

to demand. CO₂ even controls the density of stomata; as a compensatory mechanism, their numbers increase if the concentration of CO₂ drops. Similar to animals, a major puzzle has been how plants sense CO₂. Hu *et al.* (2) found that the carbonic anhydrases β CA1 and β CA4 in the model plant *Arabidopsis thaliana* function in CO₂ sensing. Plants lacking the two enzymes were greatly impaired in their response to increases in atmospheric CO₂, showing much less stomatal pore closure. In contrast to the extracellular location of the mouse carbonic anhydrase, the plant enzymes are inside the cell, both adjacent to the cell membrane and inside chloroplasts. Thus, although the enzymatic function of the enzymes—as either transponder or sensor—is conserved, the site of action is very different, implying that the sensing mechanism also may be different. Astonishingly, Hu *et al.* (2) found that expressing a structurally unrelated mammalian α -carbonic anhydrase in *Arabidopsis* plants lacking carbonic anhydrases restored CO₂ responsiveness. This supports the transponder hypothesis, as it is

less probable that the downstream signaling machinery in the plant can function with this very different enzyme.

A key element of stomatal closure is the efflux of ions. Hu *et al.* (2) further showed that intracellular bicarbonate released by carbonic anhydrase activates anion channels in guard cells, allowing ions to efflux, thus triggering the closure of stomatal pores (see the figure). Plants overexpressing the β -carbonic anhydrases in guard cells also improved conservation of water, which suggests a possible means to engineer plants that use less water.

Although plants and humans diverged about 1 billion years ago, they use similar mechanisms to detect CO₂ sensing. Two main observations suggest that their common sensing mechanism must have evolved independently. There is a striking difference in the cellular location of the enzymes. Moreover, there are five classes of carbonic anhydrase enzymes that are unrelated in protein sequence and structure; plants and animals express different family members (6).

Why plants evolved this mechanism is obvious—they need to adjust the valves to optimize CO₂ uptake from the atmosphere while minimizing water loss. In humans, one may speculate that this mechanism was retained to help identify rotting food, and now serves mainly to identify carbonated drinks. The observation that carbonic anhydrase is also present in insect gustatory and olfactory cells and may cooperate with ionotropic receptors (ion channels that, when activated by a ligand, open and permit ion flow) may help to identify how insects and mammals use CO₂ sensors to discern food sources (7).

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ECOLOGY

Explaining Bird Migration

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Arctic shorebirds can travel tens of thousands of kilometers every year as they fly along intercontinental flyways from their southern wintering grounds to their remote, harsh breeding sites. How these birds solve the navigational and physiological constraints has been largely answered, but why they migrate is still a question with many possible answers (1). On page 326 of this issue, McKinnon *et al.* (2) present a continent-wide study that points to predation as a driving mechanism for migration. The study also elucidates the role of predation in shaping Arctic terrestrial biodiversity.

For migration to be sustained in evolutionary terms, the associated costs and benefits must balance. The costs—higher energetic requirements and mortality risk—increase with flyway length and, hence, with latitude. The benefits of Arctic breeding grounds include open landscapes, per-

manent daylight, time-limited but abundant resources, limited competition, lower pathogen loads, and lower predation pressure, but not all these benefits increase with latitude. For example, if Arctic migrants were just looking for rich and open habitats to be exploited under permanent daylight, they would stop in the low-Arctic zone, never reaching the northernmost regions in Greenland and Canada. Although other hypotheses still need to be properly tested (3), McKinnon *et al.* provide convincing evidence of lowered predation pressure the further north one gets. The authors focus on shorebirds, but their results might be relevant for other ground-nesting birds, because all their sites share a key predator in these ecosystems: the Arctic fox.

