

# JOURNAL OF AVIAN BIOLOGY

## Article

### Wintering space use and site fidelity in a nomadic species, the snowy owl

Audrey Robillard, Gilles Gauthier, Jean-François Therrien and Joël Bêty

A. Robillard (<http://orcid.org/0000-0002-3690-7080>) ([audrey.robillard.2@ulaval.ca](mailto:audrey.robillard.2@ulaval.ca)) and G. Gauthier (<http://orcid.org/0000-0002-2624-3508>), Dept Biologie and Centre d'études nordiques, Univ. Laval, Québec, QC, Canada. – J.-F. Therrien, Hawk mountain sanctuary, Acopian Center for Conservation Learning, Orwigsburg, PA, USA. – J. Bêty, Dept Biologie, chimie et géographie and Centre d'études nordiques, Univ. du Québec à Rimouski, Rimouski, QC, Canada.

Journal of Avian Biology

2018: e01707

doi: 10.1111/jav.01707

Subject Editor: Thomas Alerstam

Editor-in-Chief: Jan-Åke Nilsson

Accepted 20 February 2018

Migratory species can exploit many habitats over vast geographic areas and adopt various patterns of space and habitat use throughout their annual cycle. In nomadic species, determinants of habitat use during the non-breeding season are poorly known due to the unpredictability of their movement patterns. Here, we analysed variability in wintering space and habitat use by a highly nomadic species, the snowy owl, in eastern North America. Using 21 females tracked by satellite telemetry between 2007 and 2016, we 1) assessed how space use patterns in winter varied according to the type of environment (marine vs terrestrial), latitudinal zone (Arctic vs temperate), local snow conditions and lemming densities and 2) investigated winter habitat and site fidelity. Our results confirmed a high inter-individual variation in patterns of habitat use by wintering snowy owls. Highly-used areas were concentrated in the Arctic and in the marine and coastal environments. Owls wintering in the marine environment travelled over longer distances during the winter, had larger home ranges and these were divided in more smaller zones than individuals in terrestrial environments. Wintering home range sizes decreased with high winter lemming densities, use of the marine environment increased following high summer lemming densities, and a thick snow cover in autumn led to later settlement on the wintering ground. Contrary to expectations, snowy owls tended to make greater use of the marine environment when snow cover was thin. Snowy owls were highly consistent in their use of a given wintering environment and a specific latitudinal zone between years, but demonstrated flexibility in their space use and a modest site fidelity. The snowy owls' consistency in wintering habitat use may provide them with advantages in terms of experience but their mobility and flexibility may help them to cope with changing environmental conditions at fine spatial scale.

Keywords: snowy owl, *Bubo scandiacus*, fidelity, habitat use, home range, nomadism, non-breeding, satellite telemetry



[www.avianbiology.org](http://www.avianbiology.org)

© 2018 The Authors. Journal of Avian Biology © 2018 Nordic Society Oikos

## Introduction

Throughout their annual cycle, migratory species can exploit many habitats over vast geographic areas that may be separated by thousands of kilometers. In doing so, individuals adopt various tactics of movement (Newton 2008, Phillips et al. 2009), foraging (McClellan et al. 2010) and habitat use (Tranquilla et al. 2014). Defined as the way individuals use environmental components to meet their life history needs (Block and Brennan 1993, Jones 2001), habitat use can be influenced by multiple factors during winter such as food abundance or its accessibility, which can be limited by environmental factors such as snow cover in winter (Greenwood and Baillie 1991, Golawski and Kasprzykowski 2010). Despite such environmental variability, some migrating species will show relatively high fidelity to a specific wintering site because familiarity with a given site may improve foraging efficiency, predator avoidance or maintain a dominant status, which could ultimately increase individual fitness (Cresswell 2014, Blackburn and Cresswell 2016, Latta et al. 2016). Site fidelity is generally favoured when resource levels are predictable in space and time (Newton 2006, 2008).

Nomadic species show highly variable and unpredictable movements, both within and between years, often in response to large-scale fluctuations in food availability (Swingland and Greenwood 1984, Newton 2008, Rappole 2013). In those species, determinants of habitat use during the non-breeding season is poorly known due to the unpredictability of their migratory patterns (Swingland and Greenwood 1984). The snowy owl is considered one of the most nomadic bird and extreme breeding dispersal has been documented in this species (Therrien et al. 2014). In winter, snowy owls can exhibit a bewildering diversity in movement and habitat use. For instance, although snowy owls are regular winterers in the Canadian Prairies and American Great Plains, they also show periodic irruptions throughout the temperate regions of North America (Kerlinger et al. 1985, Kerlinger and Lein 1988, Holt et al. 2015). Many adult snowy owls also remain in the Arctic throughout the winter and can make extensive use of the marine environment (Therrien et al. 2011, Robillard et al. 2017). However, very little is known about individual consistency and the effect of environmental factors on patterns of space and habitat use during the winter in such nomadic species.

Snowy owls wintering in different regions (e.g. Arctic vs temperate areas) and feeding in different habitats (e.g. terrestrial vs marine) can face highly contrasted environmental conditions. During the summer, snowy owls specialize on lemmings, which show high temporal and spatial variability in abundance on the tundra (Angerbjörn et al. 2001, Krebs et al. 2002, Gruyer et al. 2008). In winter, they broaden their diet and become more generalists. In terrestrial environment, small mammals (lemmings but also mice and voles at more southern latitudes) typically remain their main prey items but they must capture them under the snow (Boxall and Lein 1982a, Detienne et al. 2008). Ptarmigans and hares

can also be part of their wintering diet (Holt et al. 2015, Doyle et al. 2017). Owls wintering in coastal and marine environments can rely on other prey such as water and sea birds (Campbell and Maccoll 1978, Smith 1997, Robertson and Gilchrist 2003, Robillard et al. 2017). These prey can often be found in high densities (Gilchrist and Robertson 2000, Therrien et al. 2011) in open water in the sea ice (e.g. polynyas), which are fairly recurrent at the same locations and periods each year (Smith and Rigby 1981, Barber and Massom 2007). Therefore, we could expect this prey base to be more predictable from year to year in the marine environment than in the tundra.

We used satellite telemetry to describe the behavior of wintering snowy owls breeding in eastern Canada and to examine factors affecting their wintering behavior. In particular, we 1) assessed how space use patterns in winter varied according to the type of environment (marine vs terrestrial), latitudinal zone (Arctic vs temperate), local snow conditions and lemming densities in summer and winter, and 2) investigated winter habitat use and site fidelity. We predicted that snowy owls would show greater fidelity to wintering than to breeding sites due to the relatively higher predictability of food resources in the former. Due to differences in migration length, we also expected individuals wintering in the Arctic to settle earlier on their wintering site in autumn and to depart later in spring than individuals wintering in southern temperate regions. Moreover, in winters with reduced food availability in the terrestrial environment (low small mammal abundance or thick snow), we expected a greater use of the marine habitat.

## Material and methods

### Study area and snowy owl captures

Between 2007 and 2014, 31 snowy owls (30 females and 1 male) were captured at three different sites in the eastern Canadian Arctic: Bylot Island, Nunavut (73°08'N, 80°00'W; High Arctic) in 2007 (n = 12) and 2014 (n = 10), Mary River, Nunavut (71°10'N, 79°21'W; High Arctic) in 2011 (n = 1) and Deception Bay, Nunavik, QC (62°02'N, 74°49'W; Low Arctic) in 2013 (n = 8; see Fig. 1 for study site locations). Landscapes of Bylot Island and Mary River are similar and dominated by broad river valleys and gently rolling hills with a mosaic of mesic and wet habitats with lush vegetation (see Gauthier et al. 2011 for a detailed description of Bylot Island's study area); these sites belong to the Arctic bioclimate subzone C (Walker et al. 2005). Deception Bay is dominated by mesic habitats and rocky terrains, with small patches of wet habitats scattered in the landscape and lush vegetation along the river banks; the site corresponds to the Arctic bioclimate subzone D. On Bylot Island, nest searching of snowy owls was carried out in suitable nesting habitat over a ~450 km<sup>2</sup> area of the south plain on foot or by helicopter. At Deception Bay and Mary River, nest searching was carried out along the

