Timing matters: phenological constraints and predation shape Arctic community structure

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Summary

Ecological theory predicts that abiotic constraints and biotic interactions jointly shape species assembly, yet empirical evidence for their combined effects on community structure remains limited. In Arctic ecosystems, spring snowmelt sets the timing and duration of the snow-free period, thereby controlling food availability, and predation often imposes strong additional pressure on prey species. Using a 10-year dataset on the occurrence of 11 bird species across a 600 km² study area, we evaluated how spring snowmelt timing and predator density influence species occurrence and community structure in the High Arctic tundra. Species occurrence declined with later snowmelt dates, with larger-bodied species being particularly constrained by short snow-free periods. Predation further modulated species occurrence, with responses varying according to body mass. Our findings highlight the combined influence of the phenology of food availability and predation as fundamental ecological filters shaping community structure. Building on species contrasted responses, we propose a conceptual framework for how phenological constraints and predation shape community assembly in highly seasonal environments.

Key-words

Community structure, Phenology, Predation risk, Snowmelt timing, Body mass, Arctic tundra, Predator-prey

Introduction

Understanding what governs the assemblage of species in ecological communities is a long standing challenge in ecology (Hutchinson, 1959). Among many influential drivers, energy availability is one of the most fundamental (Lindeman, 1942). In most ecosystems, plants absorb energy from sun radiation, which is then transferred through trophic levels by consumptive interactions. Herbivores may establish and persist in a system if the available energy is sufficient to support their growth and reproduction (Lindeman, 1942). Yet, while the total quantity of energy available may set an upper limit to the abundance and diversity of species at different trophic levels, the temporal availability of these resources is also essential.

In many biological systems, there is a limited period each year during which environmental conditions are suitable for critical life-history events like growth or reproduction (Hjort, 1914; McNamara & Houston, 2008; Visser & Gienapp, 2019). This phenological window is determined by a combination of favourable abiotic conditions (e.g., adequate pH, favourable temperature, lack of snow) and high enough resource availability (McNamara & Houston, 2008). These windows limit species occurrence based on their physiological tolerances and ability to complete energetically demanding life-history events within the restricted time available (Durant et al., 2007; McNamara & Houston, 2008). The timing and duration of phenological windows thus filter which species can locally complete their lifecycle and persist (Godsoe et al., 2017; Schneider & Frost, 1996; Williams et al., 2017).

Species vary in how they navigate constraints imposed by phenological windows due to differences in functional traits (Humphries et al., 2017). Body mass is a fundamental trait shaping both energetic demands and trophic relationships (Brose, 2010; Gravel et al., 2013; Riede et al., 2011). Because metabolic rate scales with body mass (Brown et al., 2004; Kleiber, 1932), it is a strong indicator of energy requirements and can serve as a proxy for several other traits (Peters, 1986). For example, larger bird species consistently have heavier eggs and longer incubation and chick-rearing periods (Sæther, 1987). Thus, a species' body mass should be intimately linked to the phenological window it needs to persist and reproduce.

Phenological constraints on resource availability can also propagate to higher trophic levels, as areas with longer productive periods may support more consumers, in turn

altering top-down dynamics (Fretwell & Barach, 1977; Oksanen et al., 1981). For example, in ephemeral ponds, the short availability of suitable habitats can exclude prey species that need long windows to reproduce and therefore prevent the establishment of predators (Schneider & Frost, 1996). Therefore, longer growing periods tend to support greater prey biomass, which in turn can sustain higher predator abundance (Oksanen et al., 1981). Predator density may change nonlinearly and can increase sharply once the growing season is long enough to allow new prey species. This is particularly striking in the case of large colonial prey, such as waterfowl in arctic ecosystems, which can drastically increase predator densities (Dulude-de Broin et al., 2023; Giroux et al., 2012). The ability of species to withstand predation should also be influenced by their body mass. For instance, the body mass ratio between consumers and their prey affects both the rate and success of attacks, as larger prey are generally more difficult to subdue and consume (Brose, 2010; Portalier et al., 2019). Consequently, phenological constraints not only shape resource availability for primary consumers but may also alter biotic interactions within food webs.

Understanding how phenology and predation influence the ability of species to persist in ecological systems is a major challenge in community ecology (CaraDonna et al., 2014; Visser & Gienapp, 2019). These drivers are rarely integrated when studying the structure of vertebrate communities (Ponti & Sannolo, 2023) because they require detailed information on both phenological windows, predation risk and multi-species distribution. Arctic terrestrial ecosystems offer a unique opportunity to tackle these questions as seasonal changes impose severe phenological constraints on ecological processes (Humphries et al., 2017; Saulnier-Talbot et al., 2024). Snow cover creates strong heterogeneity in the length of the growing season, leading to abrupt changes in primary production (Niittynen & Luoto, 2018). In particular, the spring snowmelt unlocks the window of opportunity for plant growth, making it the primary phenological driver of primary production (Walker et al., 2001). Snowmelt timing is also intimately linked to the duration of the snow free period, which can constrain access to terrestrial food resources for consumers (Rixen et al., 2022). Moreover, predation could affect the ability of prey species to persist in the arctic tundra landscape (Beardsell et al., 2023).

Here we benefited from a spatial gradient of snowmelt over a 600 km^2 study area and contrasted predator densities induced by the presence of a goose colony to investigate how the timing and duration of food resource availability, assessed through the timing of spring snowmelt, and predator density influence species occurrence and community structure in the High Arctic tundra. We leveraged a 10-year, high-resolution dataset on vertebrate relative occurrence to: (1) evaluate how spring snowmelt date influences the relative occurrence and distribution of 11 vertebrate species during the breeding period, and (2) assess the response of these species, differing in body mass, to both snowmelt phenology and predation. We hypothesized that snowmelt timing influences the occurrence of breeding species across the landscape by defining the temporal window during which energy is available to complete reproduction. Second, we hypothesized that predator density further modulates species occurrence, and that body mass mediates the joint response to snowmelt and predation. We predicted that the probability of occurrence would decline with later snowmelt dates, especially for larger-bodied species whose reproductive cycles require more time and resources. However, we expected larger bodied species to be less sensitive to predation, due to greater defence capacity. Together, these hypotheses emphasize the combined influence of abiotic (snowmelt) and biotic (predation) factors on the structure of Arctic vertebrate communities and set the stage for a trait-based examination of species responses across environmental gradients.