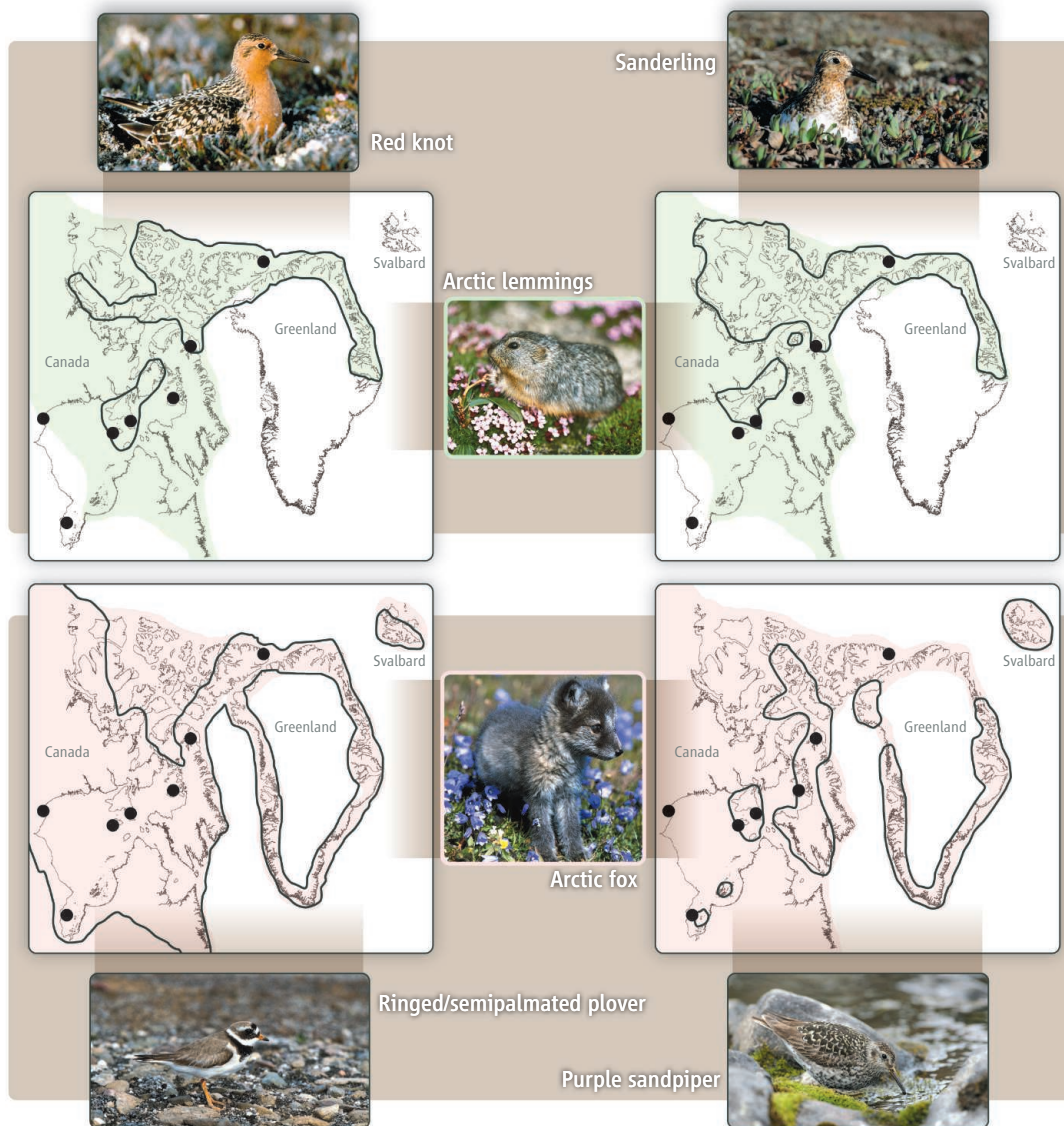
The results also shed light on the dominant role played by predation in the functioning and structuring of Arctic terrestrial vertebrate communities. In this region more than anywhere else, populations are strongly impacted, and sometimes driven, by predator-prey interactions. The key pieces of this puzzle are several species of Arctic lemmings, whose dynamics are typically cyclic. Lem-