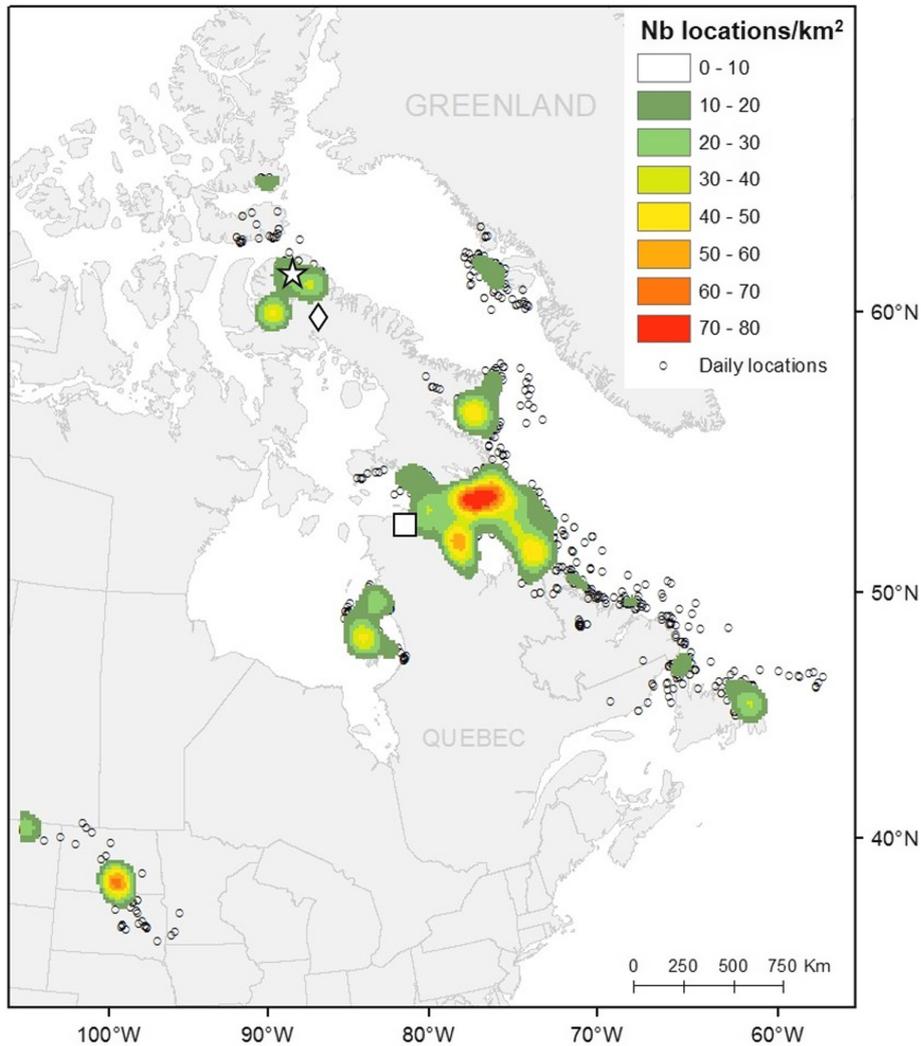


Figure 1. Highly-used areas by 21 wintering snowy owls tracked between 2007 and 2016 estimated with Kernel densities in ArcMap 10.2. Capture sites (Bylot Island: star; Mary River: diamond; Deception Bay: square) are also depicted.

roads in the vicinity of the mining facilities present at both sites. Captures of snowy owls were performed with bow-nets positioned over the nest or with a bal-chatri between 29 June and 4 August.

### Locations of radio-marked individuals

Snowy owls were fitted with ARGOS satellite transmitters (Microwave telemetry, USA, PTT-100,  $n=14$ ; North Star Science and Technology, LLC, USA, PTT-30G,  $n=17$ ). Transmitters were installed on the owls as a backpack using a harness made of Teflon strips (Steenhof et al. 2006) and weighed 40g (i.e. 1.8% of the birds' body mass). It has been shown that these transmitters do not significantly impact survival or reproductive performances of owls (Therrien et al. 2012, Heggøy et al. 2017). Between 2007 and 2010, locations were obtained over a 4–6 h period at  $\sim 2$ –3 d intervals, from mid-June to November and  $\sim 5$  d intervals from December to mid-June. Between 2011 and 2016, locations were obtained

more often during the non-breeding period (i.e. at  $\sim 2$ –3 d intervals from December to mid-June and  $\sim 5$  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; CLS 2016). Locations with a lower estimated precision (i.e. classes 0, A, B, Z) were excluded. Because of early transmission failure, 10 female owls could not be included in any of the analyses; therefore, effective sample size was 21 individuals.

As multiple locations were recorded for each transmission period, positions were averaged to a single mean daily coordinate to avoid non-independence of spatial data. Distances between consecutive daily locations were estimated using the 'as.ltraj' function in the adehabitatLT package (Calenge 2006) in R ver. 3.2.3 (R Development Core Team) and divided by the number of days between locations to evaluate the daily movement of individuals. The distance from

each daily location to the nearest coast was estimated by the Env-Data annotation system in Movebank (Dodge et al. 2013), with positive values when birds were on land and negative values when they were at sea.

## Environmental covariates

Small mammal abundance data on Bylot Island was obtained for both summer and winter periods between 2007–2016, as this is the only site in eastern Arctic of North America where it was measured annually. Summer densities of lemmings were estimated using live-trapping and winter abundance of lemmings was measured by sampling remnants of winter nests (see Supplementary material Appendix 1 for details). We considered summer abundance of lemmings because we believed that it could affect owl behaviour in winter through carry-over effects. For snow depth, we obtained data through the Movebank Env-Data system (Dodge et al. 2013) using the NCEP NARR dataset which interpolates the snow depth at small spatial resolution (i.e. 0.3 deg = 32 km; see Supplementary material Appendix 1 for details). A snow depth was associated with each owl location and averaged over specific time-frames (e.g. autumn) but was ignored for owl locations over sea ice because availability of prey in this habitat (primarily seabirds in open water) should not be affected by snow depth.

## Data analysis

### Determination of breeding and wintering periods

Annual settlement and departure dates on the breeding and wintering sites were determined for each individual. The duration of the breeding or wintering period of each individual owl was defined as the difference between its departure and settlement dates. The autumn period corresponded to the period between the departure from the breeding site and the settlement in the wintering site. Throughout the text, we make a distinction between the non-breeding season (i.e. the entire period outside the breeding season, which includes migratory periods in autumn and spring) and the wintering period as defined above. Details of the methods used to estimate settlement and departure dates are presented in Supplementary material Appendix 2.

### Determination of habitat categories

To analyse space and habitat use, each individual location was assigned to one of the two main types of environment used by owls based on its distance from the closest marine coast: land ( $\geq 0$  km from coast), and sea ( $< 0$  km from coast; negative distance values were assigned when birds were at sea, see above). We calculated the proportion of time spent by individuals in each of these environments during the wintering period and assigned birds as being terrestrial when more than 50% of locations were on land (referred to as inland) or marine when more than 50% of locations were at sea. Each bird was also categorized according to a wintering latitudinal zone as Arctic or temperate (localisations ranged from

43.7°N to 76.7°N), depending if they wintered above or below the tree line (in North America, this line runs roughly from 57°N in the east to 63°N in the central portion).

### Determination of space use parameters

Both home range (95% utilization) and core area size (50% utilization) were estimated using the Brownian bridge kernel method with the function `kernellbb` of the package `adehabitatHR` (Calenge 2006) in R (R Development Core Team) for each individual, year and period (breeding and wintering). This method takes into account the path travelled between successive locations and not only the static positions recorded (Bullard 1991, Calenge 2006, Horne et al. 2007). The Brownian bridge kernel method requires time-specific locations, a defined distribution of location errors (here assumed to be normally distributed with mean centered on the estimated location), a parameter related to the imprecision of the locations (i.e. the estimated error associated with location data; *Sig2*) and a Brownian motion variance parameter ( $\sigma_m^2$ ; *Sig1*). This latter parameter is related to the tracked individual's mobility and can be estimated with the 'liker' function in package `adehabitatHR` through maximum-likelihood (Calenge 2006, Horne et al. 2007) based on the *Sig2* parameter. Because this method characterizes individual space use very finely, we also extracted the number of distinct home ranges and core areas used by each individual in each season. Overlaps in home ranges and core areas between year  $t$  and year  $t - 1$  were calculated with the `Intersect` tool in ArcMap 10.2 (ESRI 2013).

The Kernel density tool in the spatial analyst toolbox of ArcMap 10.2 (ESRI 2013) was used to calculate and illustrate areas of low to high use by snowy owls based on mean daily locations for all birds tracked for at least one complete winter ( $n = 21$ ). The default search radius (bandwidth) was used as this approach relies on the spatial configuration and number of input points and corrects for spatial outliers, thereby selecting the relevant search radius while minimizing overestimation.

