and Labrador. The mean distance of daily locations to the nearest coast in winter (175 ± 461 km) was greater than in autumn (89 ± 280 km) or throughout the year (104 ± 330 km; Table 1), consistent with the fact that some females wintered far inland while others made extensive use of sea ice and coast. Proportion of locations at sea and along the coast also exhibited a large variability among individuals in winter, ranging from 0 to 1 (Table 1).

In terms of time spent in the marine environment (i.e. number of days between the first and last location at sea), one female spent the whole winter (i.e. 186 days) at sea, while 4 others spent a considerable amount of time there (respectively 143, 141, 138 and 122 days). For females that spent a large proportion of their time (>50 %) at sea in winter, their average distance to the coast ranged from −7 to −68 km. At the opposite end, two females that travelled to the central part of the continent spent 100 % of their time inland in winter and their average distance to the nearest coast were 617 and 1214 km.

Table 1. Mean, SD, minimum and maximum values (in parentheses) of parameters describing habitat use for each period analysed (*N* = number of individual snowy owls tracked by satellite).

Habitat parameter	Autumn Sep–Dec N = 17	Winter Jan–Mar N = 12	All year *N* = 11
Number of locations	53 ± 20 (18–77)	63 ± 20 (28–83)	213 ± 38 (153–256)
Proportion of locations at sea (< −5 km)	0.09 ± 0.10 (0–0.32)	0.43 ± 0.31 (0–0.83)	0.24 ± 0.15 (0–0.44)
Proportion of locations at sea + along the coast (<5 km)	0.41 ± 0.24 (0–0.82)	0.71 ± 0.43 (0–1)	0.49 ± 0.25 (0.04–0.85)
Distance to the coast (km; signed)	89 ± 280 (−201–1490)	175 ± 461 (−369 to 1480)	104 ± 330 (−369 to 1490)
Distance to the coast (km; absolute)	96 ± 278 (0–1490)	223 ± 440 (0–1480)	127 ± 322 (0–1490)
Latitude (°)	62.7 ± 6.3 (43.7–75.7)	58.1 ± 6.4 (44.2–71.7)	61.8 ± 6.9 (43.7–75.7)

Negative distances represent locations at sea and positive distances, locations on land.

3.2. Link between diet and habitat use

Marine prey had considerably higher δ^{13}C and δ^{15}N values than terrestrial prey (Appendix 2), and individual isotope values of owl feathers were located much closer to the isotope values expected from a diet of terrestrial than marine prey despite a large variation in isotope values among feathers type and individual owls (Appendix 3). Mean estimated proportion of marine sources in the diet of individual owls ranged from 0.04 to 0.29 when using all feathers and from 0.04 to 0.57 when using the two most marine feathers (Figure 2). Coefficients of variation were large (55 % when using all feathers and 69 % with the most marine feathers), indicating marked inter-individual variability in the contribution of the marine environment to the diet. For the individual that wintered in the Prairies, including deer mice as a third source in the mixing model slightly reduced the marine contribution to its diet (individual C, mean marine contribution for all feathers with two vs. three sources: 0.04 vs. 0.03, Figure 2).

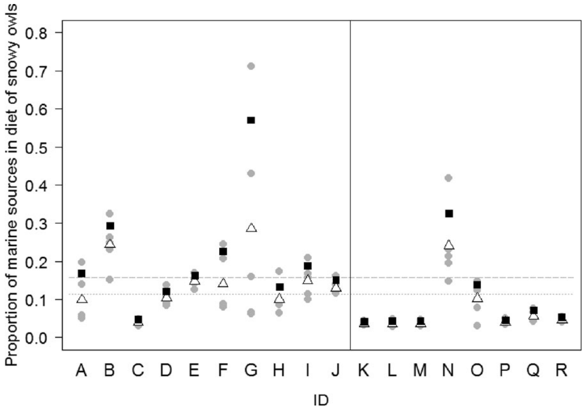

Figure 2. Proportions of marine sources in the diet of individual snowy owls (ID) inferred from each feather (gray circles) using the SIAR posterior probability distributions. Mean proportion of marine sources for each owl based on all feathers (white triangle) and from the two most marine feathers (black square) are also shown. Dotted and dashed gray lines depict respectively mean marine proportions of all feathers and the two most marine feathers. Individuals A-J were sampled in 2013; individuals K-R in 2014.