Predation pressure falls with increasing latitude, helping to explain why many birds migrate as far north as the high Arctic.

ming densities depend on, but also determine, the functional and numerical responses of predator species (mainly Arctic fox, snowy owl, jaegers, and small mustelids) (4). In turn, the 3- to 4-year lemming cycles strongly affect the dynamics of alternate prey, such as shorebirds and wildfowl, through indirect predator-prey interactions (5–7). In the low phase of the lemming cycle, the fraction of these alternate prey increases in the predators' diets; in the peak phase, predators specialize on lemmings and release their predation pressure on alternate prey. Surprisingly, the mechanisms behind latitudinal trends in predation pressure and the impact of lemming cyclic phases are not discussed by McKinnon *et al.*

In this cat-and-mouse game, shorebirds are both impacting (by contributing to increase predators' survival rates) and impacted by lemming-predator interactions. For the shorebird species that are most sensitive to predation, high predation pressure by the Arctic fox cannot be compensated by reproduction or survival. Viable populations of these species may hence occur only within the lemming distribution range, where the pressure imposed by the Arctic fox is regu-

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Follow the lemmings. Using artificial nests at several field sites in the Canadian Arctic (black dots), McKinnon *et al.* show that Arctic shorebirds face declining predation pressure toward the north (2), an important benefit for long-distance migrants whose biogeography should hence partly be driven by predator-prey interactions. The distribution ranges of several species support the latter hypothesis. In Svalbard and South and West Greenland, lemmings (light green) are absent and terrestrial predators like the Arctic fox (light pink) impose a higher predation pressure on birds. The perfect mismatch between these lemming-free areas and the ranges of some high-Arctic shorebirds (upper panels) supports such a predation-driven pattern and suggests that these species are more sensitive to predation than are species that can breed further south or within the entire distribution range of the Arctic fox (lower panels). Data are from (14–16) and additional regional sources (17–23).

larly released when lemmings are plentiful (8). Empirical data support this assumption: The highest diversity of *Calidris* species is found within the lemming distribution range (9), and some species (such as Sanderling and Knot) are absent outside of this range (see the figure). Using molecular tools to test for spatial and temporal synchrony in the postglacial expansion of lemmings, fox, and shorebirds, and measuring predation pressures on natural nests from different species and in different communities, should provide additional evidence for the hypothesis, overlooked in previous research [such as (10)], that shorebird biogeography can be explained by predator-prey interactions.

During the 2007–2008 International Polar Year, many large-scale initiatives (11) studied the importance of top-down processes such as changes in predation pressure versus bottom-up processes such as greening of vegetation. The growing evidence that predation is a driving force in structuring Arctic eco-

systems, and the quality of these programs' results, call for the continuation and extension of such circumpolar networks.

Climate change already affects many Arctic species (12). Because these ecosystems are structured by only a handful of species, these changes immediately diffuse to lower and upper trophic levels through strong direct or indirect predator-prey interactions. Scientists in the Arctic must therefore increase their efforts in documenting and modeling changes in predator behavior and dynamics, including the species currently invading from the south (13).

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Lower Predation Risk for Migratory Birds at High Latitudes

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Quantifying the costs and benefits of migration distance is critical to understanding the evolution of long-distance migration. In migratory birds, life history theory predicts that the potential survival costs of migrating longer distances should be balanced by benefits to lifetime reproductive success, yet quantification of these reproductive benefits in a controlled manner along a large geographical gradient is challenging. We measured a controlled effect of predation risk along a 3350-kilometer south-north gradient in the Arctic and found that nest predation risk declined more than twofold along the latitudinal gradient. These results provide evidence that birds migrating farther north may acquire reproductive benefits in the form of lower nest predation risk.