Centroids of all locations during the winter and breeding periods were calculated as mean latitude and longitude for each individual and year. Geodesic distances between centroids were measured in ArcMap 10.2 (ESRI 2013) and were used to estimate dispersal distance.

## Statistical analyses

To assess the effect of latitudinal zone, snow depth, lemming density and, when applicable, wintering environment, on the different wintering space use variables (i.e. marine habitat use, length of stay on a wintering site, distance travelled, winter dispersal distances, distance to the coast, number of core areas, home range and core area size), we used LMMs with bird ID as random effect (as individuals could be tracked over multiple winters). We used the same models (LMMs with bird ID as random effect) to analyse differences in annual dispersal distances (between consecutive breeding or wintering centroids), length of stay, home range and

core area sizes between summer and winter and differences in migration distances in autumn and spring. For analyses of the marine environment use, defined as proportion of locations of an individual at sea, we used GLMMs with binomial family and bird ID as a random effect. The term weights was added to account for the total number of locations per winter and per individual. To meet normality requirements, dispersal distances, distances travelled, home range and core area size were log-transformed while length of stay on a wintering site, migratory distances between breeding and wintering sites and core area numbers were square-root transformed. We also tested for possible year effects by including year as an additional random factor in all analyses. However, because results were always similar whether year was included or not, we report results without this variable to minimize the risk of having over-parameterize models. All means are presented  $\pm$  SD unless otherwise specified.

We used the package `influence.ME` (Nieuwenhuis et al. 2012) to investigate whether some individual data points could be over-influential on some parameter estimates. We identified one outlier (i.e. female J; Supplementary material Appendix 3) in the analysis linking the marine environment use with summer small mammal abundance based on the Cooks' distances (Cooks'  $D=16.1$ ; cut-off value=0.24; Van der Meer et al. 2010), the percentile change between models including and excluding the ID (155%) and the 'sigtest' function (which evaluates how an individual affects the significance of the fixed factors; Nieuwenhuis et al. 2012). This specific female spent 87% of her time in the marine environment in year 1 and 0% in year 2. We thus excluded this female in the relevant statistical analysis but nonetheless present the data points on the graphs.

## Results

### Habitat use and distance travelled

The 21 tracked owls allowed us to record 42 complete wintering periods, 25 of which were spent predominantly inland (16 in the Arctic, 9 in temperate areas) and, 17 in the marine environment (15 in the Arctic, 2 in temperate areas; Supplementary material Appendix 3 and 4). Among birds classified as marine,  $80 \pm 11\%$  (range 55 to 98%) of their locations in winter were at sea whereas for those classified as wintering in the terrestrial environment,  $85 \pm 17\%$  (range 54 to 100%) of their locations were inland. Highly-used areas were concentrated in the Arctic marine and coastal environments, especially in the Hudson strait (i.e. northern Nunavik and southern Baffin areas) and to a lesser extent in the American Midwest (i.e. North and South Dakota; Fig. 1).

Mean distance to the coast in winter ranged from  $-75$  km to 1368 km ( $171 \pm 454$  km,  $n=42$ ; negative distance values indicate birds at sea). Individuals wintering in the Great Plains were much furthest inland (distance to the coast:  $1267 \pm 75$  km;  $n=6$ ) compared to birds wintering inland in the Arctic or in temperate southeastern Canada (i.e. Newfoundland;

$7 \pm 14$  km,  $n=19$ ; Fig. 1). Individuals wintering in the marine environment were at similar distance from the coast in the Arctic ( $-31 \pm 16$  km,  $n=15$ ) and in temperate areas ( $-45 \pm 43$  km,  $n=2$ ;  $t$ -test:  $t=0.46$ ,  $p=0.7$ ).

Straight-line distances between centroids of breeding and wintering sites (autumn migration) were shorter for birds wintering in the Arctic ( $831 \pm 504$  km) than for birds wintering at temperate latitudes ( $2517 \pm 787$  km;  $\beta=21.7$ ; CI: [14.1; 29.2]) but not different for birds wintering in marine ( $1009 \pm 511$  km) or terrestrial environments ( $1451 \pm 1132$  km;  $\beta=0.7$ ; CI: [-7.7; 9.3]). On their wintering sites, mean distance travelled by individuals was greater in marine ( $2729 \pm 1378$  km) than in terrestrial environments ( $1190 \pm 695$  km) but not different between the Arctic ( $1817 \pm 1036$  km) and temperate areas ( $1801 \pm 1838$  km; Table 1). Snow depth in winter and summer lemming densities on Bylot did not affect the distance travelled in winter but there was a trend for shorter distances travelled at high densities of lemmings in winter (Table 1; Fig. 2a).

Individuals that wintered outside the Great Plains were highly variable in their use of the marine environment (i.e. range 0–98%; mean  $48.2 \pm 33.5\%$ ;  $n=36$ ). One female (M) spent up to 169 d at sea in the High Arctic and only 4 individuals were never located at sea during a given wintering season. Individuals made a greater use of the marine environment when snow depth on land was low but this relationship was driven by only two data points at very high snow density (Table 1, Fig. 2b). Use of the marine environment in winter also increased when lemming density during the previous summer was high (Table 1, Fig. 2c).

### Settlement and departure dates

The average settlement and departure dates from the wintering ground were 16 November and 7 April, and from the breeding ground 27 May and 23 August, respectively (Fig. 3). Settlement dates on the wintering grounds were on average earlier for birds wintering in terrestrial environment than those wintering in marine environment, and tended to be earlier for birds that wintered in the Arctic than for birds in temperate areas (Table 1; Fig. 3). Settlement on a wintering site also occurred later when snow on land was deep in autumn (Table 1; Fig. 2d). Inversely, arctic birds departed later from their wintering site than temperate ones and terrestrial winterers also tended to depart earlier than marine wintering birds (Table 1; Fig. 3). Departure dates from wintering sites were not affected by snow depth or lemming density in winter.

Length of stay on the wintering ground for all individuals averaged  $142 \pm 32$  d and was longer than the length of stay on the breeding site ( $86 \pm 22$  d;  $\beta = 2.7$ , CI = 2.2, 3.2;  $n=98$ ). Owls wintering at temperate latitudes tended to have shorter wintering periods than owls wintering in Arctic (Table 1), but neither the wintering environment, snow depth nor the lemming density significantly affected length of stay on wintering grounds.

Table 1. Statistical results of the relationships between different parameters of winter space and habitat use by snowy owls tracked by satellite telemetry and selected explanatory variables: type of wintering environment (Environment; marine vs terrestrial), wintering latitudinal zone (LatitudinalZone: Arctic vs temperate), snow depth (SnowAutumn: autumn and SnowWinter: winter) and small mammal abundance on Bylot Island (LemmSummer: previous summer and LemmWinter: current winter). Response variables include: distance travelled (km; n=42 winter-individual), marine environment use (n=36 winter-individual; excluding the birds wintering in the prairies), settlement and departure dates (n=42 winter-individual), length of stay (days; n=42 winter-individual), home range and core area size (km<sup>2</sup>; n=42 winter-individual) and number of core areas (n=42 winter-individual). Bird ID was included in all models as random effect. Latitudinal zone of reference=Arctic. Environment of reference=marine. Complete results with all explanatory variables are presented in Supplementary material Appendix 6.

Response variables	Explanatory variables	$\beta$	Lower CI	Upper CI
Distance travelled within wintering area	Environment	-0.788	-1.195	-0.381
	LemmWinter	-0.027	-0.059	0.006
Marine environment use	SnowWinter	-0.089	-0.110	-0.068
	LemmSummer <sup>1</sup>	0.121	0.056	0.185
Dates of settlement on wintering ground	Environment	-14.393	-28.025	-0.761
	LatitudinalZone	11.745	-3.849	27.339
	SnowAutumn	2.732	1.623	3.841
Dates of departure from wintering ground	Environment	-8.733	-21.922	4.456
	LatitudinalZone	-18.812	-37.397	-0.227
Length of stay on wintering site	LatitudinalZone	-0.907	-1.859	0.045
Wintering home range size	Environment	-1.452	-2.229	-0.675
	LemmWinter	-0.077	-0.149	-0.005
Wintering core area size	Environment	-1.698	-2.579	-0.817
	LemmWinter	-0.083	-0.161	-0.005
Number of core areas in wintering area	Environment	-0.571	-0.977	-0.165
	LatitudinalZone	-0.426	-0.881	0.029
	LemmWinter	-0.044	-0.082	-0.005

<sup>1</sup> Female J was removed from this model (n=34).

