

An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter

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Top predators of the arctic tundra are facing a long period of very low prey availability during winter and subsidies from other ecosystems such as the marine environment may help to support their populations. Satellite tracking of snowy owls, a top predator of the tundra, revealed that most adult females breeding in the Canadian Arctic overwinter at high latitudes in the eastern Arctic and spend several weeks (up to 101 d) on the sea-ice between December and April. Analysis of high-resolution satellite images of sea-ice indicated that owls were primarily gathering around open water patches in the ice, which are commonly used by wintering seabirds, a potential prey. Such extensive use of sea-ice by a tundra predator considered a small mammal specialist was unexpected, and suggests that marine resources subsidize snowy owl populations in winter. As sea-ice regimes in winter are expected to change over the next decades due to climate warming, this may affect the wintering strategy of this top predator and ultimately the functioning of the tundra ecosystem.

The Arctic tundra is characterized by strong seasonal variations in productivity, which nonetheless remains relatively low throughout the year compared to other ecosystems (Bliss 1986, Gauthier et al. 1996, Krebs et al. 2003). Considering that, the relatively high abundance and diversity of vertebrate predators in the tundra is impressive (Krebs et al. 2003). Terrestrial predators, such as the snowy owl *Bubo scandiacus* or the Arctic fox *Vulpes lagopus*, need to find sufficient prey throughout the year to sustain their basic metabolic needs and withstand the extreme Arctic conditions. This is especially critical during the long Arctic winter because the availability of the primary prey species of the tundra such as small mammals and migratory birds becomes very low due to protection offered by the snow cover or the departure of migratory species.

While wintering at high latitudes can reduce migration costs and allow a quick return to tundra breeding sites in spring, terrestrial predators have to cope with very low prey availability at that time. Even if snowy owls are able to withstand midwinter Arctic conditions out in the open (Gessaman 1972), their regular presence during winter in different regions of southern Canada and northern United States suggests that owls are migrating out of the Arctic when food availability is reduced (Kerlinger et al. 1985, Parmelee 1992). Throughout their breeding range those birds have a narrow, specialised diet almost entirely made of small mammals during summer (Parmelee 1992). For that reason, it has long been thought that snowy owls were moving to southern areas to prey upon similar prey type during the winter (Parmelee 1992). Despite some reports of

predation on birds and especially waterfowl (Gross 1944, Campbell and MacColl 1978, Mehlum and Gjertz 1998), several studies analysed snowy owl diet during winter and they all found that small mammals comprised the bulk of the food consumed (reviewed by Detienne et al. 2008).

By tracking several individual owls marked with satellite transmitters over a 2-year period, we have uncovered a hitherto unknown wintering strategy for a typically terrestrial species, the extensive use of Arctic sea-ice. Even if it has been previously reported that snowy owls could feed on seabirds at polynyas and open leads in the ice during the winter in the Arctic (Hudson Bay area of Canada; Gilchrist and Robertson 2000, Robertson and Gilchrist 2003), here we show that this strategy is commonly used among adult female snowy owls breeding in the eastern Canadian Arctic. We also discuss the implications of this wintering strategy for the conservation of Arctic predators in the context of global warming and retreating sea-ice.

Methods

In July 2007, we marked 12 breeding female snowy owls on their nest with satellite transmitters over a 115 km² area on the southern portion of Bylot Island, Nunavut, Canada (73°N, 80°W), using a bow-net trap. We fixed the transmitters (PTT-100, 30 g battery-powered; Microwave Telemetry, USA) on the owls using a back-pack harness (Steenhof et al. 2006) made of Teflon ribbon. All animal

manipulations were conducted in accordance with the animal care committee of Univ. Laval (CPAUL permit no. 84921). We received transmissions at 5-d intervals and retained locations of accuracy ranging from 150 to 1000 m to generate maps of winter movements and to determine the proportion of locations that were over the sea.