Life history theory predicts that the costs of migration must be compensated for by benefits to lifetime reproductive success (1, 2). Costs of migration include the metabolic and energetic requirements of flight (3), high mortality risk (4, 5), and exposure to extreme weather events (6, 7). Such negative effects are expected to be important for migrant birds that breed in the Arctic, where severe weather events during migration or upon arrival at the breeding grounds can lead to poor body condition, breeding failure, complete reverse migration, and even death (8). Bird migration patterns have been thought to be determined mainly by food availability (9), habitat-related parasite pressures (10), and predation risk during migration (4).

Arctic-nesting birds exhibit some of the most impressive migratory strategies, such as flying from wintering areas at the southern tip of South America, southern Africa, and Oceania to their breeding grounds in the Arctic (11, 12). The physiological costs of migrating to and breeding at these arctic sites have been well documented for species such as shorebirds (7, 13, 14). Birds could reduce these costs by breeding at more southerly latitudes, thereby decreasing both migration costs and the metabolic costs of breeding in the extreme arctic environment. However, if competition for food resources, risk of parasite infection, and predation at southern sites are high, then increasing migration distance could have repro-

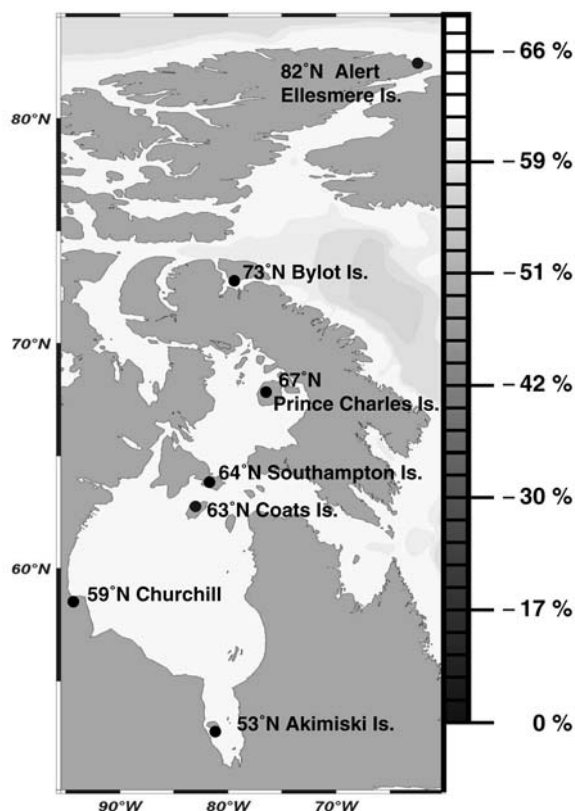
ductive and/or survival benefits. Potential fitness benefits of breeding at higher latitudes have been quantified in terms of reduced parasite loads (15) and greater food availability due to longer daylight hours (16).

Reduced predation at higher-latitude sites has yet to be quantified. Predation risk has emerged as a dominant force in the evolution of avian life history, influencing the selection of nest sites and underlying latitudinal clines in the clutch size of passerines (17). We thus predicted that the risk of nest predation could also play a key role in balancing the costs of long-distance migration. If so, we would expect a negative relationship between nest predation risk and latitude in arctic

ground-nesting shorebirds. To test for this relationship, we systematically measured predation risk by monitoring the survival of 1555 artificial nests for a minimum of two summers at seven shorebird breeding sites (table S1) (18) over a latitudinal gradient of 29° (~3350 km) from sub-Arctic to High-Arctic regions of Canada (Fig. 1). By monitoring artificial nests, we controlled for the heterogeneity in survival associated with real nests [temporal, spatial, interspecific, and intraspecific behavioral differences (19)] to yield a controlled effect of predation risk. We monitored artificial nests during early and late shorebird incubation periods. We then tested for the effect of latitude on predation risk, using Cox proportional hazards regression (18, 20).