## Home range size

The average winter home range size was  $7.11 \times 10^4$  km<sup>2</sup> ( $\pm 8.77 \times 10^4$ ; n=42; Fig. 4). Home range sizes were greater in winter than summer (summer =  $2.02 \pm 4.57 \times 10^2$  km<sup>2</sup>,  $\beta=6.28$ , 95% CI=5.71, 6.84, n=52). Home range size was greater for owls wintering in the marine environment ( $11.6 \pm 9.0 \times 10^4$  km<sup>2</sup>, n=17) than inland ( $4.1 \pm 7.4 \times 10^4$ , n=25) but did not vary among wintering latitudinal zones (Fig. 4) and was greater in winters of low lemming density (Table 1, Fig. 2e). The number of distinct home ranges within a given winter ranged from 1 to 5 (i.e.  $1.9 \pm 1.0$ ; Supplementary material Appendix 5).

Similarly, the mean winter core area size was  $9.4 \times 10^3$  km<sup>2</sup> ( $\pm 13.5 \times 10^3$ ; Fig. 4) and was also greater in marine habitats than inland as well as in winters of low lemming density (Table 1). Generally, multiple core areas were present in individual home ranges ( $4.6 \pm 2.8$  core areas per individual; range: 1–12). The number of core areas were greater in the marine ( $5.8 \pm 2.3$ ) than the terrestrial environment ( $3.8 \pm 2.9$ ) and also tended to be greater for birds wintering in the Arctic ( $5.1 \pm 3.0$ ) than in temperate regions ( $3.3 \pm 2.0$ ; Table 1). The number of core areas decreased with increasing lemming density in winter (Fig. 2f).

## Fidelity

Most individuals that were tracked for two consecutive years used the same wintering environment and latitudinal zone (16 out of 21 cases; Table 2). Two individuals switched from the marine to the terrestrial Arctic environment the

following year whereas one switched from a terrestrial to a marine environment and back to a terrestrial environment in the third winter. Only one individual changed latitudinal zone in the following winter, from the Arctic to temperate latitudes.

The mean distance between centroids of wintering locations for individuals tracked in consecutive years was 389 km  $\pm$  624 km (i.e. winter dispersal; range=20–2731 km, n=21), and was lower than breeding dispersal which was 710 km  $\pm$  466 km (range=85–1617 km, n=35; [ $\beta=-1.00$ , 95% CI=-1.55, -0.44]; Fig. 5). However, if we excluded the individual that switched wintering latitudinal zone from one year to the next (Table 2), mean distance between centroids of wintering birds was 271  $\pm$  327 km (range=20–1479 km).

Mean home range overlap for individual tracked over two consecutive winters was 29  $\pm$  28% (range 0–100%) and mean core areas overlap was 12  $\pm$  17% (range 0–62%; n=21; Supplementary material Appendix 5). These values remained highly similar if we excluded the five individuals that changed wintering environment or latitudinal zone between consecutive winters. In comparison, breeding home range or core area never overlapped in consecutive summers (n=29). Neither the wintering environment nor the latitudinal zone affected the level of home range overlap.

## Discussion

Our study is the first to examine the large-scale spatial wintering ecology of a highly nomadic species like the snowy owl. We found that space use patterns strongly differed

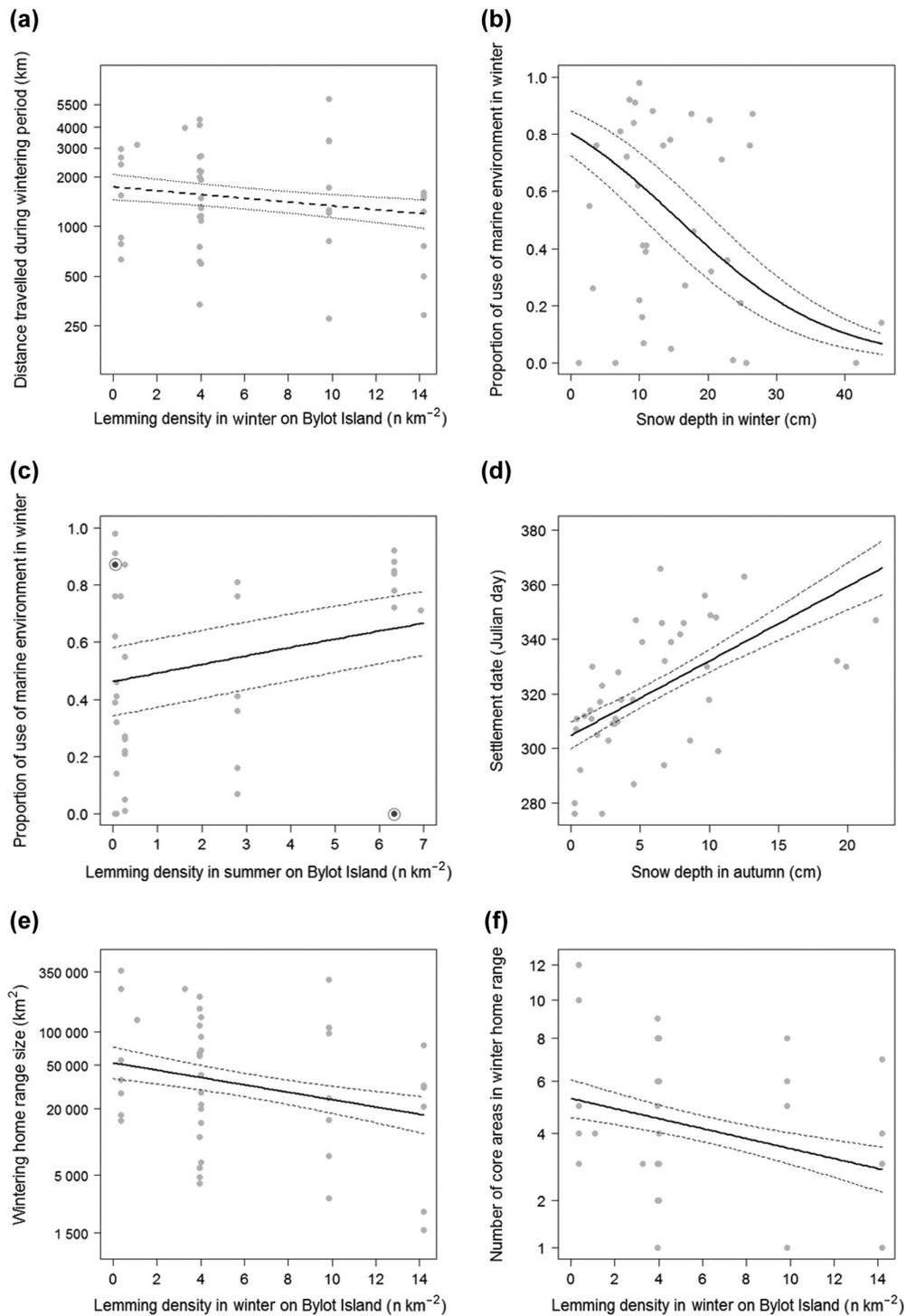


Figure 2. Relationships between distance travelled (a), proportion of use of the marine environment (b, c), dates of settlement on wintering site (c), wintering home range size (d), number of core areas in winter (e) and lemming densities on Bylot Island (previous summer or current winter) or snow depth (autumn or winter). Coefficients were predicted with LMM or GLMM (from Table 1). Regressions with confidence intervals excluding zeros (full lines) and trends (dashed lines) are depicted along with their SE (dotted lines). Confidence levels are 0.95 in all graphs. Raw data points (pale gray dots) and outliers (encircled dark gray dots; removed from analysis) are also depicted.

among individuals using different types of wintering environment (marine vs terrestrial) and latitudinal zones (Arctic vs temperate) and part of this variability could be explained by environmental factors like snow depth and density of their

main terrestrial prey (lemmings). We also found that individuals were generally faithful to their wintering environment and latitudinal zone, and to some extent to their specific wintering location.