We characterized the ice cover around the highest quality owl locations (accuracy of ≤ 150 m; $n = 32$) using sea-ice images with a 50-m resolution taken by Radarsat satellites provided by the Canadian Ice Service (Radarsat-1 2007–2008, Radarsat-2 2009). We selected satellite images taken within a 2-d window of each owl location. We associated each location with 10 random points (Fortin et al. 2009) within either a 10, or a 100-km radius (encompassing 80 and 100% of the maximum daily distance traveled by owls during winter, respectively) and we measured distances of all points to the nearest open water patch > 0.2 km² (the minimum open water patch size where owls had been observed in winter (Gilchrist and Robertson 2000)). For random points located over open water, we attributed a distance of 0. We confirmed that open water patches could be reliably identified from Radarsat images by comparing pairs of images of the same area taken < 2 d apart under different environmental conditions (because wind, for example, creates ripples on the surface water that change the color on the image). We detected the same open water patches on both images in $> 95\%$ of the cases ($n = 130$). We compared the observed and random distances using conditional logistical regressions with empirical standard errors and individual locations nested within each owl ID to account for repeated measures (Fortin et al. 2009). We performed spatial analyses with ArcGIS 9.2 software (ESRI, Redlands, USA) and statistical analyses with SAS 9.1.3 software (SAS Inst. 2005).

Results

We successfully tracked nine owls during the first winter following marking (2007/2008) (Fig. 1), and eight of them for a second winter (2008/2009; Fig. 2). All tracked birds wintered at high latitudes ($> 55^\circ\text{N}$) in the eastern Canadian Arctic except for two birds that wintered in temperate areas (one in Newfoundland and one in North Dakota, between 45°N and 51°N). Over the two years, birds that wintered in the Arctic and in temperate areas were located on average 1100 km ($n = 13$; range: 410 to 1970 km) and 2900 km ($n = 4$; range: 1715 to 3520 km) from their previous summer nesting site.

All birds but one that overwintered in the Arctic were located over the sea for several weeks during both winters, as well as one of the two birds that wintered in more temperate areas (F8; median = 41 d, range = 8 to 71 d in winter 2007/2008, and median = 59 d, range = 30 to 101 d, in winter 2008/2009; Table 1). At the time that these locations were recorded (from early Dec to late Apr), the area used by owls is almost entirely covered by sea-ice. Owls concentrated their activity in the Hudson and Davis straits and in Hudson Bay at a median distance of 40 km from the coast but sometimes as far as 210 km (Fig. 1, 2). Individuals that spent the most time on the sea-ice during the first

winter adopted the same behavior the following winter (Pearson correlation, $r = 0.74$, $p = 0.04$, $DF = 8$). During both winters, owls were significantly closer (average distance \pm SEM = 0.48 ± 0.11 km, $n = 32$) to open water patches identified on the Radarsat images than random points at both spatial scales (1.50 ± 0.09 km, $\beta = -1.49 \pm 0.30$, $\chi^2 = 24.3$, $DF = 1$, $p < 0.001$; 4.10 ± 0.39 km, $\beta = -1.40 \pm 0.22$, $\chi^2 = 40.7$, $DF = 1$, $p < 0.001$, for the 10 and 100-km scales respectively; Fig. 3).

Discussion

Our study presents the first quantitative results showing that extensive use of the sea-ice is a common and important wintering strategy for snowy owls in North America, a surprising result for a terrestrial species. Although a previous study revealed that owls could cross between land masses over the sea-ice, the time spent on sea-ice was short and was not indicative of potential resource use in this habitat (Fuller et al. 2003). Considering the length of time spent on sea-ice by our birds, they must be able to find prey in this environment despite the extremely cold temperatures and winter darkness. Small patches of open water areas at those latitudes are often used by high density of wintering seabirds such as eiders *Somateria* spp., long-tailed ducks *Clangula hyemalis* and black guillemots *Cepphus grylle*, and snowy owls have been observed attacking seabirds there (Gilchrist and Robertson 2000, Robertson and Gilchrist 2003). Considered a small mammal specialist during the breeding period (Parmelee 1992), this predator thus seems to switch to a more generalist or opportunistic strategy during the winter. Wintering at high latitudes may be advantageous to owls by allowing them to start prospecting very early in spring for areas with high lemming densities, a prerequisite for a breeding attempt (Gilg et al. 2003, Gauthier et al. 2004, Hakala et al. 2006).