As predicted, nest predation risk was negatively correlated with latitude. For an increase in 1° of latitude, the relative risk of predation declined by 3.6% (coefficient -0.0360 , SE 0.0045 , $\chi^2_1 = 63.77$, $P < 0.0001$; Figs. 1 to 3). This equates to a decrease in predation risk of 65% over the studied latitudinal transect of 29°. Previous studies investigating latitudinal trends in predation risk on the nests of temperate-breeding neotropical migrants failed to detect any clear south-north gradient (21). These differences in results could be attributed to differences in real patterns of predation risk between temperate versus arctic environments, or they could be due to differences in methodological approaches. In our study, artificial nests enabled us to measure a standardized predation risk, as opposed to the nest success of

Fig. 1. Average latitudinal decrease in nest predation risk and map of the shorebird breeding sites where artificial nests were monitored. The decrease in predation risk (3.6% per degree relative to the southernmost site, Akimiski Island) is indicated at 5° intervals on the latitudinal scale at right.



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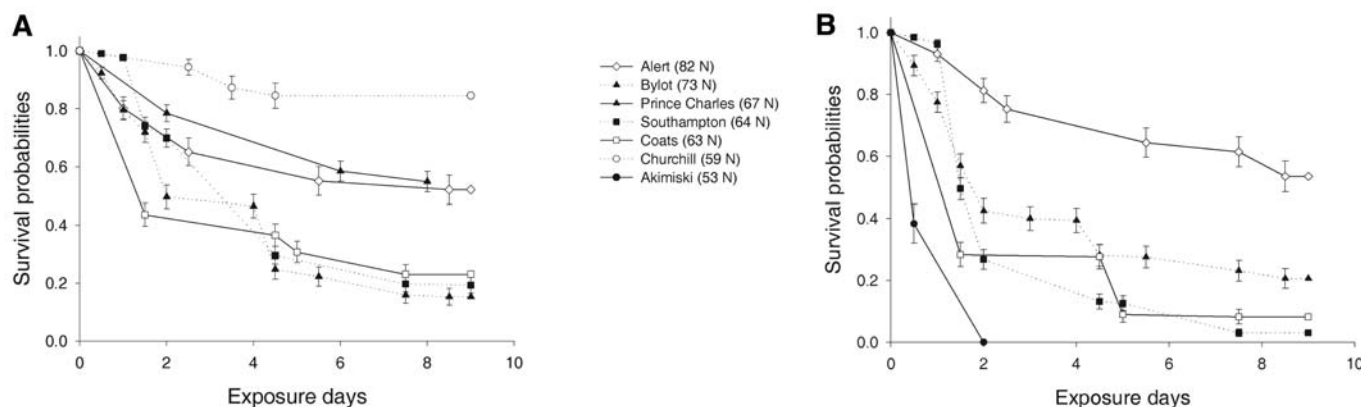
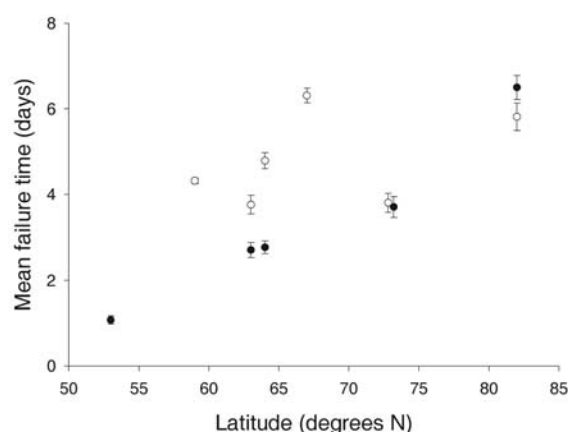


Fig. 2. Kaplan-Meier survival probabilities over 9 exposure days for artificial nests by site for all years during early (A) and late (B) shorebird incubation periods. Each data point on the curve represents the Kaplan-Meier survival

estimate at time t (\pm SEM), which provides the probability that a nest will survive past time t . Survival probabilities are based on 2 to 4 years of data per site [see table S1 for details (18)]

Fig. 3. Mean failure time in days (\pm SEM) for depredated artificial nests by latitude for all years during early (open circles) and late (solid circles) shorebird incubation periods. Low mean failure times indicate rapid nest loss (high predation risk). Each data point is based on 2 to 4 years of data per site [see table S1 for details (18)]. Overlapping data points for Bylot Island (73° N) have been offset by $\pm 0.2^\circ$.



real nests, which is affected by several factors other than predation pressure [for example, parent birds can compensate for an increased risk of predation by increasing the defense of their nest (22)].