We found no link between marine proportions in the diet and habitat use during the autumn period (Table 2). In winter, however, we found a negative relationship between the proportion of marine sources in the diet of snowy owls and the distance to the coast when using either all body feathers or the most marine feathers (Table 2). Feathers of birds wintering far from the coast (one in the Prairies and one in northern Quebec) had a relatively low contribution of marine resources in their diet compared to birds that were close to or in the marine environments, though we noted a large variability in the latter group (Figure 3). The relationships were significant even if we excluded the 2 most extreme inland birds (i.e. the two birds wintering at an average of 617 and 1214 km from the coast) using the most marine feathers (Est.: −4.01, CI low: −8.00, CI up: −0.002; Figure 3). In addition, we also found a positive relationship between the proportion of marine sources in the diet and the proportion of locations at sea and along the coast, and a near significant relationship when using the proportion of locations strictly at sea (Table 2, Figure 3). When using locations throughout the year, we also found an inverse relationship between marine proportions estimated in feathers and distance to the coast (Table 2).

We repeated the previous analyses using the marine contribution estimated by the three-sources rather than the two-sources model for the bird that wintered in the Prairies. Results with the three-sources model are consistent with the previous analysis although most relationships were actually stronger (Appendix 4). Moreover, the marine proportion in the diet was negatively related to distance to the coast in autumn.

3.3. Carry-over effects on reproduction

Clutch size of individuals at the time of capture ranged from 1 to 9 eggs (mean: 6.1 ± 1.8 eggs) and their body mass at capture varied from 1.92 to 2.49 kg (mean: 2.18 ± 1.12 kg). The mean laying date in 2013 was 31 May ($N = 10$) and 25 May in 2014 ($N = 6$) but ranged from 17 May to 13 June in both years. Clutch size and laying date were not related to inferred marine proportions in the diet but a trend for an inverse relationship was found for body mass (Table 3). Birds with a high proportion of marine source in their feathers tended to be lighter than those with a low proportion (Appendix 5) and we observed the same trends if we used all feathers or only the most marine feathers (Appendix 5).

4. Discussion

By combining data on habitat use derived from satellite telemetry with those on the diet inferred by stable isotope analyses of feathers, we showed a link between the intra-population variability in the use of the coastal and marine environments in winter and the contribution of these environments to the diet of snowy owls. This confirms our hypothesis that inter-individual variability in diet during the non-breeding season is linked with individual wintering habitat use. However, we found no evidence of carry-over effects of variability in the contribution of the marine environment to the diet inferred from feathers on reproduction.

Table 2. Coefficients (β with their 95 % confidence intervals) of linear regressions relating the mean marine proportions in the snowy owl diet inferred from all body feathers sampled or the two feathers with the highest marine contribution (Most marine feathers) to different habitat use variables (**Prop_locSea**: proportion of locations at sea; **Prop_LocSea + Coast:** proportion of locations at sea and along the coast; **DistcoastSTD**: standardized mean distance to the coast in km; positive value over land, negative value over the sea; **DistcoastAbsSTD**: absolute standardized mean distance to the coast in km; and **Latitude** in °) and for different periods of the annual cycle. Year was added as fixed effect in all models.

	Autumn 1 Sep–31 Dec *N* = 17				Winter 1 Jan–31 Mar *N* = 12				All year *N* = 11			
Explanatory variables	β	Lower CI	Upper CI	AIC	β	Lower CI	Upper CI	AIC	β	Lower CI	Upper CI	AIC
All feathers												
Prop_locSea[a]	−0.28	−3.13	2.56	29.18	0.72	−0.32	1.76	20.96	1.93	−0.52	4.38	19.52
Prop_locSea + Coast[b]	0.64	−0.77	2.06	28.13	0.68	−0.15	1.51	19.96	1.10	−0.63	2.84	20.69
DistcoastSTD	−0.21	−0.48	0.05	25.93	**−0.34**	**−0.62**	**−0.06**	**16.59**	**−0.36**	**−0.68**	**−0.04**	**16.56**
DistcoastAbsSTD	−0.22	−0.48	0.04	25.67	**−0.33**	**−0.62**	**−0.04**	**17.37**	**−0.35**	**−0.68**	**−0.02**	**17.07**
Latitude	0.03	−0.04	0.09	28.46	0.02	−0.04	0.09	23.05	0.01	−0.10	0.13	23.22
Marine feathers												
Prop_locSea[a]	−0.12	−3.48	3.25	34.92	0.96	−0.22	2.15	24.08	2.48	−0.26	5.23	22.02
Prop_locSea + Coast[b]	1.09	−0.52	2.70	32.52	**0.95**	**0.04**	**1.85**	**22.14**	1.55	−0.35	3.46	22.78
DistcoastSTD	−0.28	−0.59	0.02	30.63	**−0.41**	**−0.74**	**−0.07**	**20.51**	**−0.44**	**−0.80**	**−0.08**	**19.25**
DistcoastAbsSTD	−0.29	−0.59	0.01	30.33	**−0.38**	**−0.73**	**−0.03**	**20.51**	**−0.42**	**−0.80**	**−0.05**	**20.11**
Latitude	0.03	−0.05	0.11	34.19	0.02	−0.06	0.10	27.55	0.00	−0.14	0.14	26.80