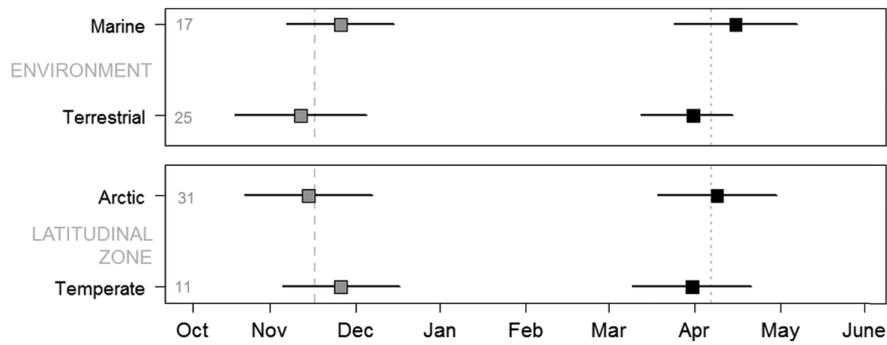


Figure 3. Settlement (gray squares; mean = dashed line) and departure (black squares; mean = dotted line) dates from wintering areas of snowy owls ( $n = 21$  individuals tracked over one to three wintering periods) in different types of wintering environment (top) or at different latitudinal zones (bottom).

### Intraspecific variation in space and habitat use in winter

Adult female snowy owls that bred in the eastern Canadian Arctic showed a clear latitudinal dichotomy in their use of wintering areas. Most tracked owls wintered in the Arctic (74%) whereas the rest wintered in temperate regions of North America. Wintering in the Arctic rather than at temperate latitudes may confer several advantages. First, travelling distances during migration are shorter for birds wintering in the Arctic and thus such migration should be physiologically

less demanding (Pennycuik 1989). The longer migration of birds travelling to temperate areas can explain why they tended to settle later on their wintering site and departed earlier than birds spending the wintering season in the Arctic. This result is consistent with the general pattern of latitudinal variation in timing of migration reported in other bird species (King and Mewaldt 1981, Newton 2008). Second, birds wintering in the Arctic are close to potential future breeding sites, which should facilitate prospecting for suitable settling areas in spring (Therrien et al. 2014) and may ultimately confer reproductive advantages (Mehl et al. 2004, Bregnballe et al.

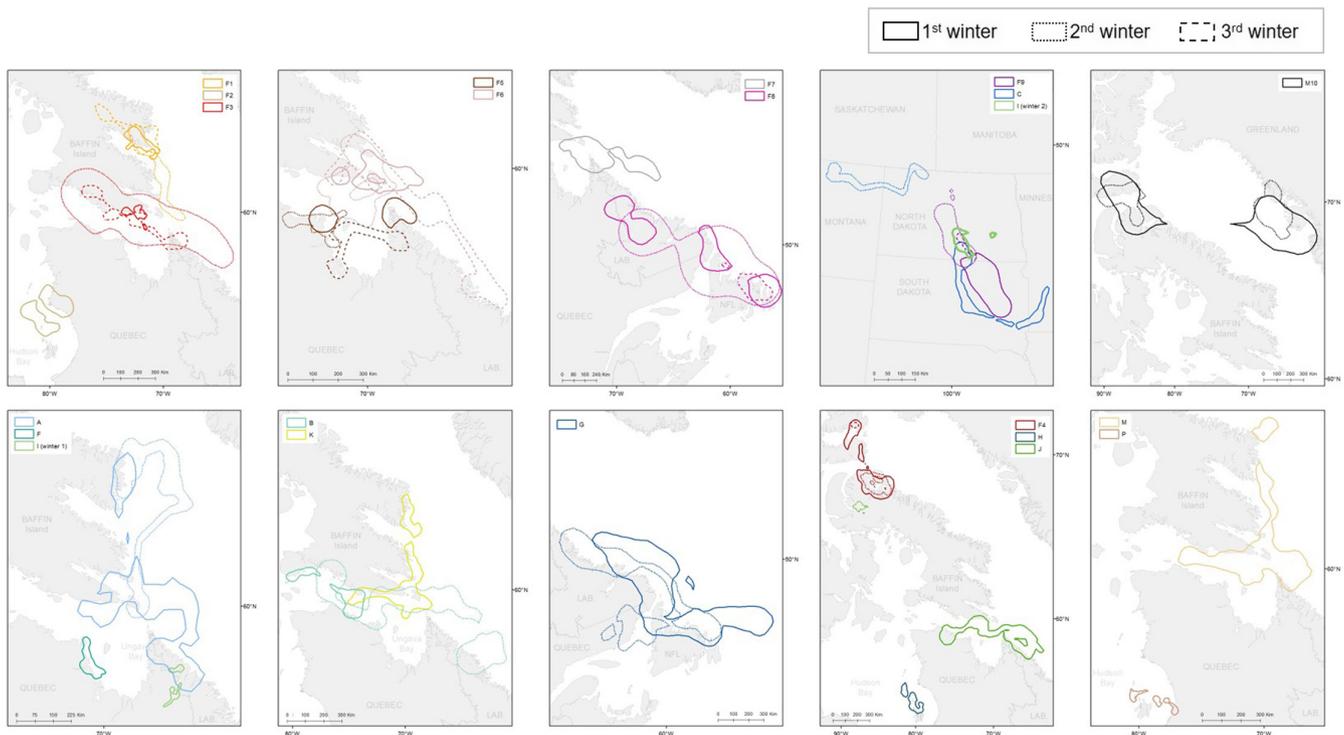


Figure 4. Overlapping wintering home range contours of individuals tracked for at least one complete winter between 2007 and 2016 ( $n = 21$  individuals tracked over one to three wintering periods). One to three individuals only are plotted in the same graph (different color for each individual) to facilitate visual assessment of home range overlaps of the same individuals between years. Solid line = 1st winter, small dashed line = 2nd winter, large dashed line = 3rd winter for each individual. Wintering environments and latitudinal zones of each individual are listed in Supplementary material Appendix 3.

Table 2. Individual consistency in winter habitat use (main wintering environment and latitudinal zones) by snowy owls tracked over consecutive years. Bold numbers represent individuals that use the same habitat in consecutive years.

		Winter 2				Total
		Marine Arctic	Marine Temperate	Terrestrial Arctic	Terrestrial Temperate	
Winter 1	Marine Arctic	<b>4</b>	0	<u>3</u>	0	7
	Marine Temperate	0	<b>1</b>	0	0	1
	Terrestrial Arctic	<u>1</u>	0	<b>6</b>	<u>1</u>	8
	Terrestrial Temperate	0	0	0	<b>5</b>	5
	Total	5	1	9	6	21

X: environment switch between 2 consecutive winters.

X: latitude switch between 2 consecutive winters.

2006). Third, being an archipelago, the Canadian High Arctic is rich in coastal habitats, which may provide access to both marine and terrestrial food sources. Even though half of the owls wintering in the Arctic were classified as inland birds, most were located close to coasts (Fig. 1) and made use of the marine environment (e.g. up to 46% of their locations were there), which likely allowed them to exploit both marine and terrestrial prey (Holt et al. 2015, Doyle et al. 2017). Despite the availability of marine food sources in the Arctic, the diversity of terrestrial prey may be lower than in temperate regions and snow cover may reduce their accessibility. In contrast, the Prairies and Great Plains are thought to provide snowy owls with a relatively high abundance of small mammals and birds easily accessible due to a thin snow cover (Boxall and Lein 1982a, Detienne et al. 2008, Naughton 2012), but further away from their arctic breeding sites.

Exploitation of the marine environment in winter may confer several benefits. First, food supply may be abundant and offer highly profitable prey as sea birds wintering at northern latitudes are much larger than small mammals and often aggregate at high local densities in small polynyas (Gilchrist

and Robertson 2000, Mallory and Gilchrist 2005). Second, the fidelity of sea ducks to wintering sites in ice-free areas provides a potentially predictable prey base in this environment (Petersen et al. 2012). Third, few predators have been documented exploiting this food source in winter except for gyrfalcons *Falco rusticolus* (Burnham and Newton 2011) and ravens *Corvus corax* (Gilchrist and Robertson 2000), which should reduce interspecific competition and energetic costs associated with territorial strife.