These results provide evidence that the costs of migrating farther north could be compensated for by decreases in predation risk at higher latitudes. However, can lower predation risk at higher latitudes really compensate for the increased migration distances and increased metabolic harshness experienced by High-Arctic-nesting species? Though we may have good estimates of the energetic costs of flying (23) and how standard metabolic rates change with latitude (they increase by 1% per degree of latitude) (24), we still lack the basic understanding of how these variables affect adult survival. The apparent cost associated with migrating to Arctic breeding areas is indicated by the reduced survival of adults that fail to achieve adequate condition before leaving the last spring staging area (7, 13); however, it is not known whether the increased mortality is associated with migration, breeding, or both. To explore these trade-offs, we require better estimates of demographic parameters for birds breeding at various latitudes,

so that we can model the contrasting effects of adult survival versus reproductive components. By combining studies on marked individuals with systematic sampling of ecological conditions experienced on the breeding grounds, we will better be able to link individual itineraries with life history events, thus improving our theoretical understanding of the ecology and evolution of long-distance migration.

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Lower Predation Risk for Migratory Birds at High Latitudes

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Materials and Methods

Heterogeneity in nest density, camouflage, incubation length and constancy (exposure time), parental care (uniparental/biparental), and nest defence all contribute to variation in rates of predation on shorebird nests(S1, S2). In order to measure the relative risk of predation across sites, we controlled for these factors by monitoring artificial nests. In the Arctic, artificial nests exhibit lower survival rates than real shorebird nests, however, they have been shown to be a reliable index for both temporal(S3) (inter-annual) and spatial(S4) trends in predation risk of real shorebird nests. Artificial nest monitoring was conducted for 2 to 4 years at each of the 7 study sites providing a measure of average predation risk, taking into account the potentially high inter-annual variability in predation pressure. Monitoring was conducted following similar protocols. At most sites (see Table S1 for site-specific details), 40 artificial nests were positioned randomly in suitable shorebird nesting habitat, covering an area of approximately 4 km². This density of artificial nests was within the range of observed nesting densities of shorebirds across the study sites considered. Each artificial nest consisted of 4 Japanese Quail (*Coturnix japonica*) eggs placed in a small depression made in the ground. Quail eggs resemble those of shorebirds in colouration and size, and the depressions made are similar to the simple nest scrapes used by shorebirds. Nests were deployed within the same time period, and were relocated by small sticks or natural objects (rocks or feathers) placed between 5 and 7 m from the nest. Once deployed, artificial nests were checked at 12 hours, 24 hours, 72 hours, and then every 3 days up to 9 exposure days. For visit intervals greater than 24 hours, failure times were assumed to occur at the midpoint between sampling intervals as the exact date of failure was not known. At most sites, artificial nest monitoring occurred twice during the breeding season, corresponding to the early and late incubation periods for shorebirds at each site (Table S1).

Analyses

The effect of latitude on artificial nest survival was tested using Cox proportional hazards regression models (PROC PHREG in SAS)(S5) which test for a relationship between Kaplan-Meier survival estimates and explanatory variables. One assumption of the Cox approach is that the survival and hazard functions being compared are proportional to each other.

Violation of this assumption was tested graphically(S6). As survival and hazard functions for season (early or late) were not proportional, analyses were stratified by season. Stratifying by season permitted the testing of a latitudinal trend while controlling for the effect of season.