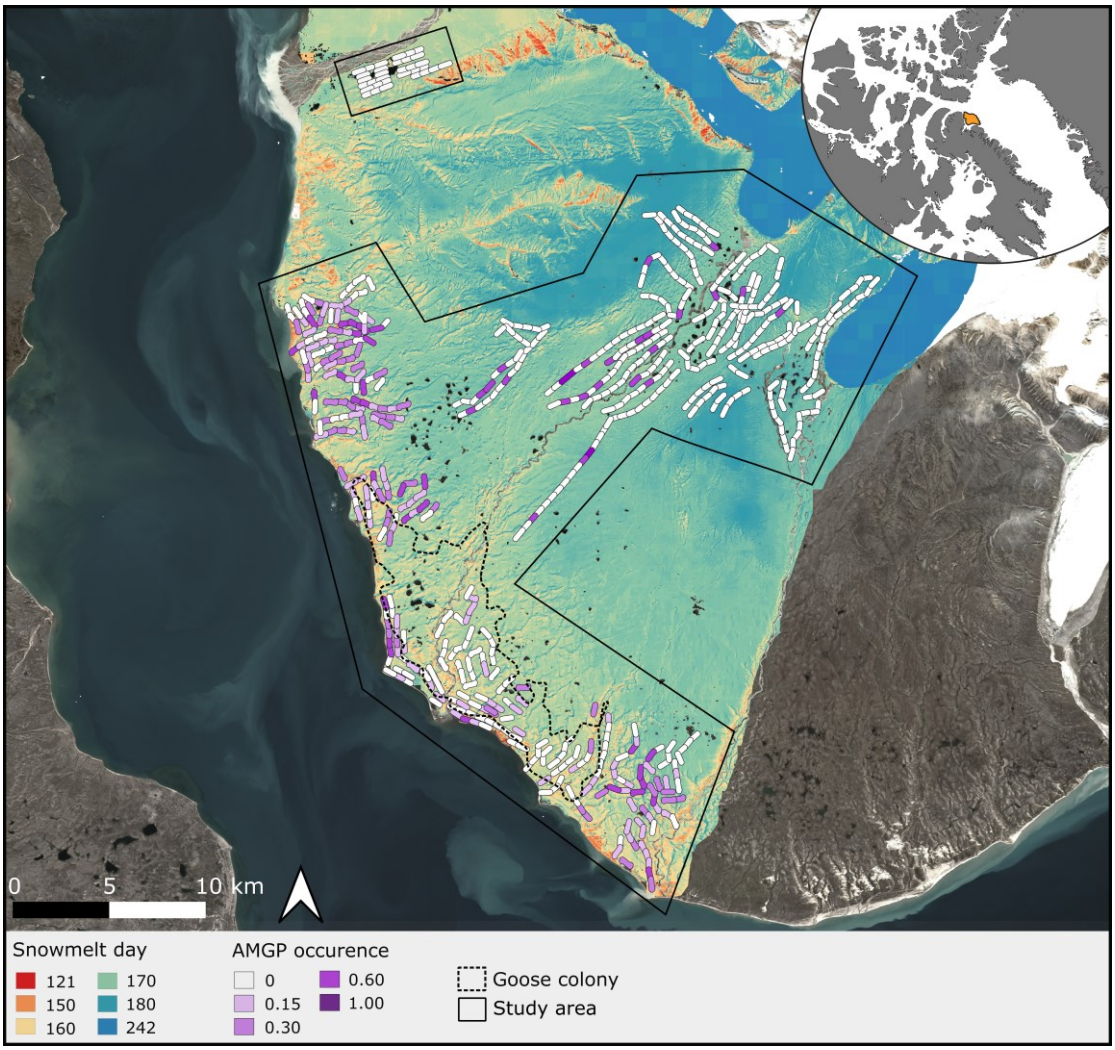

Figure 1. Map of the study area (inside solid black lines) on Bylot Island (Nunavut, Canada) showing the location of sampling transects (coloured lines), the greater snow goose colony boundary (black dashed line), and the average snowmelt day. The occurrence of each species was recorded within 150 m on each side of the 500 m-long transects. For illustrative purposes, line colours indicate the relative occurrence (i.e., the proportion of surveys with a sighting) of the American golden plover (AMGP), one of 11 surveyed species. Snowmelt day refers to the day of the year (counting from January 1) and was derived from combined Sentinel-2 and MODIS imagery. Areas where snow did not melt were assigned a value of 242. The top-right inset illustrates the location of the study area at a broader geographic scale.

Materials and Methods

Study system

Field work was conducted in the southwest plain of Bylot Island (72.93° N, 79.76° W), in Sirmilik National Park, Nunavut, Canada (Fig. 1). The ~600 km² area consists of rolling hills, plateaus, and lowlands separated by glacial valleys (Gauthier et al., 2011). It is mostly covered by mesic tundra, with wet meadows commonly found in valley bottoms. Lakes, ponds, and polygonal wetland complexes are scattered throughout the landscape. Elevation increases from the coast inland and from valley bottoms to plateaus, up to 600m asl. Mesic tundra and wet meadows are well vegetated with diverse plant communities, and rocky substrates associated with xeric tundra become more common with altitude. Nonetheless, all major habitat types are broadly distributed throughout the study area.

Arctic fox is the main terrestrial predator and feeds primarily on lemmings (brown lemming, *Lemmus trimucronatus*, and collared lemming, *Dicrostonyx groenlandicus*) and snow goose eggs, but also opportunistically consume the eggs of all other tundra nesting birds (Gauthier et al., 2011). We assessed the occurrence of 11 bird species, which share the arctic fox as primary predator: greater snow goose (*Anser caerulescens*), cackling goose (*Branta hutchinsii*), glaucous gull (*Larus hyperboreus*), red-throated loon (*Gavia stellata*), long-tailed jaeger (*Stercorarius longicaudus*), American golden plover (*Pluvialis dominica*), Baird's sandpiper (*Calidris bairdii*), white-rumped sandpiper (*Calidris fuscicollis*), Lapland longspur (*Calcarius lapponicus*), horned lark (*Eremophila alpestris*), and snow bunting (*Plectrophenax nivalis*). These species vary in body size, nesting habitat, diet, and vulnerability to fox predation (See Appendix S1 for detailed descriptions). Shorebirds, passerines, and jaegers nest in mesic to xeric tundra, while cackling goose, glaucous gull, and red-throated loon nest near lakes and wetlands. Snow geese use both mesic tundra and wetlands, often in large colonies but also nest individually away from the colony center. Ground-nesting shorebirds and passerines are highly vulnerable to fox predation (McKinnon & Bêty, 2009), whereas larger and water-associated birds have partial defences and may benefit from nesting microhabitats less accessible to foraging foxes (Corbeil-Robitaille et al., 2024).

174 *Nesting bird occurrence*

175 We conducted surveys along transects to assess the occurrence of species commonly
176 found nesting in mesic and xeric habitats, and we surveyed lake shores to assess the
177 occurrence of species nesting near lakes and ponds (i.e. cackling goose, glaucous gull,
178 red-throated loon).

179

180 *Transects*

181 Observers walked at constant speed along 500 m transects and recorded all bird
182 sightings, along with reproductive status (see Appendix S1 for breeding criteria), within
183 150 m on either side of the transect line (distances estimated by observers trained with
184 a range finder). For each species, detection probability was assumed constant across
185 observers and habitats, given the use of standardized protocols, trained observers, and
186 the open tundra landscape. Most species were highly detectable often responding to
187 observers' presence, and the open tundra provided excellent visibility, minimizing
188 potential influence of habitat structure on detection rates. We nonetheless remained
189 cautious and avoided comparing absolute occurrence across species, as differences in
190 detection rates due to species-specific traits and behaviour are likely. We also included
191 transect ID and year as random effects in the analyses to reduce potential biases from
192 residual spatial or temporal variation in occurrence (see Statistical Analyses).

193 Surveys along transects were carried out annually between 2010 and 2024, except in
194 2020 and 2021, with an average of 243 transects per year (range: 146-295).
195 Additionally, in 2022, 2023, and 2024, we added 331, 322, and 291 transects,
196 respectively, in areas with later snowmelt. For all years but 2024, surveys took place
197 during bird incubation period from 20 June to 14 July. We alternated surveys between
198 early and late snowmelt areas, as well as between areas with high and low fox densities
199 (see below), to minimize bias from potential seasonal decline in nest detection due to
200 nest failure (Lamarre et al., 2017). Some data from 2024 had to be excluded because
201 field work was delayed on that year (see Appendix S1).

202 For analyses, we used the occurrences of breeding individuals along transects for
203 plovers, jaegers, and passerines, and both breeding and unknown-status individuals for
204 other species, excluding non-breeders. Only high lemming years (see below) were
205 included for jaegers as they do not nest at low lemming density (Seyer et al., 2023).

Snow bunting analyses focused on data from 2022 and 2023, as the addition of transects in late snowmelt areas provided most observations for that species, with only 11 observations recorded during the other nine years.

Lake surveys

Lakes across the study area were surveyed for nesting cackling goose, glaucous gull, and red-throated loons from 2022 to 2024 (n = 288 lakes in 2022, 399 in 2023, and 117 in 2024). Observers walked the perimeter of each lake, carefully searching for nests along the shoreline and on islets. The presence or absence of a nest for each species was recorded at each lake.

Nesting phenology

For snow geese, American golden plovers and Lapland longspurs, intensive nest searches independent of transect surveys were conducted, providing a large sample of laying dates (snow goose: n= 8496 over 27 years, American golden plover: n=566 over 15 years, Lapland longspur n=766 over 25 years). For those species, we present the distribution of laying dates alongside the occurrence-snow relationships and discuss the snowmelt threshold in relation to the latest laying date observed.

Snowmelt phenology

To assess the influence of snowmelt patterns on spatiotemporal variation in species occurrence, we mapped the date of snow disappearance (hereafter snowmelt date) by calculating, for each year from 2010 to 2024, the median snowmelt date of all pixels within 150 m of surveyed transects and lakes. We focused on snowmelt date rather than snow cover duration because it is the dominant phenological driver of primary production in the Arctic (Walker et al., 2001). Snowmelt date and snow cover duration were, however, highly correlated at our study sites (Appendix S1, Figure S10, Estimate [95%CI] = –1.05 [–1.08, –1.03], n = 3298, R^2 = 0.65).

Snowmelt dates can be derived from Sentinel-2 imagery from 2017 onward (spatial resolution: 20 m, revisit frequency: 1-2 d on Bylot, Drusch et al., 2012) and from MODIS data between 2000 and 2024 (resolution: 500 m, revisit frequency: 1 d on Bylot, (Hall & Riggs, 2021). To benefit from the high spatial resolution of Sentinel-2 products along with the frequent revisit and longer temporal coverage of MODIS, we obtained enhanced snowmelt maps by combining information from both satellites.

Comprehensive details on how MODIS and Sentinel-2 snow products were integrated and validated are available in Appendix S1.

Predator density

Arctic fox density varies within the study area, largely due to the presence of the snow goose colony. Foxes with dens located within the snow goose colony have home ranges that are half the size of those outside the colony, resulting in higher local densities and a sharp increase in predation risk (Dulude-de Broin et al., 2023).

To quantify variations in fox local density, we used spatial variations in home range size compiled from fox tracking data (Berteaux, 2020, 2021). Between 2008 and 2023, we captured 165 foxes within the study area and equipped them with ARGOS or GPS collars (see Clermont et al., 2021; Lai et al., 2015 for details). We measured their annual home range (95% isopleth) using autocorrelated kernel density estimation implemented in the ctmm R package (Calabrese et al., 2016) as described in Dulude-de Broin et al. (2023). This allowed us to delineate 248 individual fox home ranges over 16 years, which collectively overlapped with 56% of transects and 75% of lakes surveyed.