[a] locSea: < −5 km.

[b] SeaCoast: < 5 km.

Significant relationships are shown in bold (*N* = number of females).

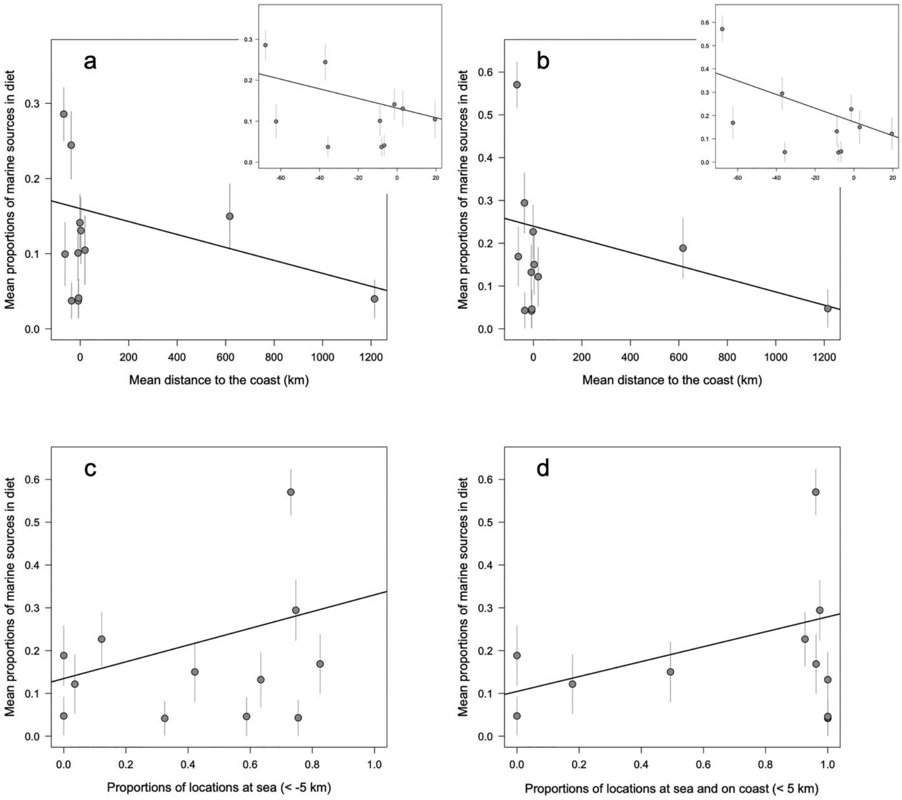

Figure 3. Relationships between proportion of marine sources in the diet inferred from all body feathers (a) or the two most marine feathers (b, c, d) and distance to nearest coast (a, b), proportions of locations at sea (c) and proportions of locations both at sea and along the coast (d) Proportions of locations at sea and on coast (< 5km) during winter. Insets represent the relationships between proportion of marine sources in the diet inferred from feathers and distance to the coast excluding the two individuals wintering far inland. Regression lines are from models in Table 2. Gray lines depict the 95 % credible intervals estimated by SIAR. Positive distance values represent locations on land, while negative distance values are associated to locations at sea.

Table 3. Coefficients (β with their 95 % confidence intervals) of linear regressions relating clutch size, laying date and body mass (kg) of snowy owls to the mean marine proportions in their diet inferred from all body feathers sampled or the two most marine feathers only (N = number of females).