Kerlinger and Lein (1986) showed that despite a large overlap, the winter distribution of snowy owls in North America varies according to age and sex, with adult females remaining predominantly in the northernmost part of the wintering range while young, immature birds in the southernmost part. In our study, only adult females that had previously bred were tracked and thus it remains to be seen if the strategy of wintering at high latitude and of using sea-ice is also used by adult males and/or immature birds. Given their larger size than males, females may be more capable or suited to feed on relatively large size prey such as seabirds (Lind 1993) and may thus be more inclined to winter over sea-ice than males. Similarly, the cost of wintering in the Arctic may be greater in immature birds and especially first-year ones due to their inexperience, which may explain why they tend to winter further south (Kerlinger and Lein 1986). Therefore, further investigations are needed to determine the extent of this wintering strategy in males or immature owls.

Exchanges of energy and nutrients between ecosystems, such as between the marine and terrestrial ecosystems, may be relatively common and may have a strong impact on the functioning of the ecosystems involved (Huxel 2002, Loreau 2003). These exchanges are often asymmetric and

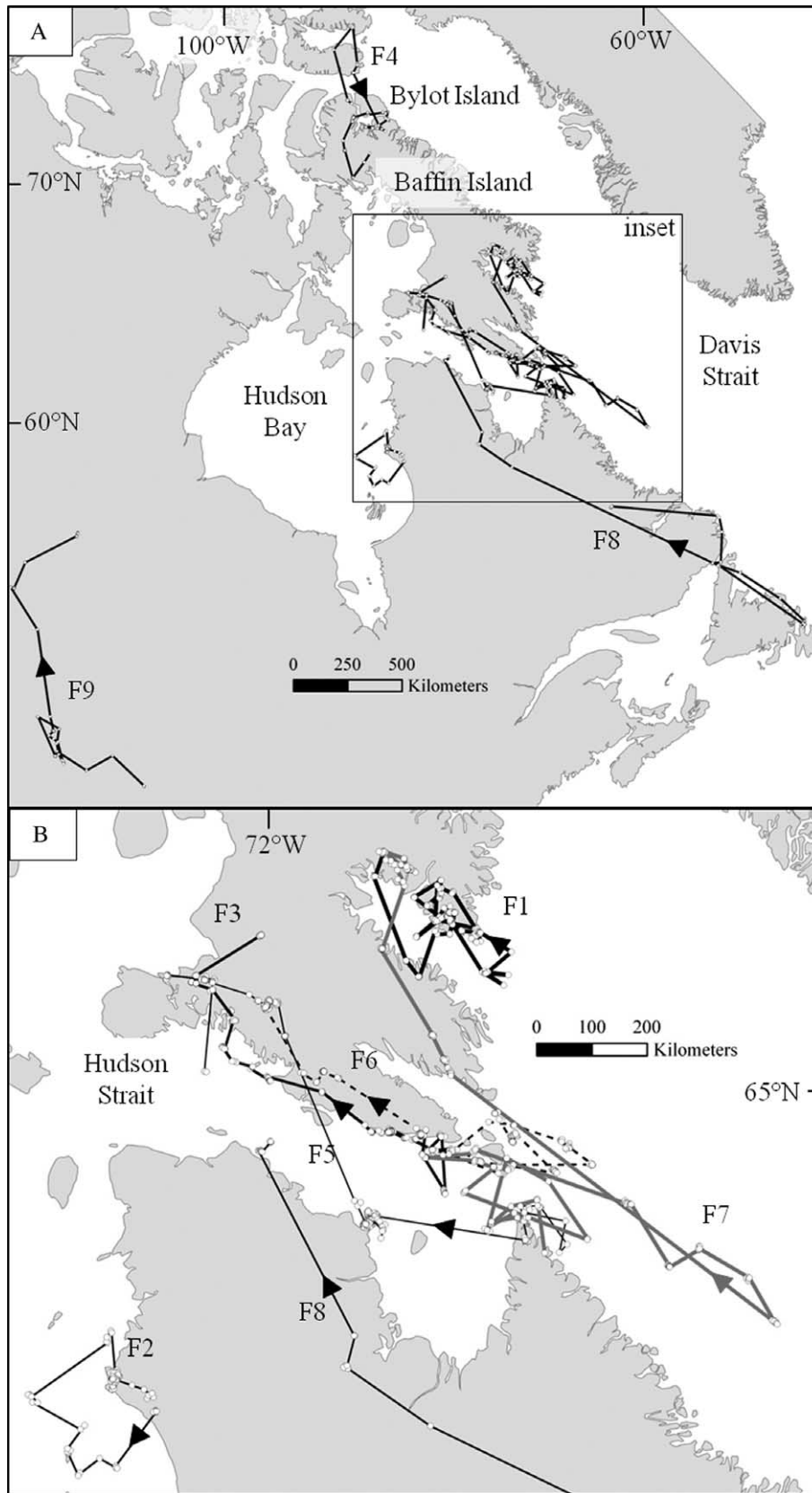


Figure 1. Satellite-tracked movements of nine adult female snowy owls showing extensive use of sea-ice from 11 Dec 2007 to 28 Apr 2008 in the eastern Canadian Arctic (A). The Hudson and Davis Strait regions where most of the marked owls used the sea-ice during winter are presented in more details (B). All birds were marked on the southern portion of Bylot Island in summer 2007.