For transects and lakes with spatially overlapping home ranges ($n_{transect}$=372, n_{lake}=332), we calculated the average size of fox home ranges, regardless of the year. Estimates were based on a mean of 16 overlapping home ranges per transect (range: 3-39) and 15 per lakes (range: 1-35). Home range analysis allowed the classification of transects and lakes in two categories, large and small home ranges, largely related to fox access to the goose colony (see Appendix S1). Transects and lakes that did not overlap with documented home ranges ($n_{transect}$=288, n_{lake}=112) were assigned to the large home range size category because they were at least 10 km from the goose colony, and all five nearest home ranges fell within that category. To facilitate interpretation, we refer to high and low predator density throughout the manuscript.

Lemming density

Lemmings represent a major and cyclic food resource for arctic foxes (Gauthier et al., 2011). We therefore used lemming abundance as a covariate in our analysis. Lemmings were live-trapped in two 11-ha permanent grids, one in wet and one in mesic habitat, to obtain spatially explicit mark–recapture estimates of density as described in Fauteux et

al. (2015). Trapping sessions were conducted in June, July and August with 144 Longworth traps deployed in each grid and checked twice a day during three consecutive days. We used the average density for all three sessions and both lemming species to obtain annual lemming density. We then classified each transect and lake survey into one of two classes of lemming density, that is low (<18 lemming/km^2) or high (>174 lemmings/km^2). No intermediate lemming density was observed during the study period. Although some spatial variations in lemming abundance likely exists, systematic records of incidental field observations suggest that these two categories remain consistent over the study area (Dulude-de Broin et al., 2023). Moreover, these two lemming density categories closely reflect fox breeding propensity throughout the study area (Giroux et al., 2012; Juhasz et al., 2020).

Statistical analyses

For each bird species, we identified the latest snowmelt date compatible with reproduction (hereafter snowmelt threshold), defined as the latest snowmelt date across all transects or lakes with a nesting individual. To obtain a measure of variability, we resampled the entire dataset 500 times with replacement, calculated the threshold for each resample, and used the median as the final threshold with 95% quantiles as confidence intervals. A species with only one nesting observation near the threshold and no others close in time would yield a wide confidence interval. In contrast, if multiple transects or lakes with nesting individuals shared the same latest snowmelt date, the threshold would be more robust, resulting in a narrower confidence interval.

We modelled the influence of snowmelt date and predator density on the probability of occurrence of a species on individual transects and lakes using generalized linear mixed models with a binomial distribution and a logit link. Each species was analysed separately, and we used model selection to evaluate the contribution of each variable.

Our analysis followed a two-step approach. First, because we expected non-linear relationships between snowmelt dates and the probability of occurrence, we fitted the full model (see below) using natural cubic splines with degrees of freedom ranging from 1 to 5. The most parsimonious model was selected based on AICc. Second, we compared a set of models with different combinations of snowmelt dates (fitted with the selected spline), predator and lemming density (both, high vs. low), and the

interaction between predator density and lemming density. All models included year as a random intercept. Models based on transect data also included transect ID as a random intercept to account for repeated surveys over the years. For lake data, lake ID was not included because nearly half the lakes (42%) were surveyed only once. We considered models with $\Delta AICc < 2$ to be equally supported (Burnham & Anderson, 2002) and discussed all variables included in these models. To illustrate the effect, or lack of effect, of the main variable of interests (i.e. snowmelt date and fox density), we present predictions and model summary from the most parsimonious model that includes both variables, rather than from the single best-fitting model overall. All predictions are shown for high lemming density.

To assess the relative influence of snowmelt date and predation pressure across species with different body masses, we plotted the snowmelt threshold and the effect size of fox density against species body mass.

Results

We monitored 637 unique transects and 444 lakes resulting in 4097 transect-year and 804 lake-year (total number of sightings on transect for each bird species are provided in Appendix S1). Median snowmelt dates ranged from day 140 (May 20) to day 203 (July 22) for transects and from day 155 (June 4) to day 194 (July 13) for lakes. On average, snowmelt timing varied by 18 days [95%CI: 8, 27] across years for the same transect and by 9 days [95%CI: 4, 16] for the same lake. Within a given year, snowmelt timing varied on average by 24 days [95%CI: 14, 43] among transects and 29 days [95%CI: 25, 32] among lakes.

Transects and lakes were well distributed in terms of predator density with 30% of transects and 43% of lakes monitored in areas with high fox densities, and 48% of transects and 15% of lakes surveyed during years of high lemming density. The occurrence of foraging foxes on transect was on average 4.2 times higher in areas of high fox densities compared to areas with low fox densities (Appendix S1, Figure S1).

Occurrence probability of nesting species was generally high in early snowmelt areas and declined with later snowmelt dates until reaching a threshold beyond which a species was no longer observed (Figure 2 and 3, see Appendix S1, Table S1 for threshold values). Waterfowls had the earliest snowmelt thresholds and did not nest in areas that only became snow-free at the beginning of July, a pattern also observed in gulls and jaegers. Red-throated loons and American golden plovers nested in regions with later snowmelt, while smaller species, including sandpipers and passerines, nested across the study area, with reproductive occurrences declining only under very late snowmelt (Figures 2 and 3). Notably, passerine thresholds were near the latest snowmelt dates sampled. For species with intensive nest search data independent from transects surveys (Lapland longspur, American golden plover, and snow goose), the snowmelt threshold closely matched the latest observed lay dates (Figure 2). As expected, larger-bodied species were most affected by a late snowmelt and had the earliest thresholds (Figure 4).

Snowmelt date was an important predictor of occurrence probability in all species except glaucous gulls and red-throated loons (Figure 2 and 3) for which snow was included among the top models, but not in the most parsimonious (Appendix S1, Table S2). Lapland longspurs, American golden plovers, long-tailed jaegers, cackling geese,

346 and snow geese had a high and consistent occurrence probability in early snowmelt
347 areas followed by a steep decline in late snowmelt areas, while the decline was more
348 gradual for horned larks and Baird's sandpipers (Figures 2 and 3). White-rumped
349 sandpipers showed a humped shaped relationship, with low occurrence in early and late
350 snowmelt sites. Notably, snow buntings were largely absent from areas with early
351 snowmelt and occurrence only increased in sites where snowmelt took place after day
352 180 (June 29), before declining again.

353 Predator density was also an important predictor of occurrence probability, although
354 associations were either positive or negative depending on species (Figures 2 and 3).
355 As expected, snow geese occurrence and areas of high fox density were strongly
356 positively associated (Odds ratio (OR) = 140.85 [72.74, 272.73], 95% CI). Fox density
357 was included in the most parsimonious model for all species except Lapland longspur,
358 snow bunting, and white-rumped sandpiper, where it appeared among the top-ranked
359 models, but not in the most parsimonious (Appendix S1, Tables S2). Horned larks (OR
360 = 0.70 [0.55, 0.90]), Baird's sandpipers (OR = 0.25 [0.13, 0.46]), American golden
361 plovers (OR = 0.28 [0.21–0.37]), and long-tailed jaegers (OR = 0.68 [0.51, 0.91]) were
362 less likely to occur in areas of high fox density, with reductions in the probability of
363 occurrence ranging from 26% to 74%. Lapland longspurs showed a similar trend (22%
364 reduction in high fox density areas, OR = 0.78 [0.60, 1.01]). In contrast, cackling geese
365 (OR = 2.47 [1.57, 3.87]), glaucous gulls (OR = 3.99 [1.67, 9.53]), and red-throated
366 loons (OR = 3.62 [1.69, 7.74]) were more likely to occur in high fox density areas. Fox
367 density did not affect the occurrence of white-rumped sandpipers and snow buntings
368 (Tables S2 and S3). Lemming density had a lesser effect on species occurrence than fox
369 density as it was in the most parsimonious model only for snow goose and Baird's
370 sandpiper (Appendix S1, Table S2).

371 Larger bodied species (≥ 1855 g) were generally less sensitive to predation than smaller
372 ones (Figure 5), even showing positive associations with areas of high fox densities.
373 Interestingly, although smaller species were generally negatively affected by fox
374 densities, the strongest negative associations occurred among species of intermediate
375 body size (50-150 g; Figure 5).