Dependent variables	β	Lower CI	Upper CI
All feathers			
Clutch size ($N = 18$)	0.24	−1.22	1.70
Laying date ($N = 16$)	4.07	−1.09	9.23
Body mass ($N = 17$)	−0.08	−0.17	0.01
Most marine feathers			
Clutch size ($N = 18$)	0.28	−0.98	1.54
Laying date ($N = 16$)	3.34	−1.16	7.83
Body mass ($N = 17$)	−0.07	−0.15	0.01

4.1. Seasonal habitat use and diet

Our study confirms previous reports that snowy owls breeding in the eastern North American Arctic can winter in a wide spectrum of habitats, including the arctic tundra, the arctic marine environment and the North American Prairies [17,18]. In this study, most owls (i.e. 80 %) used the marine environment to some extent in winter with some individuals (i.e. 8/12 owls) spending over 95 % of their time over sea ice or along the coast. Our isotope analyses showed that a significant part of the owls' diet comes from the marine environment. This establishes that marine prey are a major food source for wintering owls in the eastern Canadian Arctic. Although owls also used the marine and coastal environments to some extent during autumn, we found few relationships between the use of this habitat in autumn and the marine contribution to their diet as inferred from the isotope composition of feathers. It is possible that few of the sampled feathers grew in autumn and thus provided little information on the diet at that time of the year [20]. Alternatively, and perhaps more likely, the relative use of marine prey by owls is lower in autumn than in winter in the Arctic.

Although the total abundance of marine prey like seabirds may be greater in autumn, before some of them migrate south, than in winter, they may be harder to catch at that time. In autumn, sea ice only began to freeze and therefore seabirds are likely scattered over large expanses of water, rendering prey catching more difficult for owls. On the other hand, snow cover is still low or nonexistent during the autumn season, which allows owls to easily feed on terrestrial prey like small mammals or land birds [43]. In winter, ice cover becomes more extensive, leaving only small areas of open-water (i.e. polynyas and leads) where seabirds often concentrate in dense aggregations [44], thereby facilitating prey capture by owls. Robertson and Gilchrist [45] reported that the number of snowy owls near polynyas of the Belcher Island in Hudson Bay was positively related to the local abundance of sea ducks in winter. In contrast, the availability and vulnerability of prey in the tundra, primarily lemmings, decrease between autumn and winter. Lemming populations are often at their lowest seasonal density at the beginning of the snow season after suffering intense predation pressure during summer and autumn [19,46,47]. In addition, catching lemmings may become harder once snow covers the ground [48,49]. Snowy owls using mainly the marine environments also tended to settle later during the non-breeding season than birds using terrestrial environments [18]. Therefore, some owls may progressively switch from a primarily terrestrial-based diet in autumn to a predominantly marine one during winter.

Our results confirm that snowy owls can show a great flexibility in their diet during the non-breeding season, and possibly more than previously recognized [16], in response to variations in prey availability. However, the extensive use of sea ice and reliance on marine prey observed in owls wintering in the eastern Canadian Arctic contrast with observations made in Norway, Russia and the western North American Arctic. In those areas, use of the sea ice by owls in winter is limited or negligible [50–52]. These differences may arise due to variability in prey availability or accessibility among these regions in winter. For instance, the marine environment of the eastern Canadian Arctic is more productive than in the western Arctic [53] and may thus harbour a higher density of seabirds in winter (e.g. [54,55]). Alternatively, other continental areas may offer a higher density and diversity of prey for owls such as high density of snowshoe hares *Lepus americanus* and ptarmigans in Alaska and Yukon [52].

4.2. Potential limitations of the study

An important assumption in our analyses was that individuals were consistent in their winter habitat use from year to year because feather stable isotopes reflected diet prior to the period of satellite tracking (Figure 1). Even though fidelity of snowy owls to a specific habitat (marine vs. terrestrial) is high [18] and they show a high inter-annual repeatability in their habitat use pattern, some individuals could have changed wintering habitats between years (i.e. individual wintering in the marine/coastal environment one year and far inland the next year or *vice versa*). Such habitat shifts may be more likely for young individuals that breed for the first time because immature individuals generally move to southern inland areas rather than remaining in the Arctic [56,57]. The possible occurrence of habitat shifts in some birds could account for part of the unexplained variability in our relationships. However, this likely rendered our analyses more conservative because the 'wrong' wintering habitat would have been associated with the isotopic signatures of feathers recorded in the previous year. The fact that we still find several significant relationships despite such potential limitation suggests that they are robust. Nonetheless, when the biology of the study species allows it, we recommend sampling feathers that grew during the same time period than the satellite transmitters were active.