Variation in climatic conditions and sea ice extent or thickness can influence polynyas and leads within and among years (Barber and Massom 2007). Although polynyas are generally recurrent ice structures at large scale due to local topography, at a smaller spatial scale and within a given winter they may open or close depending on local wind or current, thus forcing seabirds to move among different patches of open water (Gilchrist et al. 2006, Lovvorn et al. 2014). The mobility of large avian predators like owls allows them to move quickly and potentially over large areas to track variations in the distribution of their prey. This may explain why we found that owls wintering in the marine environment

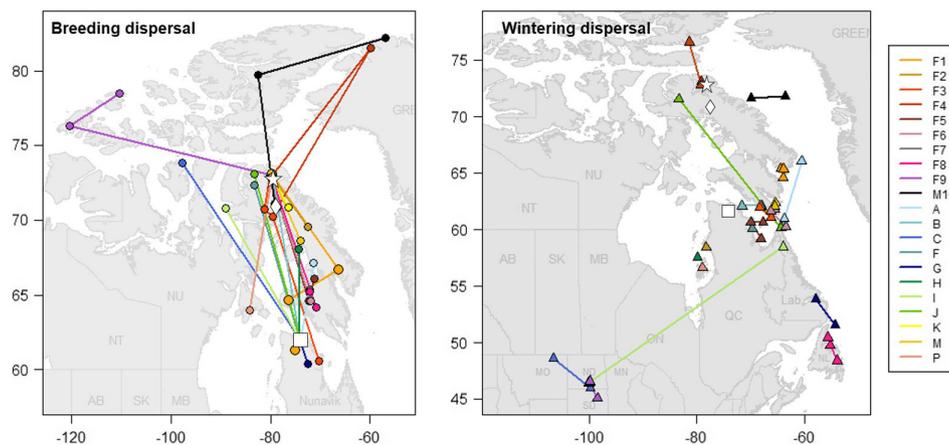


Figure 5. Summer (circles, left panel) and winter (triangles, right panel) centroids of locations for individual snowy owls tracked by satellite. The dispersal distance between consecutive seasons (lines) is also indicated for birds tracked over successive years. Capture sites (Bylot Island: star; Mary River: diamond; Deception Bay: square) are also depicted. Individuals' colour identification are the same as in Fig. 4.

travelled over longer distances during the winter, had larger home ranges and used more core areas than those wintering inland.

Home range size of wintering snowy owls in eastern North America are among the largest ever reported in strigidae, and possibly in all raptors, with a maximum extent of 363 915 km<sup>2</sup>. This far exceeds the maximum winter home ranges reported for other avian predators such as gyrfalcons (172 007 km<sup>2</sup>; Burnham and Newton 2011) or lesser spotted eagle *Aquila pomarina* (22 500 km<sup>2</sup>; Meyburg et al. 2004), but is surprisingly close to a mammalian predator, the polar bear *Ursus maritimus*, which also predominantly uses the marine environment (367 547 km<sup>2</sup>; Auger-Méthé et al. 2016). We found a large inter-individual variability in home range size, with some owls having relatively small ranges with few core areas whereas other had large ranges with up to 12 core areas. Burnham and Newton (2011) also reported a large variability in gyrfalcon winter home ranges around Greenland where variable ice conditions forced some individuals to track sea bird prey over large areas. Overall, individuals wintering in a marine environment may need to use multiple centers of activities and move more to fulfill their needs than those wintering in a terrestrial environment.

Timing of sea ice formation may also limit the ability of snowy owls to exploit the marine environment. As autumn progresses, sea ice will expand and eventually force sea birds to aggregate in relatively small ice-free areas. Sea ice phenology may therefore explain why owls wintering in the marine environment tend to settle later than birds in terrestrial environments. Similarly, in spring, the persistence of sea-ice and the late onset of sea ducks' pre-breeding migration from polynyas (e.g. king eiders *Somateria spectabilis* in April; Oppel 2008) may extend the time of prey availability and explain the later departure by birds wintering in marine environments compared to terrestrial ones.

### Fidelity to wintering site and environment

Migratory birds often show a high level of fidelity to their breeding and wintering sites (Greenwood 1980, Weatherhead and Forbes 1994). The concept of site fidelity, when applied to breeding birds, is typically defined at a relatively fine spatial scale as migratory birds often use sites separated by few meters from one year to another (Greenwood 1980). In contrast, snowy owls are considered a nomadic species (Holt et al. 2015), as shown by the extreme breeding dispersal distance between consecutive breeding attempts, on the order of several hundred km (Therrien et al. 2014; this study). Therefore, applying the concept of winter site fidelity to snowy owl must be done at a spatial scale relevant to the biology of the species, which is much larger than in most other bird species when considering breeding dispersal.

The extreme breeding dispersal observed in snowy owl is likely due to cyclic, large amplitude population fluctuations of lemmings in the Arctic, leading to a highly unpredictable summer food supply both spatially and temporally (Krebs 2011). Because snowy owls show a greater flexibility in their

use of prey, habitat and geographical areas in winter than in summer and because the abundance of some of their winter prey is more predictable than the availability of their main summer prey, we expected a greater fidelity of owls to their wintering sites compared their breeding sites. This prediction was supported because inter-annual distances between centroids of winter home ranges were about half of the breeding dispersal observed in summer. Nonetheless, these inter-annual distances were still quite lengthy (i.e. of the order of ~200–300 km) and overlap in winter home ranges between consecutive years was moderate (~30%), despite their very large size. We also observed no difference in overlap extent between birds wintering in marine vs terrestrial environments, nor for birds that wintered in the Arctic vs temperate areas. Considering the geographic range and the diversity of environments where snowy owls can be found in winter (Fig. 4 and 5; Boxall and Lein 1982b, Fuller et al. 2003, Holt et al. 2015), it is interesting that these birds even overlapped their wintering home ranges and core areas at all. Therefore, although owls showed a propensity to partly reuse the same wintering site from one year to the next, some factors may limit their ability to do so (see below).

At a broader scale, individuals were quite consistent in their wintering habitat use, predominantly using the same environment (marine or terrestrial) and latitudinal zones from one winter to the next (76%). Nonetheless, some individuals switched in the use of their main environment between winters and most individuals have been located in both environments each winter. Switching from the terrestrial to the marine environment may be facilitated in the Canadian Arctic because both habitats are highly intertwined and thus often close to each other. Age and experience are other factors that can affect habitat use patterns in birds (Dolbeer 1982, Cresswell 2014). In snowy owls, it is believed that young of the year and immatures predominantly migrate to temperate areas in winter whereas a high proportion of adult breeders spend the winter in the Arctic (Fuller et al. 2003, Doyle et al. 2017). However, this is unlikely to be a factor in our study because all our birds were experienced breeders and the only switch detected between latitudinal zones was from the Arctic to temperate areas, the opposite of what is expected as birds get older.

### Environmental determinants of space and habitat use

In top predators like the snowy owl, variation in food availability is thought to be a major factor affecting space and habitat use pattern (Schliebe et al. 2008, Trierweiler et al. 2013, Lopez-Lopez et al. 2014). Annual variations in sea ice dynamics may change the spatial distribution of seabirds and could explain the moderate site fidelity shown by snowy owls in the marine environment. Unfortunately, quantitative information on the annual variation in the abundance of seabirds wintering in the Canadian Arctic is too scarce to address this question.

In terms of terrestrial prey, longitudinal data on small mammal densities in winter and summer are rare and Bylot

Island was the only site in the whole eastern Canadian Arctic where this information was available. This is clearly a limitation to our analysis because owls range over a large portion of the Canadian Arctic in winter, although we note that lemming population fluctuations may be spatially synchronous at a relatively large scale, (i.e. hundreds of kilometers, Krebs et al. 2002). Despite these limitations, we found evidences that lemming densities on Bylot Island affected some aspects of habitat use by wintering owls. Home range sizes were smaller in years of high lemming densities in winter as found in other predatory birds. For instance, prairie falcons *Falco mexicanus* dramatically reduced their home range size in years of high ground squirrels *Spermophilus townsendii* densities (Marzluff et al. 1997).

Use of the marine environment increased during winters following high summer densities of small mammals. Fauteux et al. (2015) showed that lemming populations in the Canadian Arctic often declined during the autumn following peak summer densities to reach very low densities in the subsequent winter. Therefore, low lemming abundance after a summer peak may explain the previous result rather than a carry-over effect from the previous summer lemming abundance. A good knowledge of the ecology of prey species in all periods of the annual cycle is thus important when attempting to infer carry-over effects (Norris and Taylor 2006).

Over land, snow cover is another factor that may greatly affect food availability for snowy owls, both directly and indirectly. On the one hand, a thick snow cover may limit the ability of owls to prey on small mammals living underneath (Chamberlin 1980) as it does for other avian predators (Sonerud 1986) or foxes (Duchesne et al. 2011). On the other hand, a thick snow cover offers refuges from predators and a good thermal insulation for lemmings, which should favor their winter survival and positively affect their population (Reid et al. 2012, Bilodeau et al. 2013). A thick snow cover in autumn during the period of settlement for the winter may hinder the ability of snowy owls to find suitable areas, as suggested by their earlier settlement when snow in autumn was thin. Similarly, snow cover and depth have been shown to affect the pre-breeding movements of snowy owls when prospecting for suitable breeding sites (Therrien et al. 2015). However, a thin snow cover through the winter may eventually reduce small mammal populations by limiting their reproduction and reducing their survival, which could explain why snowy owls tended to make greater use of the marine environment under these conditions.