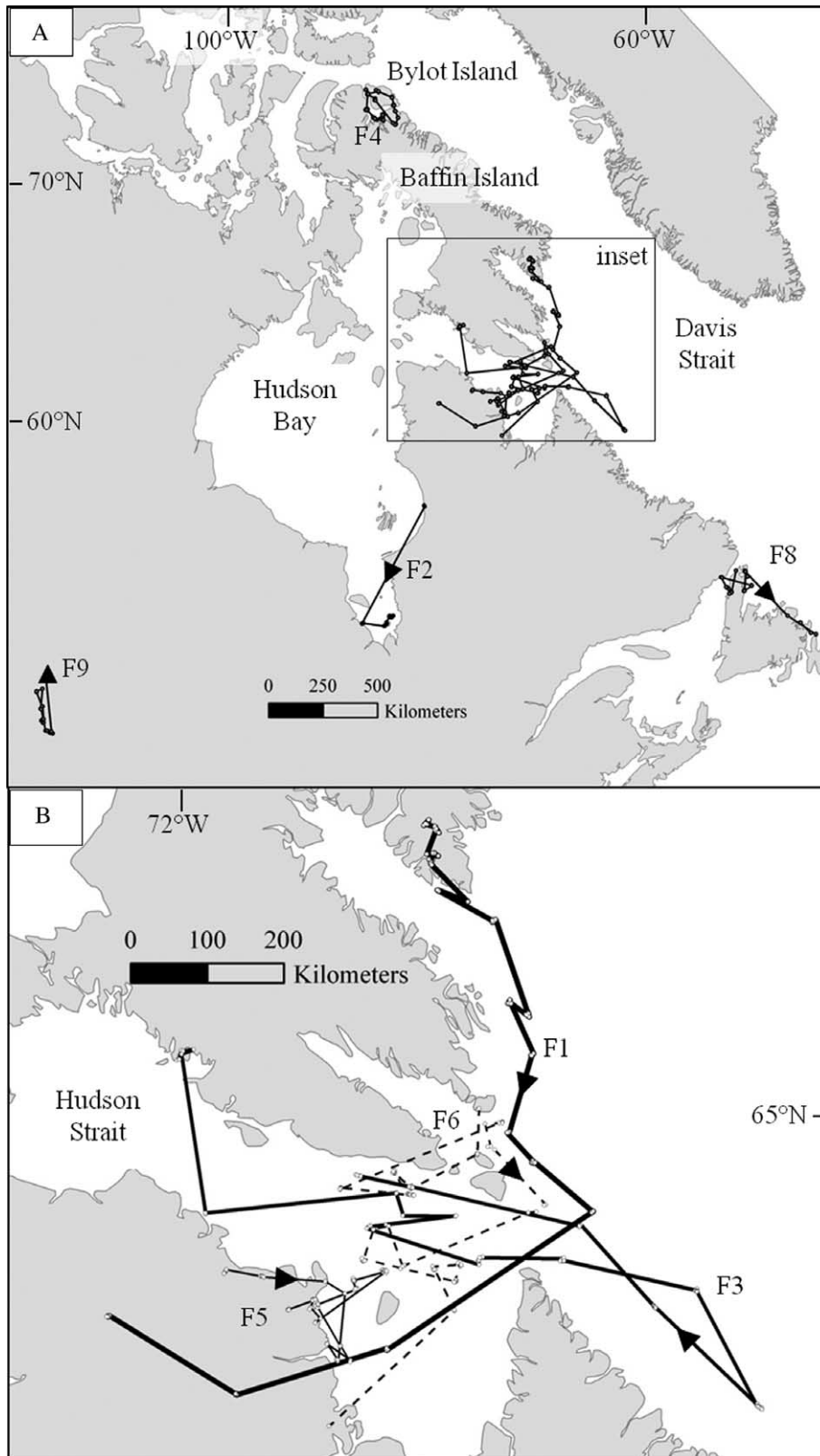


Figure 2. Satellite-tracked movements of eight adult female snowy owls showing extensive use of sea-ice from 4 Dec 2008 to 27 Mar 2009 in the eastern Canadian Arctic (A). The Hudson and Davis Strait regions where most of the marked owls used the sea-ice during winter are presented in more details (B). All birds were marked on the southern portion of Bylot Island in summer 2007.

may be especially important for the food web of low productivity ecosystems such as isolated oceanic islands or the Arctic tundra (Sanchez-Pinero and Polis 2000, Stapp

and Polis 2003). The Arctic fox represents another example of a terrestrial animal that can use the sea-ice in some regions of the Arctic, preying on seal pups or scavenging

Table 1. Movement parameters of nine adult female snowy owls tracked during the winter period (from 11 Dec 2007 to 28 Apr 2008 and from 4 Dec 2008 to 27 Mar 2009) in Canada.

Period	ID	No. of locations	Proportion of locations over sea-ice	Time spent over sea-ice (d)
Winter 2007–2008	F1	165	0.33	25
	F2	122	0.26	52
	F3	236	0.34	37
	F4	230	0.05	<1
	F5	194	0.20	41
	F6	261	0.44	71
	F7	182	0.48	88
	F8	133	0.20	8
	F9	94	0.00	0
Winter 2008–2009	F1	86	0.60	73
	F2	17	0.94	30
	F3	72	0.93	86
	F4	116	0.03	<1
	F5	71	0.45	44
	F6	85	0.92	101
	F7	– ^a	–	–
	F8	64	0.25	34
	F9	51	0.00	0

^atransmitter stopped during summer 2008.

polar bear kills, thus living essentially upon marine resources in winter (Roth 2002, Roth 2003, Tarroux et al. 2010). Therefore, our results suggest that energy subsidies from the marine ecosystem may be a general feature of terrestrial Arctic predators and could be essential for the long-term persistence of their populations.