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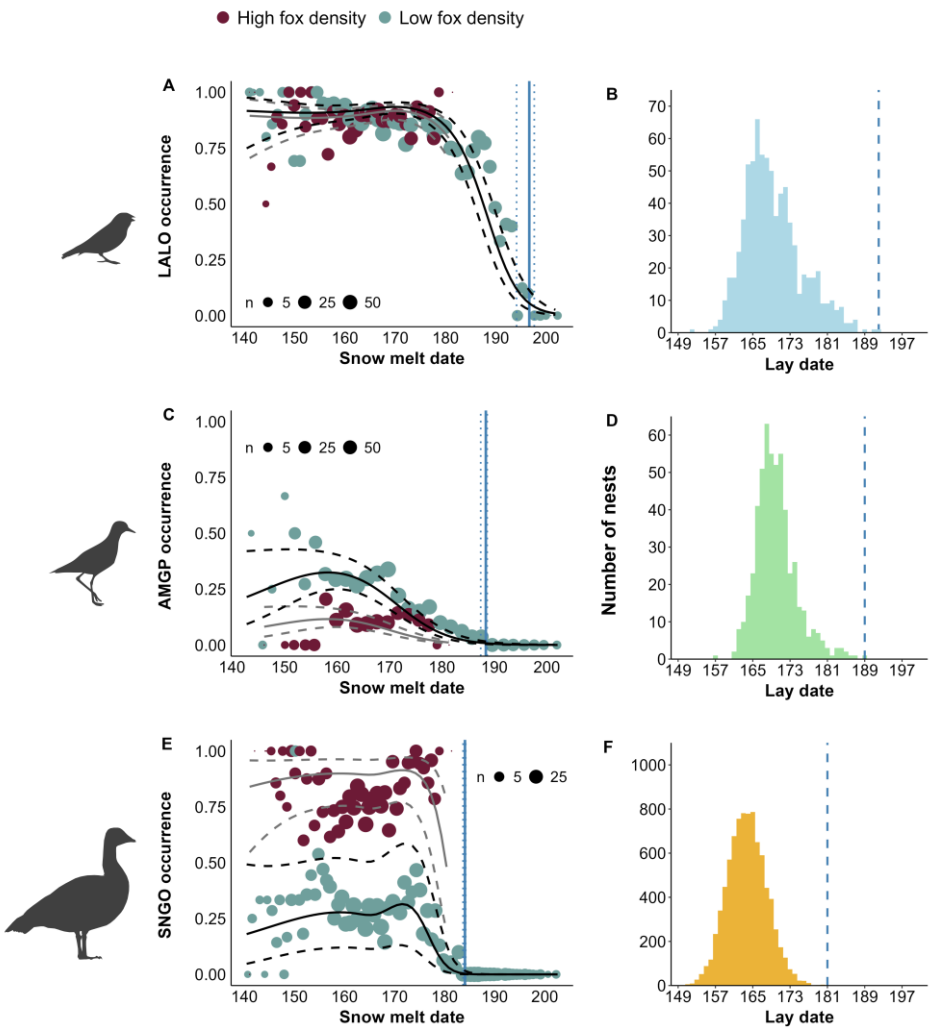


Figure 2. Influence of snowmelt date on occurrence probability of breeding (A) Lapland longspur (LALO), (B) American golden plover (AMGP), and (C) greater snow goose (SNGO) on Bylot Island, Nunavut (2010–2024). The full and dotted lines show model predictions along with their 95% confidence intervals for transects located in low (black) or high (grey) fox density areas. The dots are raw species detection averaged over equally sized intervals for transects located in low (green) and high (dark red) fox density areas. Circle size is proportional to log(n). Snowmelt date refers to the median snowmelt date within 150 m on each side of the 500 m transects. The vertical solid and dashed lines are the snowmelt threshold with the 95% CI. For each species, the distribution of nest laying dates is shown to illustrate correspondence with the snowmelt threshold (vertical dashed lines on these graphs; panels B, D, F).

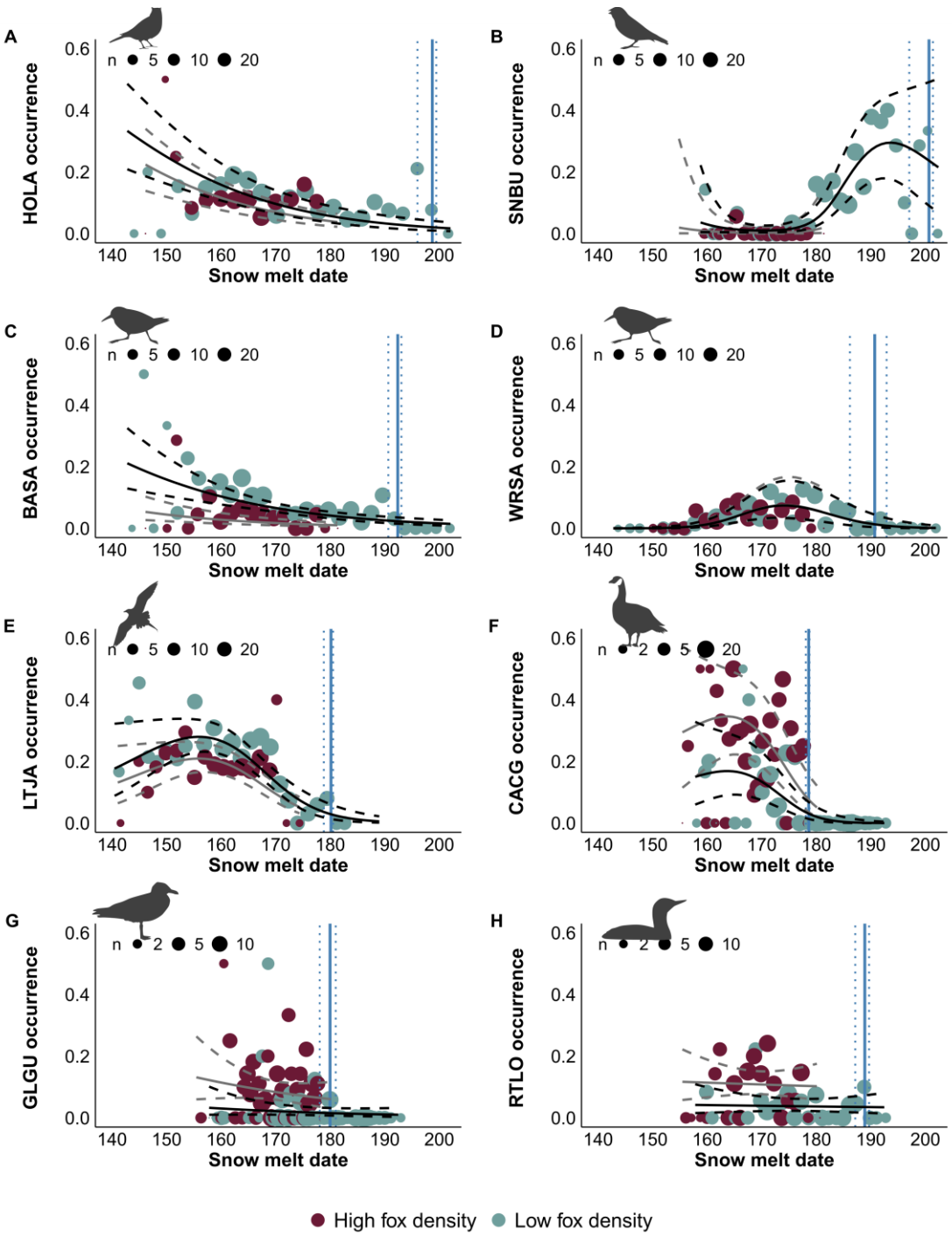


Figure 3. Influence of snowmelt date on occurrence probability of breeding (A) horned lark (HOLA), (B) snow bunting (SNBU), (C) Baird's sandpiper (BASA), (D) white-rumped sandpiper (WRSA), (E) long-tailed jaeger (LTJA), (F) cackling goose (CACG), (G) glaucous gull (GLGU), and (H) red-throated loon (RTLO) on Bylot Island, Nunavut (2010–2024). The full and dotted lines show model predictions along with their 95% confidence intervals for transects or lakes located in low (black) or high (grey) fox density areas. The dots are raw species detection averaged over equally sized intervals for transects located in low (green) and high (dark red) fox density areas. Circle size is proportional to log(n). Snowmelt date refers to the median snowmelt date within 150 m on each side of the 500 m transects (species A-E) or around surveyed lakes (species F-H). The vertical solid and dashed lines are the snowmelt threshold with the 95% CI.