### Future perspectives in a changing climate context

Consistency in habitat use may provide advantages in terms of familiarity and experience in exploiting specific prey but some flexibility can also help to cope with changing environmental conditions. Sea ice extent is known to show a long-term decline (Stroeve et al. 2012) and changes in ice structure have already been shown to affect seabirds (Bump and Lovvorn 2004) and marine mammals (Laidre et al. 2008,

Hunter et al. 2010, Amstrup et al. 2013). The reliance of wintering snowy owls on both the marine and terrestrial arctic environments may expose them to changes occurring in both but their high mobility may also allow them to adapt to changes at a fine scale. Further investigations are needed to understand the effects of changing winter conditions on the survival and subsequent reproductive performances of snowy owls.

*Acknowledgements* – We thank Glencore for their hospitality and support at the Raglan mine, QC. We also thank Andréanne Beardsell and Yannick Seyer for their help in the field.

*Funding* – This study was financially supported by the Natural Sciences and Engineering Research Council of Canada (NSERC; 36784), the network of center of excellence ArcticNet, the Polar Continental Shelf Program of Natural Resources Canada, the Fonds de Recherche du Québec Nature et Technologies, EnviroNorth, First Air and the Fonds Écologique Anne Vallée.

### References

- Amstrup, S. C., Marcot, B. G. and Douglas, D. C. 2013. A bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. – In: DeWeaver, E. T., Bitz, C. M. and Tremblay, L.-B. (eds), Arctic sea ice decline: observations, projections, mechanisms, and implications. American Geophysical Union, pp. 213–268.
- Angerbjörn, A., Tannerfeldt, M. and Lundberg, H. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. – *Ecography* 24: 298–308.
- Auger-Méthé, M., Lewis, M. A. and Derocher, A. E. 2016. Home ranges in moving habitats: polar bears and sea ice. – *Ecography* 39: 26–35.
- Barber, D. G. and Massom, R. A. 2007. The role of sea ice in Arctic and Antarctic polynyas. – In: Smith Jr, W. O. and Barber, D. G. (eds), Polynyas: windows to the world. Elsevier Oceanography Series, pp. 1–54.
- Bilodeau, F., Reid, D. G., Gauthier, G., Krebs, C. J., Berteaux, D. and Kenney, A. J. 2013. Demographic response of tundra small mammals to a snow fencing experiment. – *Oikos* 122: 1167–1176.
- Blackburn, E. and Cresswell, W. 2016. High winter site fidelity in a long-distance migrant: implications for wintering ecology and survival estimates. – *J. Ornithol.* 157: 93–108.
- Block, W. M. and Brennan, L. A. 1993. The habitat concept in ornithology: theory and applications. – Plenum Press.
- Boxall, P. C. and Lein, M. R. 1982a. Feeding ecology of snowy owls (*Nyctea scandiaca*) wintering in southern Alberta. – *Arctic* 35: 282–290.
- Boxall, P. C. and Lein, M. R. 1982b. Territoriality and habitat selection of female snowy owls (*Nyctea scandiaca*) in winter. – *Can. J. Zool.* 60: 2344–2350.
- Bregnballe, T., Frederiksen, M. and Gregersen, J. 2006. Effects of distance to wintering area on arrival date and breeding performance in great cormorants *Phalacrocorax carbo*. – *Ardea* 94: 619–630.
- Bullard, F. 1991. Estimating the home range of an animal: a Brownian bridge approach. – MSc thesis, Univ. of North Carolina at Chapel Hill.

- Bump, J. K. and Lovvorn, J. R. 2004. Effects of lead structure in Bering Sea pack ice on the flight costs of wintering spectacled eiders. – *J. Mar. Syst.* 50: 113–139.
- Burnham, K. K. and Newton, I. 2011. Seasonal movements of gyrfalcons *Falco rusticolus* include extensive periods at sea. – *Ibis* 153: 468–484.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. – *Ecol. Model.* 197: 516–519.
- Campbell, R. W. and Maccoll, M. D. 1978. Winter foods of snowy owls in southwestern British Columbia. – *J. Wildl. Manage.* 42: 190–192.
- Chamberlin, M. L. 1980. Winter hunting behavior of a snowy owl in Michigan. – *Wilson Bull.* 92: 116–120.
- CLS 2016. Argos user's manual: worldwide tracking and environmental monitoring by satellite. – Collecte Localisation Satellite.
- Cresswell, W. 2014. Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis. – *Ibis* 156: 493–510.
- Detienne, J. C., Holt, D., Seidensticker, M. T. and Pitz, T. 2008. Diet of snowy owls wintering in west-central Montana, with comparisons to other North American studies. – *J. Raptor Res.* 42: 172–179.
- Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D. and Wikelski, M. 2013. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. – *Mov. Ecol.* 1: 3.
- Dolbeer, R. A. 1982. Migration patterns for age and sex classes of blackbirds and starlings. – *J. Field Ornithol.* 53: 28–46.
- Doyle, F. I., Therrien, J. F., Reid, D., Gauthier, G. and Krebs, C. J. 2017. Seasonal movements of breeding snowy owls in the western north American Arctic. – *J. Raptor Res.* 51: 428–438.
- Duchesne, D., Gauthier, G. and Berteaux, D. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. – *Oecologia* 167: 967–980.
- ESRI 2013. ArcGIS desktop: release 10.2. – Redlands, CA.
- Fauteux, D., Gauthier, G. and Berteaux, D. 2015. Seasonal demography of a cyclic lemming population in the Canadian Arctic. – *J. Anim. Ecol.* 84: 1412–1422.
- Fuller, M., Holt, D. and Schueck, L. 2003. Snowy owl movements: variation on the migration theme. – Springer.
- Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J. F., McKinnon, L., Legagneux, P. and Cadieux, M. C. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. – *Ecoscience* 18: 223–235.
- Gilchrist, G., Heath, J., Arragutainaq, L., Robertson, G., Allard, K., Gilliland, S. G. and Mallory, M. 2006. Combining scientific and local knowledge to study common eider ducks wintering in Hudson Bay. – In: Riewe, R. and Oakes, J. (eds), *Climate change: linking traditional and scientific knowledge*. Aboriginal Issues Press, pp. 284–303.
- Gilchrist, H. G. and Robertson, G. J. 2000. Observations of marine birds and mammals wintering at polynyas and ice edges in the Belcher Islands, Nunavut, Canada. – *Arctic* 53: 61–68.
- Golawski, A. and Kasprzykowski, Z. 2010. The influence of weather on birds wintering in the farmlands of eastern Poland. – *Ornis Fenn.* 87: 153–159.
- Greenwood, J. J. D. and Baillie, S. R. 1991. Effects of density-dependence and weather on population-changes of English passerines using a non-experimental paradigm. – *Ibis* 133: 121–133.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – *Anim. Behav.* 28: 1140–1162.
- Gruyer, N., Gauthier, G. and Berteaux, D. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. – *Can. J. Zool.* 86: 910–917.
- Heggøy, O., Aarvak, T., Øien, I. J., Jacobsen, K.-O., Solheim, R., Zazelenchuk, D., Stoffel, M. and Kleven, O. 2017. Effects of satellite transmitters on survival in snowy owls *Bubo scandiacus*. – *Ornis Norvegica* 40: 33–38.
- Holt, D., Larson, M. D., Smith, N., Evans, D. and Parmelee, D. F. 2015. The snowy owl (*Bubo scandiacus*). – In: Poole, A. (ed.), *The birds of North America online*. Cornell Lab of Ornithology, <<http://bna.birds.cornell.edu/bna/species/010>>.
- Horne, J. S., Garton, E. O., Krone, S. M. and Lewis, J. S. 2007. Analyzing animal movements using Brownian bridges. – *Ecology* 88: 2354–2363.
- Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Amstrup, S. C. and Stirling, I. 2010. Climate change threatens polar bear populations: a stochastic demographic analysis. – *Ecology* 91: 2883–2897.
- Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. – *Auk* 118: 557–562.
- Kerlinger, P. and Lein, M. R. 1988. Population ecology of snowy owls during winter on the Great Plains of North America. – *Condor* 90: 866–874.
- Kerlinger, P., Lein, M. R. and Sevick, B. J. 1985. Distribution and population fluctuations of wintering snowy owls (*Nyctea scandiaca*) in North America. – *Can. J. Zool.* 63: 1829–1834.
- King, J. R. and Mewaldt, L. R. 1981. Variation of body-weight in gambel white-crowned sparrows in winter and spring: latitudinal and photoperiodic correlates. – *Auk* 98: 752–764.
- Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. – *Proc. R. Soc. B* 278: 481–489.
- Krebs, C. J., Kenney, A. J., Gilbert, S., Danell, K., Angerbjorn, A., Erlinge, S., Bromley, R. G., Shank, C. and Carriere, S. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. – *Can. J. Zool.* 80: 1323–1333.
- Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, O., Heide-Jorgensen, M. P. and Ferguson, S. H. 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. – *Ecol. Appl.* 18: S97–S125.
- Latta, S. C., Cabezas, S., Mejia, D. A., Paulino, M. M., Almonte, H., Miller-Butterworth, C. M. and Bortolotti, G. R. 2016. Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana waterthrush *Parus motacilla*. – *Ibis* 158: 395–406.
- Lopez-Lopez, P., Garcia-Ripolles, C. and Urios, V. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. – *Ecol. Appl.* 24: 938–949.
- Lovvorn, J. R., Anderson, E. M., Rocha, A. R., Larned, W. W., Grebmeier, J. M., Cooper, L. W., Kolts, J. M. and North, C. A. 2014. Variable wind, pack ice, and prey dispersion affect the long-term adequacy of protected areas for an Arctic sea duck. – *Ecol. Appl.* 24: 396–412.
- Mallory, M. L. and Gilchrist, H. G. 2005. Marine birds of the Hell Gate Polynya, Nunavut, Canada. – *Polar Res.* 24: 87–93.
- Marzluff, J. M., Kimsey, B. A., Schueck, L. S., McFadzen, M. E., Vekasy, M. S. and Bednarz, J. C. 1997. The influence of habitat,