Another factor that may have contributed to unexplained inter-individual variability in marine contribution to the diet of owls wintering near the coasts is differential prey selection. Among snowy owls' potential marine prey items, long-tailed ducks, common murres and thick-billed murres, which feed mainly on crustaceans and fish [58,59,60], are considered higher trophic-level prey than common eiders that feed on bivalve and mollusk [61,62]. If some individuals specialized on marine prey at specific trophic levels, this could have affected our estimation of the marine contribution to their diet. For instance, high δ^{15}N values in the feathers of some owls could be due to those individuals feeding on prey of higher trophic level at the time of feather growth [61], and this greater ratio would bias our estimates of marine proportion in their diet.

Another possible bias in the study is that one owl wintered in the continental Prairies rather than in the Arctic, where the isotope values of small mammals are higher than in the Arctic [20,36]. Including the Prairies small mammals as a third source for this individual slightly reduced the marine contribution to its diet in an *a posteriori* analysis and may have better estimated its diet than the two-source model. This could explain why relationships between habitat use and diet inferred from the isotopic analyses became stronger in this situation. However, links uncovered between diet and habitat use remained significant even when birds wintering inland were excluded (Figure 3).

4.3. Winter diet and carry-over effects

We did not find evidence that variability in the winter habitat use of owls inferred from their diet affected subsequent reproduction. However, there are some indications that using the marine environment may lead to lighter body mass in breeding snowy owls, which could have implications for subsequent reproduction. Carry-over effects of wintering conditions on subsequent reproduction have been shown in several migratory avian species [11,12,63–65] but not in others [66,67]. Similar to our results, no impact of the winter habitat use was found on the breeding phenology and productivity of Yellow warblers *Setophaga petechia* breeding in High Arctic as opposed to those breeding in Low

Arctic, and the authors suggested that the increased migration distance dampened carry-over effects rather than penalizing long-distance breeders [67].

Differences in the quality of habitat used in winter among individuals is often a key factor leading to reproductive carry-over effects in migratory birds [11,12,68]. In the case of snowy owls however, it is unclear whether the arctic marine environment is of higher quality than the terrestrial one in winter, especially when the latter is located much further south (i.e. the Prairies). Wintering conditions in the Arctic or over sea ice may be more rigorous than in the Prairies and increase physiological costs. Similarly, spatial distribution of prey (seabirds at polynyas) may also be more patchy than in the terrestrial environment, thereby explaining the trend for a reduced body mass in those birds. However, seabirds are much larger prey than small mammals and their temporal occurrence rather predictable as they use polynyas (i.e. fairly recurrent sea ice openings at the same locations and periods each year [69,70]). Moreover, wintering in the Arctic also reduces migration distance and may allow individuals to arrive earlier on the breeding site in spring [71].

Overall, it is possible that the advantages of wintering in one habitat or the other may not differ much for owls, or may change from one winter to the other, for instance in response to fluctuating lemming abundance. This may explain the absence of reproductive carry-over effects and the persistence of such diverse tactics. However, sample size was small in these analyses and further investigations would be needed to confirm the lack of association between wintering tactics and subsequent breeding.

5. Conclusion

Coupling feather isotopic signatures and satellite tracking of individuals has revealed multi-season linkage and provided detailed information on intra-population variability in resource use over a relatively large spatio-temporal scale in a nomadic species. Merging these two techniques allowed us to explain some of the variability in wintering diet based on the relative use of two contrasted habitats, the terrestrial and marine environment. Caron-Beaudoin et al. [72] also showed the usefulness of combining such approaches in a population of ring-billed gull *Larus delawarensis* exhibiting large inter-individual variability in foraging behaviours, but few avian studies have coupled those techniques to explore linkage between seasons [73–75]. This integrated approach could have interesting ecological implications, such as extending the temporal coverage of resource use prior to sampling and allowing the identification of habitat types or important food resources for species targeted by conservation measures.