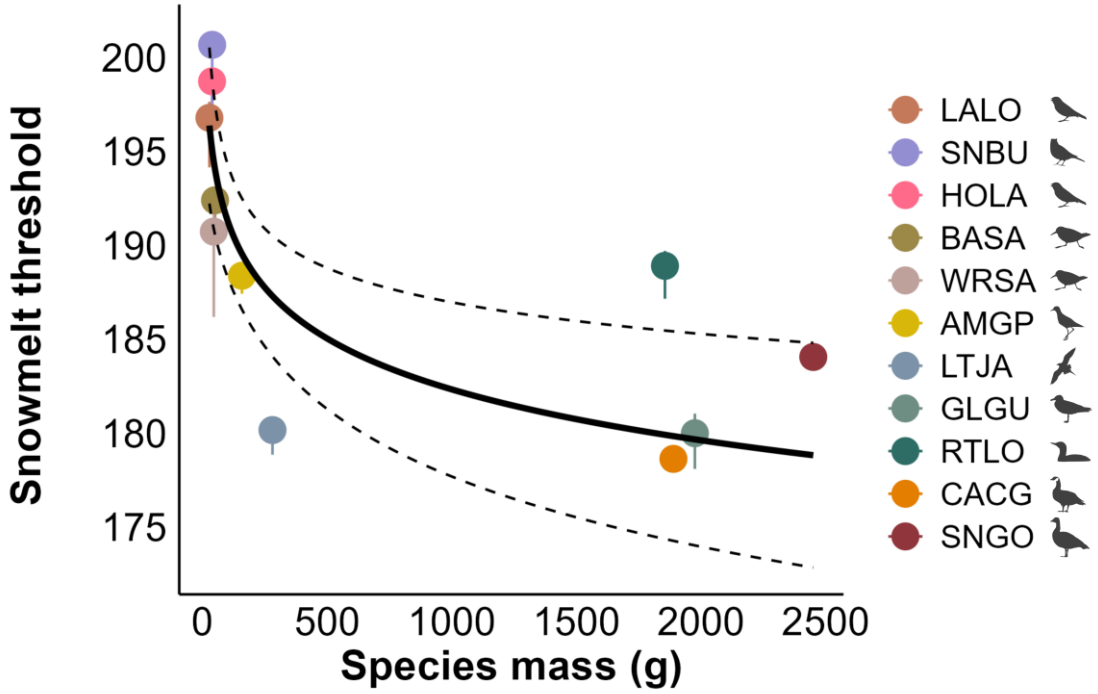


Figure 4. Relationship between the snowmelt threshold date for reproduction and body mass of individual species. Snowmelt threshold corresponds to the last date at which a breeding individual was sighted. Dots represent the threshold for each species shown with 95% confidence intervals obtained through non-parametric bootstrap. Solid and dashed curves are predictions from a simple linear model relating snowmelt threshold to body mass (intercept = 209.28 [95% CI: 199.89, 218.67]; slope = –3.90 [–5.71, –2.09]; $R^2 = 0.72$).

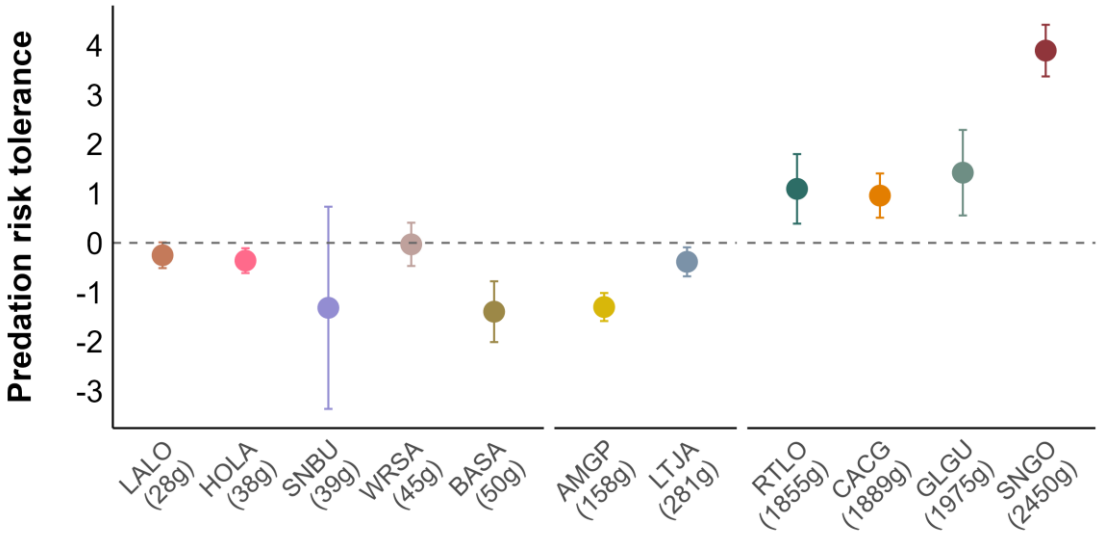


Figure 5. Predation risk tolerance of species ordered by body mass. Predation risk tolerance is the coefficient for the relationship between fox density and species occurrence probability (values in Appendix S1, Table S3). Dots represent effect size shown with 95% confidence intervals. A positive value indicates a higher probability of occurrence in high fox density area.

Discussion

Benefiting from a 10-year dataset on the relative occurrence of 11 vertebrate species across 600 km^2 in the Arctic tundra, we found that species occurrence generally declined with later snowmelt dates before reaching a threshold after which breeding individuals were no longer observed, and that larger-bodied species were most affected by late snowmelt. The relative occurrence of breeding species was further shaped by predation, with responses varying according to body mass. Our findings highlight the combined influence of the phenological timing of resource availability and predation risk as fundamental ecological filters structuring vertebrate communities.

Snowmelt timing

Our results are consistent with the hypothesis that the local assemblage of breeding species depends on the phenological window of resource availability determined by snowmelt timing. The ecological impacts of snowmelt timing is well documented for multiple species that reproduce in boreal and Arctic ecosystems (Slatyer et al., 2022). In both birds and mammals, earlier snowmelt has been linked to earlier reproduction (Dickey et al., 2008; Liebezeit et al., 2014) and higher breeding success (Anderson et al., 2015; Keyser et al., 2022; Post & Forchhammer, 2008) with potential impacts on species distribution (Keyser et al., 2022). In extreme cases, abrupt changes in snowmelt timing can cause ecosystem-wide reproductive failure (Schmidt et al., 2019). Our results support these findings and highlight the role of snow as a critical driver of community structure in the arctic tundra.

Food availability duration constrained by snow cover was likely more limiting for nesting species than total available biomass from primary production. At early snowmelt sites within our study area, where herbivory pressure is the highest, only a small fraction (<10%) of primary production is consumed annually (Legagneux et al., 2012). This suggests that other processes than total food availability are limiting. The issue is likely not how much, but rather how long these resources are available. Once biogeographical filters have operated, similar mechanisms could shape community structure in other highly seasonal systems where reproductive success is tightly linked to the temporal availability of food resources. One such example is songbird

communities relying on synchronized insect emergence in temperate ecosystems (e.g. Visser & Both, 2005).

Species had a clear snowmelt threshold for reproduction as observed in other systems (Smith et al., 2010), and larger-bodied species were generally more sensitive to a late snowmelt. The inverse association between the snowmelt threshold and body mass supports the hypothesis that species with higher energetic demands and especially longer developmental periods are more constrained by the duration and timing of resource availability as they require more time to complete their vital cycle. However, other traits such as diet and energy storage capacity may also shape species-specific responses to the duration of phenological windows. Some species such as the red-throated loon had thresholds that did not align well with their mass. Species phenological tolerance should be closely tied to and overlap with that of their food resources (Altermatt, 2010; Diamond et al., 2011). As such, species such as loons (Davis, 1972) and gulls (Gauthier et al., 2015) that can forage at sea might be less affected by terrestrial snowmelt than herbivores or terrestrial insectivores. The accumulation of energy stores or ability to forage in presence of snow can also extend a species phenological window by providing access to resources during less productive periods (Kerby & Post, 2013; Williams et al., 2017). For instance, snow geese and cackling geese would likely need a much longer pre-breeding foraging period without body stores. Similarly, species such as the snowy owl (*Bubo scandiacus*) that can forage effectively despite snow cover should be less constrained by snowmelt timing.

To minimize potential biases associated with imperfect detection and nest failure, we focused on presence/absence data over broad areas (transect: 500 m x 300 m and 150 m buffer around lakes) and alternated surveys across gradients of snowmelt timing and predator densities. However, differences in detectability across species are likely and the raw occurrence probabilities we report should not be compared between species. Importantly, such cross-species differences in detectability are unlikely to have biased estimated snowmelt thresholds, as the larger, more easily detected species showed earlier thresholds than the smaller, more cryptic ones. The pattern is thus conservative, as imperfect detection would be expected to advance threshold estimates rather than delay them.

In addition to the direct impact of annual snowmelt timing on resource availability, other multi-annual processes could also contribute to the observed patterns in species occurrence. Prolonged snow cover duration can impact habitat types by altering soil dynamics and plant communities (Niittynen et al., 2018, 2020). Although surveys were designed to minimize habitat differences by sampling species in comparable terrain across the snowmelt gradient, fine-scale vegetation variation may still contribute to some observed patterns. For example, the occurrence of white-rumped sandpipers was low in the earliest snowmelt areas, potentially because of local nest site preferences (Smith et al., 2007). Similarly, snow buntings occurred only in late-melt areas, consistent with their reliance on rock cavities (Montgomerie & Lyon, 2020) which are mainly found in areas where prolonged snow cover exposes rocky ledges. These associations could suggest an indirect link between snow-free period length and nesting habitat availability, or reflect underlying factors that influence both snowmelt and habitat. Other processes such as colonial nesting or site fidelity may also decouple relative occurrence from annual snowmelt dynamics. Comparing the explanatory power of annual and long-term averaged snowmelt dates could help disentangle the influence of short-term phenological shifts from longer-term habitat effects, and clarify the timescale over which vertebrate communities respond to environmental changes. Although the mechanisms linking snowmelt to species may vary, snowmelt timing appears to play a central role in shaping community structure by influencing both short- and long-term resource availability and habitat conditions.