Year was not entered as a covariate because we wanted to test for trends in a multi-year average predation risk across sites due to high inter-annual variability. The most southern site (Akimiski Island 53° N) had the highest nest predation rate (lowest survival curve). When this site is excluded from the analyses, there is still a significant negative relationship between latitude and predation risk (latitude coefficient -0.0274, SE 0.0048, $\chi^2_1 = 32.60$, $p < 0.0001$).

Because sample sizes were not always equal between years and sites (Table S1), we also re-conducted the analyses using all sites on a stratified random sub-sample of artificial nests (n=18 for each site, year and incubation stage; 18 was the smallest sample size at any one site and year). Thus, years of high or low predation were equally weighted within sites. Similar results were found using these random sub-samples (predation risk declined 2.8% per degree latitude; coefficient -0.0277, SE 0.0067, $\chi^2_1 = 17.29$, $p < 0.0001$).

Table S1: Detailed summary of artificial nest monitoring protocols for each study site.

Study Site	Lat. Long.	Year	Season	Study Design ^a	N	Eggs per Nest	Nest Density (/km ²)	Inter-nest Distance (m)	Visit Schedule (days)	End of Monitoring (days)
Akimiski Island	53° N 81° W	2006	late	B	20	4		200	4	4 ^b
		2008	late	B	40	4		100	0.5	1 ^c
Churchill	59° N 94° W	2004	early	A	32	3	10		7	7
		2008	early	A	39	4	10		0.5, 1, 3, 6, 9	9
Coats Island	63° N 82° W	2004	early	A	66	4	16.5		3, 7, 9	9
		2004	late	A	66	4	16.5		3, 7, 9	9
		2005	early	A	90	4	22.5		3, 6, 9	9
		2005	late	A	68	4	17		3, 6, 9	9
Southampton Island	64° N 81° W	2004	early	A	37	4	10		3, 6, 9	9
		2004	late	A	18	4	10		3, 6, 9	9
		2005	early	A	59	4	10		3, 6, 9	9
		2005	late	A	60	4	10		3, 6, 9	9
		2006	early	A	80	4	10		3, 6, 9	9
		2006	late	A	80	4	10		3, 6, 9	9
		2008	early	A	40	4	10		0.5, 1, 3, 6, 9	9
		2008	late	A	40	4	10		0.5, 1, 3, 6, 9	9
Prince Charles Island	67° N 80° W	1996	early	B	100	2		50	4, 8	8 ^d
		1997	early	B	100	2		50	4, 8	8 ^d
Bylot Island	73° N 80° W	2005	early	A	38	4	10		3, 6, 9	9
		2005	late	A	40	4	10		3, 6, 9	9
		2006	early	A	40	4	10		0.5, 1, 3, 4, 7, 9 ^f	9
		2006	late	A	40	4	10		0.5, 1, 2, 3, 4, 7, 9 ^f	9
		2007	early	A	39	4	10		0.5, 1, 3, 6, 9	9
		2007	late	A	40	4	10		0.5, 1, 3, 6, 9	9
		2008	early	A	40	4	10		0.5, 1, 3, 6, 9	9
		2008	late	A	40	4	10		0.5, 1, 3, 6, 9	9
Alert, Ellesmere Island	82° N 62° W	2007	early	A	61	4	10		1, 4, 7, 9	9 ^e
		2007	late	A	63	4	10		1, 4, 7, 9	9
		2008	early	A	40	4	10		1, 3, 5, 7, 9	9 ^f
		2008	late	A	39	4	10		1, 3, 6, 9	9

^a Study design A refers to the protocol outlined in the methods summary (Nest Density is provided), whereas study design B indicates that artificial nests were deployed along a transect (Inter-nest Distance is provided) instead of in 4 – 1 km² blocks.

^b All nests depredated by day 4

^c All nests depredated by day 1

^d Nests were monitored up to 12 days however nests surviving past 8 days were censored at day 8 for statistical analysis

^e Nests were monitored up to 10 days however nests surviving past 9 days were censored at day 9 for statistical analysis

^f Nests were monitored up to 11 days however nests surviving past 9 days were censored at day 9 for statistical analysis

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