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References

[1] Bolnick DI, Svanback R, Fordyce JA, et al. The ecology of individuals: incidence and implications of individual specialization. Am Nat. 2003;161(1):1–28.
[2] Newton I. Migration within the annual cycle: species, sex and age differences. J Ornithol. 2011;152:169–185.
[3] Metcalfe NB, Monaghan P. Compensation for a bad start: grow now, pay later? Trends Ecol Evol. 2001;16(5):254–260.
[4] Norris DR, Taylor CM. Predicting the consequences of carry-over effects for migratory populations. Biol Lett. 2006;2(1):148–151.
[5] Harrison XA, Blount JD, Inger R, et al. Carry-over effects as drivers of fitness differences in animals. J Anim Ecol. 2011;80(1):4–18.
[6] Sorensen MC, Hipfner JM, Kyser TK, et al. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. J Anim Ecol. 2009;78(2):460–467.
[7] Davis SE, Nager RG, Furness RW. Food availability affects adult survival as well as breeding success of Parasitic jaegers. Ecology. 2005;86(4):1047–1056.
[8] Penteriani V, Rutz C, Kenward R. Hunting behaviour and breeding performance of northern goshawks *Accipiter gentilis*, in relation to resource availability, sex, age and morphology. Naturwissenschaften. 2013;100(10):935–942.
[9] Cooper NW, Sherry TW, Marra PP. Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology. 2015;96(7):1933–1942.
[10] Marra PP, Hobson KA, Holmes RT. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science. 1998;282(5395):1884–1886.
[11] Norris DR, Marra PP, Kyser TK, et al. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc R Soc B Biol Sci. 2004;271(1534):59–64.
[12] Inger R, Harrison XA, Ruxton GD, et al. Carry-over effects reveal reproductive costs in a long-distance migrant. J Anim Ecol. 2010;79(5):974–982.
[13] Marra PP, Cohen EB, Loss SR, et al. A call for full annual cycle research in animal ecology. Biol Lett. 2015;11(8):4.
[14] Newton I. Advances in the study of irruptive migration. Ardea. 2006;94(3):433–460.
[15] Newton I. The migration ecology of birds. London: Academic Press; 2008.
[16] Holt D, Larson MD, Smith N, et al. The snowy owl (*Bubo scandiacus*). In: Poole A, editor. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; 2015. Retrieved from the Birds of North America Online: http://birds.cornell.edu/bna/species/010doi:10.2173/bna.10.
[17] Therrien JF, Gauthier G, Bêty J. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. J Avian Biol. 2011;42(4):363–369.
[18] Robillard A, Gauthier G, Therrien JF, et al. Wintering space use and site fidelity in a nomadic species, the snowy owl. J Avian Biol. 2018;49(5):jav-01707.
[19] Therrien JF, Gauthier G, Korpimäki E, et al. Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. Ecology. 2014;95(1):56–57.
[20] Robillard A, Gauthier G, Therrien J-F, et al. Variability in stable isotopes of snowy owl feathers and contribution of marine resources to their winter diet. J Avian Biol. 2017;48(6):759–769.
[21] Gauthier G, Berteaux D, Bêty J, et al. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience. 2011;18(3):223–235.

[22] Therrien JF, Gauthier G, Bêty J. Survival and reproduction of adult snowy owls tracked by satellite. J Wildl Manage. 2012;76(8):1562–1567.

[23] Heggøy O, Aarvak T, Øien IJ, et al. Effects of satellite transmitters on survival in snowy owls *Bubo scandiacus*. Ornis Norv. 2017;40:33–38.

[24] Steenhof K, Bates KK, Fuller MR, et al. Effects of radiomarking on prairie falcons: Attachment failures provide insights about survival. Wildl Soc Bull. 2006;34(1):116–126.

[25] CLS (Collecte Localisation Satellite). Argos user's manual: worldwide tracking and environmental monitoring by satellite; 2016. Available from: http://www.argos-system.org/manual/.

[26] Pyle P. Identification guide to North American birds: part I Columbidae to Ploceidae. Bolinas: Slate Creek Press; 1997.

[27] Pyle P. Flight-feather molt patterns and age in North American owls. Colorado Springs: American Birding Association; 1997; (Monographs in Field Ornithology; No. 2).

[28] Tieszen LL, Boutton TW, Tesdahl KG, et al. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia. 1983;57(1–2):32–37.

[29] Post DM, Layman CA, Arrington DA, et al. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia. 2007;152 (1):179–189.

[30] Petersen MR, Douglas DC, Wilson HM, et al. Effects of sea ice on winter site fidelity of pacific common eiders (*Somateria mollissima V-nigrum*). Auk. 2012;129(3):399–408.

[31] Tranquilla LAM, Montevecchi WA, Fifield DA, et al. Individual winter movement strategies in two species of murre (*Uria* spp.) in the Northwest Atlantic. PLoS One. 2014;9(4):13.