Predation

Predation further shaped the relative occurrence of most nesting birds although the influence varied depending on species. Previous studies in this (Beardsell et al., 2023; Clermont et al., 2021; É. Duchesne et al., 2021; Dulude-de Broin et al., 2023; Lamarre et al., 2017) and other Arctic tundra ecosystems (Etchart et al., 2025; Flemming et al., 2019) have shown that predation is a strong driver of nesting success and can shape the distribution of breeding birds. At our study site, early snowmelt areas are characterized by abundant food resources for predators provided in large part by the presence of a goose colony, which allows foxes to maintain smaller home ranges, thereby increasing their density and leading to increased predation risk (Dulude-de Broin et al., 2023). American golden plovers and Baird's sandpipers were the species most affected by fox density, likely because they are large enough to facilitate detection by foxes, but cannot

513 efficiently defend their nest (Beardsell et al. 2021). The negative effect of predation risk
514 was also clear for long-tailed jaegers, which are highly detectable and have limited
515 defences against foxes. Smaller passerines cannot defend their nests either, but they
516 may be harder to detect (Beardsell et al., 2021) and their shorter breeding cycles (20-
517 25 days) than shorebirds (36-55 days) could lead to as much as 50% reduction in
518 exposure to predation. We found no effect of predation risk on white-rumped sandpiper.
519 White-rumped sandpipers may lower detectability by using microhabitats with dense
520 lateral cover (Smith et al., 2007), yet the lack of effect remains puzzling given their
521 overall similarity to Baird's sandpipers.

522 In contrast with previous negative associations, the occurrence of the largest species
523 (i.e. gull, loon, and geese) was positively associated to areas of high predator density.
524 For colonially nesting snow geese, the abundance, clumping, predictability, and storage
525 potential of eggs likely attract foxes to the colony and shift cost-benefit trade-offs
526 towards the formation of smaller home ranges, resulting in higher fox densities
527 (Dulude-de Broin et al., 2023). Snow goose eggs also provide additional food resources
528 for glaucous gulls (Gauthier et al., 2015) and may promote nest formation in areas of
529 high snow goose and fox densities. In addition, risk-taking behaviours by arctic foxes,
530 such as attacking glaucous gulls, red-throated loons or cackling goose nests, appear to
531 decrease when their energy acquisition rates are high (Beardsell et al., 2025). Predation
532 risk could thus be lower for larger bodied species nesting in lakes and wetlands located
533 in areas that offer abundant alternative prey for foxes. Overall, the positive associations
534 indicate that these species can tolerate high arctic fox densities likely because they can
535 effectively defend their nest and often use islet to reduce predation risk (Beardsell et
536 al., 2025; Beaudoin, 2025; Corbeil-Robitaille et al., 2024). These potential mechanisms
537 illustrate how abiotic constraints (snowmelt timing) can rapidly propagate and create
538 complexity, even within simple food webs.

539 We found limited effect of lemming density on species occurrence. While nest
540 predation release at high lemming densities is well known (Beardsell et al., 2022; Bety
541 et al., 2002; McKinnon et al., 2014), the reduction in predation rates it induces (0.5-1
542 fold reduction; Beardsell et al., 2022; McKinnon et al., 2014) is small compared to the
543 sharp increase driven by fox numerical response near the goose colony (up to six-fold;
544 Dulude-de Broin et al., 2023). Our monitoring was based on species presence–absence

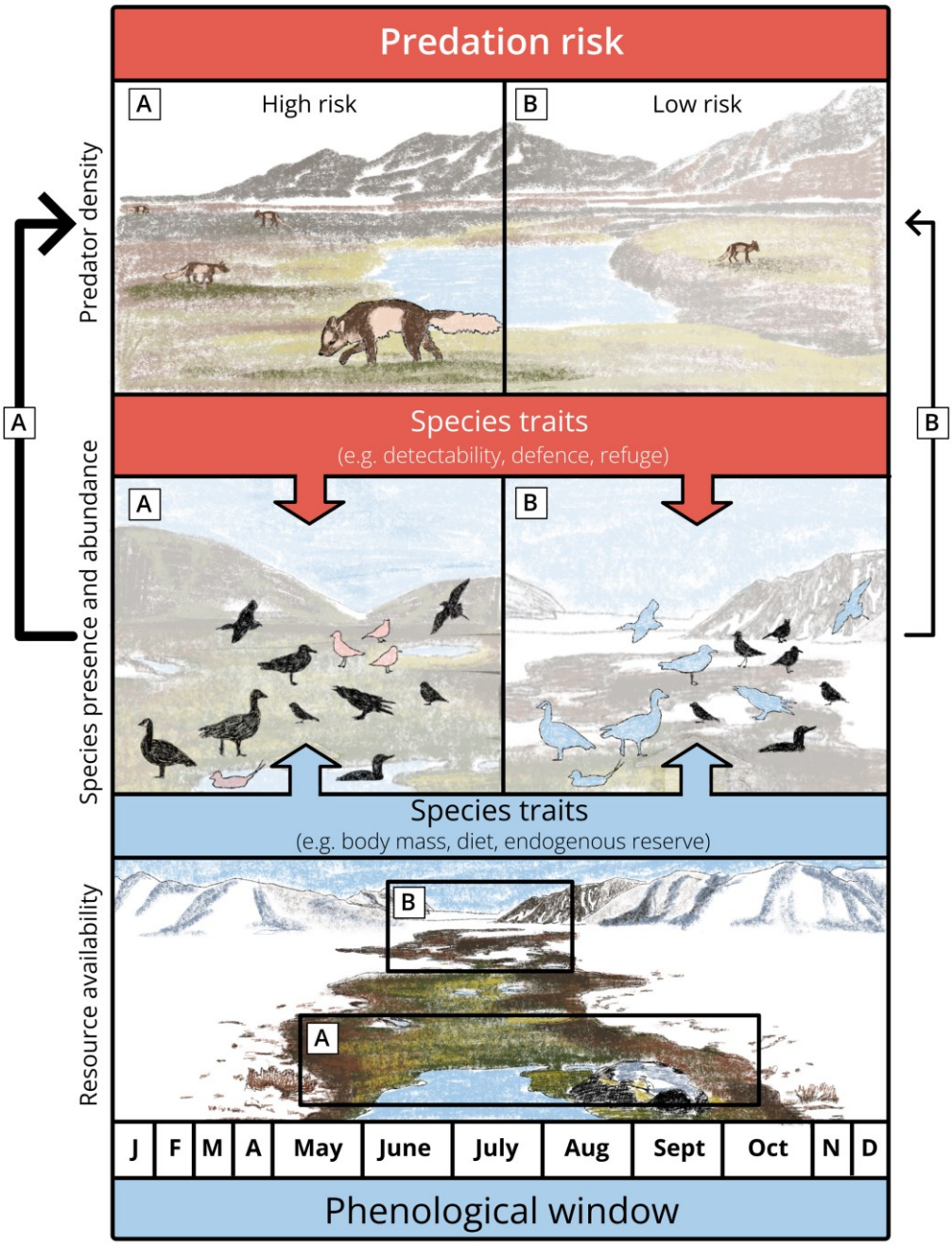
along transects or around lake shores rather than abundance, which may have limited our ability to detect such smaller predator release at high lemming density.

In our study system, the snow goose colony strongly amplified predation pressure, which helped assess how variation in predation risk influence species occurrence across the landscape. As highlighted by our results, early snowmelt was necessary for the establishment of such a colony. However, not all early snowmelt areas would experience the same level of predator density in the absence of snow geese. Still, even in the absence of the goose colony, the relative occurrence of other nesting species indicates that combined prey biomass could be higher in early snowmelt areas (e.g. cackling goose, gull, loon, plover, jaeger). Early snowmelt could also promote predator access to prey sheltered by the snow pack, such as lemmings (Duchesne et al., 2011). Together, the increased prey availability driven by snowmelt timing may positively influence predator density.

Proposed framework

We propose that, once biogeographic constraints are considered, the phenological window of resource availability acts as a secondary ecological filter shaping community structure, setting the stage for a third filter driven by predation (Figure 6). Together, these interacting filters shape the occurrence and relative abundance of nesting species according to their traits, particularly body mass. In late snowmelt areas, the short breeding window limits opportunities for successful reproduction, excluding larger species that require more time and energy to complete their breeding cycle. In contrast, early snowmelt areas may support more species, including large-bodied and colonial herbivores, which contribute to a higher overall prey biomass. Elevated prey biomass can in turn support greater densities of predators, such as arctic foxes, resulting in stronger predation pressure. This predation pressure further shapes community composition. However, not all species are equally affected by predation, and its influence should also be modulated by species traits. Our results indicate that occurrences of large species that can defend their nest, and very small species that can reduce detection, were less affected by predation. In contrast, those of intermediate body size appeared the most vulnerable, being both unable to defend their nest and highly detectable by predators. We would therefore expect early snowmelt areas to be characterised by larger species, higher overall prey biomass, longer food chain length

578 and less vulnerable species, while late snowmelt areas would host species that are more
579 vulnerable to predation but less affected by the timing and duration of food resources
580 availability. This framework offers opportunities for hypothesis testing in arctic and
581 other seasonal study systems.