Alterations to the physical environment due to climate change appear less dramatic in the Arctic tundra than in marine ecosystems (ACIA 2005, Solomon et al. 2007). However our novel findings imply that rapid changes

occurring in the marine environment may affect terrestrial species as well. With climate warming, the extent of the sea-ice in areas used by wintering owls such as the Hudson and Davis straits has been retreating in recent years and is projected to retreat at an even faster rate in the coming decades (Johannessen et al. 2004). This will likely affect the occurrence of open water patches during winter with cascading effects on the whole associated marine food web, including the number and distribution of seabirds using these environments (Stirling 1997, Mallory et al.

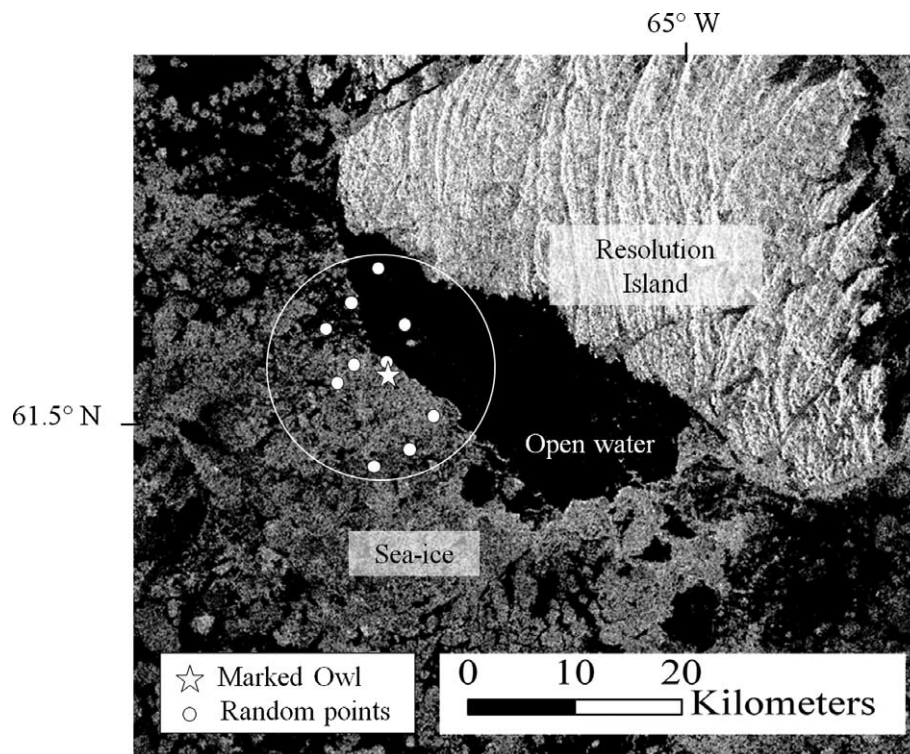


Figure 3. Example of high-resolution sea-ice image taken by Radarsat satellites within 2 d of an actual owl location. Ten random points located within a 10-km radius circle centred on the owl location are displayed.

2010). Although retreating sea-ice may lead, in the short-term, to increased open water areas in winter, it is unclear if this will be associated with an increase in primary productivity and in local seabird abundance or the opposite. For instance, more and larger open water areas could allow seabirds to spread over a wider area, possibly decreasing the local density of prey for owls. Consequently, this could lead to the degradation of an important wintering habitat for them. Alternatively, warmer temperature in the Arctic Ocean may result in an increase in primary productivity and in seabird densities, therefore increasing prey availability for snowy owls during winter. We thus believe that the potential consequences of changes in sea-ice regime on the functioning of the tundra ecosystem have been largely overlooked, and are likely underestimated due to a lack of basic knowledge on several Arctic wildlife species.

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