[32] Blackburn E, Cresswell W. High winter site fidelity in a long-distance migrant: implications for wintering ecology and survival estimates. J Ornithol. 2016;157(1):93–108.

[33] Blackburn GS, Wilson DJ, Krebs CJ. Dispersal of juvenile collared lemmings (*Dicrostonyx groenlandicus*) in a high-density population. Can J Zool. 1998;76(12):2255–2261.

[34] Predavec M, Krebs CJ. Microhabitat utilisation, home ranges, and movement patterns of the collared lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic. Can J Zool. 2000;78(11):1885–1890.

[35] Schmidt NM, Berg TB, Jensen TS. The influence of body mass on daily movement patterns and home ranges of the collared lemming (*Dicrostonyx groenlandicus*). Can J Zool. 2002;80 (1):64–69.

[36] White AJ, Poulin RG, Wissel B, et al. Agricultural land use alters trophic status and population density of deer mice (*Peromyscus maniculatus*) on the North American Great Plains. Can J Zool. 2012;90(7):868–874.

[37] Dodge S, Bohrer G, Weinzierl R, et al. The environmental-data automated track annotation (Env–DATA) system: linking animal tracks with environmental data. Mov Ecol. 2013;1:3.

[38] Parnell A, Jackson A. Stable isotope analysis in R. R package version 4.2. https://CRAN.R-project.org/package=siar; 2013.

[39] Parnell AC, Inger R, Bearhop S, et al. Source partitioning using stable isotopes: coping with too much variation. PLoS One. 2010;5(3):e9672.

[40] Therrien JF, Fitzgerald G, Gauthier G, et al. Diet-tissue discrimination factors of carbon and nitrogen stable isotopes in blood of snowy owl (*Bubo scandiacus*). Can J Zool. 2011;89 (4):343–347.

[41] R Development Core Team. R: a language and environment for statistical computing. Vienna; 2015.

[42] Stoffel MA, Nakagawa S, Schielzeth H. Rptr: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Meth Ecol Evol. 2017;8:1639–1644.

[43] Potapov E, Sale R. The snowy owl. London: T & AD Poyser; 2012.

[44] Gilchrist HG, Robertson GJ. Observations of marine birds and mammals wintering at polynyas and ice edges in the Belcher Islands, Nunavut, Canada. Arctic. 2000;53(1):61–68.

[45] Robertson GJ, Gilchrist HG. Wintering snowy owls feed on sea ducks in the Belcher Islands, Nunavut, Canada. J Raptor Res. 2003;37(2):164–166.

[46] Gilg O, Hanski I, Sittler B. Cyclic dynamics in a simple vertebrate predator–prey community. Science. 2003;302(5646):866–868.

[47] Fauteux D, Gauthier G, Berteaux D. Seasonal demography of a cyclic lemming population in the Canadian Arctic. J Anim Ecol. 2015;84(5):1412–1422.

[48] Chamberlin ML. Winter hunting behavior of a snowy owl in Michigan. Wilson Bull. 1980;92(1):116–120.

[49] Therrien JF, Pinaud D, Gauthier G, et al. Is pre-breeding prospecting behaviour affected by snow cover in the irruptive snowy owl? A test using state–space modelling and environmental data annotated via Movebank. Mov Ecol. 2015;3:1.

[50] Fuller M, Holt D, Schueck L. Snowy owl movements: variation on the migration theme. In: Berthold P, Gwinner E, Sonnenschein E, editor. Avian migration. Berlin: Springer; 2003. p. 359–366.

[51] Jacobsen KO, Solheim R, Øien IJ. Snøuglas vandringsmønster og habitatvalg [Movements and habitat choice of Snowy owls *Bubo scandiacus*]. Annual report 2008. Trondheim: Norwegian Institute for Nature Research; 2009. (NINA report; 458). Norwegian.

[52] Doyle FI, Therrien JF, Reid D, et al. Seasonal movements of breeding snowy owls in the western north American Arctic. J Raptor Res. 2017;51(4):428–438.

[53] Frey KE, Comiso JC, Cooper LW, et al. Arctic Ocean primary productivity. National Oceanic and Atmospheric Administration (NOAA); 2015. Available from: http://www.arctic.noaa.gov/reportcard/ocean_primary_productivity.html.

[54] Fort J, Cherel Y, Harding AMA, et al. Geographic and seasonal variability in the isotopic niche of little auks. Mar Ecol Prog Ser. 2010;414:293–302.