582

583 **Figure 6** Conceptual model illustrating how phenological constraints and predation
584 shape community composition. Early snowmelt sites (A) allow a longer period of
585 resource availability that can support a broad range of breeding species including those

with large body size. This results in higher overall prey biomass than later snowmelt areas, which in turn sustains more predators. Predation then acts as an additional ecological filter, excluding the most vulnerable species (in red) or reducing their abundance. In contrast, sites with shorter phenological windows (B) exclude larger species (in blue), but still offer sufficient resources for smaller species. These smaller species, including those that are more vulnerable to predation, may persist in late snowmelt areas because the absence of larger species reduces predator densities.

Conclusion

Our study demonstrates that both the timing of snowmelt, a variable strongly associated with the duration of primary production, and predation act as key ecological filters shaping avian communities in the Arctic tundra. By linking species responses to environmental cues and predation with body mass, we show that the timing and duration of resource availability can impose sharp constraints on breeding opportunities especially for larger species, while intermediate body size species appear more vulnerable to predation. These ideas may extend more broadly to both terrestrial and aquatic ecosystems, providing a framework for understanding how seasonal constraints on primary production can propagate through food webs via biotic interactions and shape ecological communities.

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Conflict of Interest

None.

Author Contributions

Conceptualization: FDB, PL, JB, Formal analysis: FDB, Data curation: FDB, ED, MBB, Visualization: FDB, ED, JB, Writing – original draft: FDB, Writing – review & editing: FDB, PL, ED, MBB, GG, DB, DG, SG, AD, JB, Funding acquisition: PL, GG, DB, JB, Supervision: PL, JB

Data availability

Data and code will be published in a public repository upon manuscript acceptance.

References

Altermatt, F. (2010). Tell me what you eat and I'll tell you when you fly: Diet can predict phenological changes in response to climate change. *Ecology Letters*, *13*(12), 1475–1484. https://doi.org/10.1111/j.1461-0248.2010.01534.x

Anderson, H. B., Madsen, J., Fuglei, E., Jensen, G. H., Woodin, S. J., & van der Wal, R. (2015). The dilemma of where to nest: influence of spring snow cover, food proximity and predator abundance on reproductive success of an arctic-breeding migratory herbivore is dependent on nesting habitat choice. *Polar Biology*, *38*(2), 153–162. https://doi.org/10.1007/s00300-014-1574-y

Beardsell, A., Berteaux, D., Dulude-De Broin, F., Gauthier, G., Clermont, J., Gravel, D., & Bêty, J. (2023). Predator-mediated interactions through changes in predator home range size can lead to local prey exclusion. *Proceedings of the Royal Society B: Biological Sciences*, *290*, 20231154. https://doi.org/10.1098/rspb.2023.1154

Beardsell, A., Dulude-de Broin, F., Gauthier, G., Gravel, D., Legagneux, P., DeLong, J., Berteaux, D., & Bety, J. (2025). Integrating predator energetic balance, risk-taking behavior and microhabitat in functional response to untangle indirect interactions in a multispecies vertebrate community. *Accepted with Minor Revisions in Functional Ecology*.

Beardsell, A., Gravel, D., Clermont, J., Berteaux, D., Gauthier, G., & Bêty, J. (2021). Multi-species mechanistic model of functional response provides new insights into predator-mediated interactions in a vertebrate community. *BioRxiv*, *October*, 1–34. https://doi.org/10.1101/2021.10.22.464289

Beardsell, A., Gravel, D., Clermont, J., Berteaux, D., Gauthier, G., & Bêty, J. (2022). A mechanistic model of functional response provides new insights into indirect interactions among arctic tundra prey. *Ecology*, *103*(8), 1–16. https://doi.org/10.1002/ecy.3734

Beaudoin, M. (2025). *Impact des îlots-refuges et des proies disponibles sur le risque de prédation des nids par le renard arctique*. Université du Québec à Rimouski.

Berteaux, D. (2020). Data from: Arctic fox Bylot - Argos tracking. *Movebank Data Repository*. https://doi.org/10.5441/001/1.3gg33bd4

Berteaux, D. (2021). Data from: Arctic fox Bylot - GPS-UHF tracking. *Movebank Data Repository*. https://doi.org/https://www.movebank.org/panel_embedded_movebank_webapp?study_id=1241071371

Bety, J., Gauthier, G., Korpimaki, E., & Giroux, J.-F. (2002). Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *Journal of Animal Ecology*, *71*(1), 88–98. https://doi.org/10.1046/j.0021-8790.2001.00581.x

Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, *24*(1), 28–34. https://doi.org/10.1111/j.1365-2435.2009.01618.x

Brown, J., Gillooly, J. F., Allen, A. P., Savage, V. M., & Geoffrey, B. W. (2004). Towards a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.4324/9781003187028-2

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach.* (Springer (ed.); 2nd editio). Springer.

CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology

reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(13), 4916–4921. https://doi.org/10.1073/pnas.1323073111

Clermont, J., Grenier-Potvin, A., Duchesne, É., Couchoux, C., Dulude-de Broin, F., Beardsell, A., Bêty, J., & Berteaux, D. (2021). The predator activity landscape predicts the anti-predator behavior and distribution of prey in a tundra community. *Ecosphere*, *12*(12). https://doi.org/10.1002/ecs2.3858

Corbeil-Robitaille, M.-Z., Duchesne, É., Fortier, D., Kinnard, C., & Bêty, J. (2024). Linking geomorphological processes and wildlife microhabitat selection : nesting birds select refuges generated by permafrost degradation in the Arctic. *Biogeosciences*, *21*, 3401–3423.

Davis, R. A. (1972). A comparative study of the use of habitat by Arctic loons and Red-throated Loons. *Digitized Thesis*, 288.

Diamond, S. E., Frame, A. M., Martin, R. A., & Buckley, L. B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, *92*(5), 1005–1012. https://doi.org/10.1890/10-1594.1

Dickey, M. H., Gauthier, G., & Cadieux, M. C. (2008). Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology*, *14*(9), 1973–1985. https://doi.org/10.1111/j.1365-2486.2008.01622.x

Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., Martimort, P., Meygret, A., Spoto, F., Sy, O., Marchese, F., & Bargellini, P. (2012). Sentinel-2: ESA's Optical High-Resolution Mission for GMES Operational Services. *Remote Sensing of Environment*, *120*, 25–36. https://doi.org/10.1016/j.rse.2011.11.026

Duchesne, D., Gauthier, G., & Berteaux, D. (2011). Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia*, *167*(4), 967–980. https://doi.org/10.1007/s00442-011-2045-6

Duchesne, É., Lamarre, J., Gauthier, G., Berteaux, D., Gravel, D., & Bêty, J. (2021). Variable strength of predator-mediated effects on species occurrence in an arctic terrestrial vertebrate community. *Ecography*, 1–13. https://doi.org/10.1111/ecog.05760

Dulude-de Broin, F., Clermont, J., Beardsell, A., Ouellet, L. P., Legagneux, P., Bêty, J., & Berteaux, D. (2023). Predator home range size mediates indirect interactions between prey species in an arctic vertebrate community. *Journal of Animal Ecology*, *92*(12), 2373–2385. https://doi.org/10.1111/1365-2656.14017

Dulude-de Broin, F., Clermont, J., Beardsell, A., Ouellet, L.-P., Legagneux, P., Bêty, J., & Berteaux, D. (2023). Data from: Predator home range size mediates indirect interactions between prey species in an arctic vertebrate community. *Dryad Data Repository*. https://doi.org/10.5061/dryad.f1vhhmh30

Durant, J. M., Hjermann, D., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, *33*(3), 271–283. https://doi.org/10.3354/cr033271

Etchart, L., Lecomte, N., Dechaume-Moncharmont, F. X., Lang, J., Moreau, J., Pagnon, T., Schmidt, N. M., Sittler, B., Bollache, L., & Gilg, O. (2025). Snowmelt and laying date impact the parental care strategy of a high-Arctic shorebird. *Scientific Reports*, *15*(1), 1–11. https://doi.org/10.1038/s41598-025-02318-y

Fauteux, D., Gauthier, G., & Berteaux, D. (2015). Seasonal demography of a cyclic lemming population in the Canadian Arctic. *Journal of Animal Ecology*, *84*(5),