- prey abundance, sex, and breeding success on the ranging behavior of prairie falcons. – *Condor* 99: 567–584.
- McClellan, C. M., Braun-McNeill, J., Avens, L., Wallace, B. P. and Read, A. J. 2010. Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. – *J. Exp. Mar. Biol. Ecol.* 387: 44–51.
- Mehl, K. R., Alisauskas, R. T., Hobson, K. A. and Kellett, D. K. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-Arctic population of king eiders. – *Condor* 106: 241–251.
- Meyburg, B. U., Meyburg, C., Belka, T., Sreibr, O. and Vrana, J. 2004. Migration, wintering and breeding of a lesser spotted eagle (*Aquila pomarina*) from Slovakia tracked by satellite. – *J. Ornithol.* 145: 1–7.
- Naughton, D. 2012. The natural history of Canadian mammals. – Univ. of Toronto Press.
- Newton, I. 2006. Advances in the study of irruptive migration. – *Ardea* 94: 433–460.
- Newton, I. 2008. The migration ecology of birds. – Academic Press.
- Nieuwenhuis, R., te Grotenhuis, M. and Pelzer, B. 2012. influence. ME: tools for detecting influential data in mixed effects models. – *R J.* 4: 38–47.
- Norris, D. R. and Taylor, C. M. 2006. Predicting the consequences of carry-over effects for migratory populations. – *Biol. Lett.* 2: 148–151.
- Oppel, S. 2008. King eider migration and seasonal interactions at the individual level. – PhD thesis, Univ. of Alaska Fairbanks.
- Pennycuik, C. J. 1989. Bird flight performance: a practical calculation manual. – Oxford Univ. Press.
- Petersen, M. R., Douglas, D. C., Wilson, H. M. and McCloskey, S. E. 2012. Effects of sea ice on winter site fidelity of pacific common eiders (*Somateria mollissima v-nigrum*). – *Auk* 129: 399–408.
- Phillips, R. A., Bearhop, S., McGill, R. A. R. and Dawson, D. A. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. – *Oecologia* 160: 795–806.
- Rappole, J. H. 2013. The avian migrant: the biology of bird migration. – Columbia Univ. Press.
- Reid, D. G., Bilodeau, F., Krebs, C. J., Gauthier, G., Kenney, A. J., Gilbert, B. S., Leung, M. C. Y., Duchesne, D. and Hofer, E. 2012. Lemming winter habitat choice: a snow-fencing experiment. – *Oecologia* 168: 935–946.
- Robertson, G. J. and Gilchrist, H. G. 2003. Wintering snowy owls feed on sea ducks in the Belcher Islands, Nunavut, Canada. – *J. Raptor Res.* 37: 164–166.
- Robillard, A., Gauthier, G., Therrien, J.-F., Fitzgerald, G., Provencher, J. F. and Bêty, J. 2017. Variability in stable isotopes of snowy owl feathers and contribution of marine resources to their winter diet. – *J. Avian Biol.* 48: 759–769.
- Schliebe, S., Rode, K. D., Gleason, J. S., Wilder, J., Proffitt, K., Evans, T. J. and Miller, S. 2008. Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the Southern Beaufort Sea. – *Polar Biol.* 31: 999–1010.
- Smith, M. and Rigby, B. 1981. Distribution of polynyas in the Canadian Arctic. – Environment Canada, Ottawa, Canada, Canadian Wildlife Service Occasional Paper no. 45.
- Smith, N. 1997. Observations of wintering snowy owls (*Nyctea scandiaca*) at Logan Airport, east Boston, Massachusetts from 1981–1997. – In: Duncan, J. R., Johnson, D. H. and Nicholls, T. H. (eds), *Biology and conservation of owls of the Northern Hemisphere: 2nd International symposium*. U.S. Dept of Agriculture, Forest Service, North Central Forest Experiment Station, pp. 591–596.
- Sonerud, G. A. 1986. Effect of snow cover on seasonal-changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. – *Holarct. Ecol.* 9: 33–47.
- Steenhof, K., Bates, K. K., Fuller, M. R., Kochert, M. N., McKinley, J. O. and Lukacs, P. M. 2006. Effects of radiomarking on prairie falcons: attachment failures provide insights about survival. – *Wildl. Soc. Bull.* 34: 116–126.
- Stroeve, J. C., Serreze, M. C., Holland, M. M., Kay, J. E., Malanik, J. and Barrett, A. P. 2012. The Arctic's rapidly shrinking sea ice cover: a research synthesis. – *Clim. Change* 110: 1005–1027.
- Swingland, I. R. and Greenwood, P. J. 1984. The ecology of animal movement. – Clarendon Press.
- Therrien, J. F., Gauthier, G. and Bêty, J. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. – *J. Avian Biol.* 42: 363–369.
- Therrien, J. F., Gauthier, G. and Bêty, J. 2012. Survival and reproduction of adult snowy owls tracked by satellite. – *J. Wildl. Manage.* 76: 1562–1567.
- Therrien, J. F., Gauthier, G., Pinaud, D. and Bêty, J. 2014. Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource. – *J. Avian Biol.* 45: 536–544.
- Therrien, J. F., Pinaud, D., Gauthier, G., Lecomte, N., Bildstein, K. L. and Bêty, J. 2015. 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.* 3: 1.
- Tranquilla, L. A. M., Montevecchi, W. A., Fifield, D. A., Hedd, A., Gaston, A. J., Robertson, G. J. and Phillips, R. A. 2014. Individual winter movement strategies in two species of murre (*Uria* spp.) in the Northwest Atlantic. – *PLoS One* 9: e90583.
- Trierweiler, C., Mullie, W. C., Drent, R. H., Exo, K. M., Komdeur, J., Bairlein, F., Harouna, A., de Bakker, M. and Koks, B. J. 2013. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. – *J. Anim. Ecol.* 82: 107–120.
- Van der Meer, T., Grotenhuis, M. T. and Pelzer, B. 2010. Influential cases in multilevel modeling: a methodological comment. – *Am. Sociol. Rev.* 75: 173–178.
- Walker, D. A., Raynolds, M. K., Daniels, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A. and Team, C. 2005. The Circumpolar Arctic vegetation map. – *J. Veg. Sci.* 16: 267–282.
- Weatherhead, P. J. and Forbes, M. R. L. 1994. Natal philopatry in passerine birds – genetic or ecological influences. – *Behav. Ecol.* 5: 426–433.

Supplementary material (Appendix JAV-01707 at <[www.avianbiology.org/appendix/jav-01707](http://www.avianbiology.org/appendix/jav-01707)>). Appendix 1–6.