[55] Hunt GL, Blanchard AL, Boveng P, et al. The Barents and Chukchi seas: comparison of two Arctic shelf ecosystems. J Mar Syst. 2013;109:43–68.

[56] Smith N. Observations of wintering snowy owls (*Nyctea scandiaca*) at Logan Airport, East Boston, Massachusetts from 1981–1997. In: Duncan JR, Johnson DH, Nicholls TH, editor. Biology and conservation of owls of the Northern Hemisphere: 2nd International symposium. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station; 1997. p. 591–596. (General Technical Report; NC-190).

[57] Robillard A, Therrien JF, Gauthier G, et al. Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the snowy owl. Oecologia. 2016;181(2):423–433.

[58] Gaston AJ, Hipfner JM. Thick-billed murre (*Uria lomvia*), version 1.0. In: Billerman SM, editor. Birds of the world. Ithaca: Cornell Lab of Ornithology; 2020.

[59] Jamieson SE, Robertson GJ, Gilchrist HG. Autumn and winter diet of long-tailed duck in the Belcher Islands, Nunavut, Canada. Waterbirds. 2001;24(1):129–132.

[60] Robertson GJ, Savard J-PL. Long-tailed duck (*Clangula hyemalis*), version 1.0. In: Billerman SM, editor. Birds of the world. Ithaca: Cornell Lab of Ornithology; 2020, https://doi.org/10.2173/bow.lotduc.01.

[61] Hobson KA. Trophic relationships among high arctic seabirds: insights from tissue-dependent stable-isotope models. Mar Ecol Prog Ser. 1993;95(1–2):7–18.

[62] Goudie RI, Robertson GJ, Reed A. Common eider (*Somateria mollissima*), version 1.0. In: Billerman SM, editor. Birds of the world. Ithaca: Cornell Lab of Ornithology; 2020, https://doi.org/10.2173/bow.comeid.01.

[63] Legagneux P, Fast PLF, Gauthier G, et al. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proc R Soc B Biol Sci. 2012;279(1730):876–883.

[64] Gurney KEB, Wood CJ, Alisauskas RT, et al. Identifying carry-over effects of wintering area on reproductive parameters in white-winged scoters: an isotopic approach. Condor. 2014;116(2):251–264.

[65] Paxton KL, Moore FR. Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. J Avian Biol. 2015;46(5):495–506.

[66] Oppel S, Powell AN. Does winter region affect spring arrival time and body mass of king eiders in northern Alaska? Polar Biol. 2009;32(8):1203–1209.

[67] Drake A, Martin M, Green DJ. Winter habitat use does not influence spring arrival dates or the reproductive success of Yellow Warblers breeding in the arctic. Polar Biol. 2014;37(2):181–191.

[68] Studds CE, Marra PP. Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. Ecology. 2005;86(9):2380–2385.

[69] Smith M, Rigby B. Distribution of polynyas in the Canadian Arctic. Ottawa: Environment Canada; 1981; (Canadian Wildlife Service Occasional Paper; Number 45).

[70] Barber DG, Massom RA. The role of sea ice in Arctic and Antarctic polynyas. In: Smith WO, Barber DG, editor. Polynyas: windows to the world. Amsterdam: Elsevier; 2007. p. 1–54. (Elsevier Oceanography Series; 74).

[71] Therrien JF, Gauthier G, Pinaud D, et al. Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource. J Avian Biol. 2014;45(6):536–544.

[72] Caron-Beaudoin E, Gentes ML, Patenaude-Monette M, et al. Combined usage of stable isotopes and GPS-based telemetry to understand the feeding ecology of an omnivorous bird, the ring-billed gull (*Larus delawarensis*). Can J Zool. 2013;91(10):689–697.

[73] Furness RW, Crane JE, Bearhop S, et al. Techniques to link individual migration patterns of seabirds with diet specialization, condition and breeding performance. Ardea. 2006;94 (3):631–638.

[74] Danckwerts DK, McQuaid CD, Connan M, et al. Intra-annual variation in the foraging ecology of the endangered endemic Barau's Petrel (*Pterodroma baraui*) from Reunion Island, south-western Indian Ocean: insights from a multifaceted approach. Mar Biol. 2016;163(1):15.

[75] Pillar AG, Marra PP, Flood NJ, et al. Moult migration in Bullock's orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. J Ornithol. 2016;157(1):265–275.