1412–1422. https://doi.org/10.1111/1365-2656.12385
Flemming, S. A., Smith, P. A., Rausch, J., & Nol, E. (2019). Broad-scale changes in tundra-nesting bird abundance in response to hyperabundant geese. *Ecosphere*, *10*(7). https://doi.org/10.1002/ecs2.2785
Fretwell, S. D., & Barach, A. L. (1977). The Regulation of Plant Communities by the Food Chains Exploiting Them. *Perspectives in Biology and Medicine*, *20*(2), 169–185. https://doi.org/10.1353/pbm.1977.0087
Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., Legagneux, P., & Cadieux, M.-C. (2011). The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. *Écoscience*, *18*(3), 223–235. https://doi.org/10.2980/18-3-3453
Gauthier, G., Legagneux, P., Valiquette, M. A., Cadieux, M. C., & Therrien, J. F. (2015). Diet and reproductive success of an Arctic generalist predator: Interplay between variations in prey abundance, nest site location, and intraguild predation. *Auk*, *132*(3), 735–747. https://doi.org/10.1642/AUK-14-273.1
Giroux, M. A., Berteaux, D., Lecomte, N., Gauthier, G., Szor, G., & Bêty, J. (2012). Benefiting from a migratory prey: Spatio-temporal patterns in allochthonous subsidization of an arctic predator. *Journal of Animal Ecology*, *81*(3), 533–542. https://doi.org/10.1111/j.1365-2656.2011.01944.x
Godsoe, W., Jankowski, J., Holt, R. D., & Gravel, D. (2017). Integrating Biogeography with Contemporary Niche Theory. *Trends in Ecology and Evolution*, *32*(7), 488–499. https://doi.org/10.1016/j.tree.2017.03.008
Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods in Ecology and Evolution*, *4*(11), 1083–1090. https://doi.org/10.1111/2041-210X.12103
Hall, D. K., & Riggs, G. A. (2021). *MODIS/Terra Snow Cover Daily L3 Global 500m SIN Grid, Version 61*. NASA National Snow and Ice Data Center Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MOD10A1.061
Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Conseil International Pour l'Exploration de La Mer*, *20*, 228.
Humphries, M. M., Studd, E. K., Menzies, A. K., & Boutin, S. (2017). To Everything There Is a Season: Summer-to-Winter Food Webs and the Functional Traits of Keystone Species. *Integrative and Comparative Biology*, *57*(5), 961–976. https://doi.org/10.1093/icb/icx119
Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds of Animals ? Published by : The University of Chicago Press for The American Society of Naturalists Stable URL : https://www.jstor.org/stable/2458768 REFERENCES Linked references are available on JSTO. *The American Naturalist*, *93*(870), 145–159.
Juhasz, C. C., Shipley, B., Gauthier, G., Berteaux, D., & Lecomte, N. (2020). Direct and indirect effects of regional and local climatic factors on trophic interactions in the Arctic tundra. *Journal of Animal Ecology*, *89*(3), 704–715. https://doi.org/10.1111/1365-2656.13104
Kerby, J., & Post, E. (2013). Capital and income breeding traits differentiate trophic match-mismatch dynamics in large herbivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624). https://doi.org/10.1098/rstb.2012.0484
Keyser, S. R., Fink, D., Gudex-Cross, D., Radeloff, V. C., Pauli, J. N., & Zuckerberg, B. (2022). Snow cover dynamics: an overlooked yet important feature of winter

bird occurrence and abundance across the United States. *Ecography*, 1–16. https://doi.org/10.1111/ecog.06378

Kleiber, M. (1932). Body size and metabolism. *Hilgardia*, *6*(11), 315–353. https://doi.org/10.3733/hilg.v06n11p315

Lai, S., Bêty, J., & Berteaux, D. (2015). Spatio-temporal hotspots of satellite- tracked arctic foxes reveal a large detection range in a mammalian predator. *Movement Ecology*, *3*(1), 1–10. https://doi.org/10.1186/s40462-015-0065-2

Lamarre, J.-F., Legagneux, P., Gauthier, G., Reed, E. T., & Bêty, J. (2017). Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. *Ecosphere*, *8*(5), e01788. https://doi.org/10.1002/ecs2.1788

Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M.-C., Bilodeau, F., Bolduc, E., McKinnon, L., Tarroux, A., Therrien, J.-F., Morissette, L., & Krebs, C. J. (2012). Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology*, *93*(7), 1707–1716. https://doi.org/10.1890/11-1973.1

Liebezeit, J. R., Gurney, K. E. B., Budde, M., Zack, S., & Ward, D. (2014). Phenological advancement in arctic bird species: Relative importance of snow melt and ecological factors. *Polar Biology*, *37*(9), 1309–1320. https://doi.org/10.1007/s00300-014-1522-x

Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, *23*(4), 399–417.

McKinnon, L., Berteaux, D., & Bêty, J. (2014). Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. *Auk*, *131*(4), 619–628. https://doi.org/10.1642/AUK-13-154.1

Mckinnon, L., Berteaux, D., Gauthier, G., & Bêty, J. (2013). Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, *122*(7), 1042–1048. https://doi.org/10.1111/j.1600-0706.2012.20708.x

McKinnon, L., & Bêty, J. (2009). Effect of camera monitoring on survival rates of High-Arctic shorebird nests. *Journal of Field Ornithology*, *80*(3), 280–288. https://doi.org/10.1111/j.1557-9263.2009.00231.x

McNamara, J. M., & Houston, A. I. (2008). Optimal annual routines: Behaviour in the context of physiology and ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 301–319. https://doi.org/10.1098/rstb.2007.2141

Montgomerie, R., & Lyon, B. (2020). Snow Bunting (Plectrophenax nivalis). In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), *Birds of the World*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.snobun.01

Niittynen, P., Heikkinen, R. K., & Luoto, M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. *Nature Climate Change*, *8*(11), 997–1001. https://doi.org/10.1038/s41558-018-0311-x

Niittynen, P., Heikkinen, R. K., & Luoto, M. (2020). Decreasing snow cover alters functional composition and diversity of Arctic tundra. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(35), 21480–21487. https://doi.org/10.1073/pnas.2001254117

Niittynen, P., & Luoto, M. (2018). The importance of snow in species distribution models of arctic vegetation. *Ecography*, *41*(6), 1024–1037. https://doi.org/10.1111/ecog.03348

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, *118*(2),

240–261.
Peters, R. H. (1986). *The ecological implications of body size* (Vol. 2). Cambridge university press.
Ponti, R., & Sannolo, M. (2023). The importance of including phenology when modelling species ecological niche. *Ecography*, *2023*(4), 1–15. https://doi.org/10.1111/ecog.06143
Portalier, S. M. J., Fussmann, G. F., Loreau, M., & Cherif, M. (2019). The mechanics of predator–prey interactions: First principles of physics predict predator–prey size ratios. *Functional Ecology*, *33*(2), 323–334. https://doi.org/10.1111/1365-2435.13254
Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1501), 2369–2373. https://doi.org/10.1098/rstb.2007.2207
Riede, J. O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C. R., & Jonsson, T. (2011). Stepping in Elton's footprints: A general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, *14*(2), 169–178. https://doi.org/10.1111/j.1461-0248.2010.01568.x
Rixen, C., Høye, T. T., Macek, P., Aerts, R., Alatalo, J. M., Jill, T., Arnold, P. A., Barrio, I. C., Bjerke, J. W., Björkman, M. P., Blok, D., Blume-werry, G., Boike, J., Bokhorst, S., Carbognani, M., Christiansen, C. T., Convey, P., Cooper, E. J., Cornelissen, J. H. C., … Zong, S. (2022). *Winters are changing : snow effects on Arctic and*. *608*(February), 572–608.
Sæther, B.-E. (1987). The Influence of Body Weight on the Covariation between Reproductive Traits in European Birds. *Oikos*, *48*(1), 79–88.
Saulnier-Talbot, É., Duchesne, É., Antoniades, D., Arseneault, D., Barnard, C., Berteaux, D., Bhiry, N., Bouchard, F., Boudreau, S., Cazelles, K., Comte, J., Corbeil-Robitaille, M.-Z., Côté, S. D., Couture, R.-M., de Lafontaine, G., Domine, F., Fauteux, D., Fortier, D., Garneau, M., … Bêty, J. (2024). Expert elicitation of state shifts and divergent sensitivities to climate warming across northern ecosystems. *Communications Earth & Environment*, *5*(1), 624. https://doi.org/10.1038/s43247-024-01791-z
Schmidt, N. M., Reneerkens, J., Christensen, J. H., Olesen, M., & Roslin, T. (2019). An ecosystem-wide reproductive failure with more snow in the Arctic. *PLoS Biology*, *17*(10), 1–8. https://doi.org/10.1371/journal.pbio.3000392
Schneider, D. W., & Frost, T. M. (1996). Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society*, *15*(1), 64–86. https://doi.org/10.2307/1467433
Seyer, Y., Gauthier, G., Bêty, J., Therrien, J. F., Legagneux, P., & Lecomte, N. (2023). Local food availability and nonbreeding carry-over effects affect breeding propensity and success of a tundra-nesting predator, the Long-tailed Jaeger. *Ornithology*, *140*(4). https://doi.org/10.1093/ornithology/ukad032
Slatyer, R. A., Umbers, K. D. L., & Arnold, P. A. (2022). Ecological responses to variation in seasonal snow cover. *Conservation Biology*, *36*(1). https://doi.org/10.1111/cobi.13727
Smith, P. A., Gilchrist, H. G., Forbes, M. R., Martin, J. L., & Allard, K. (2010). Inter-annual variation in the breeding chronology of arctic shorebirds: Effects of weather, snow melt and predators. *Journal of Avian Biology*, *41*(3), 292–304. https://doi.org/10.1111/j.1600-048X.2009.04815.x
Smith, P. A., Gilchrist, H. G., & Smith, J. N. M. (2007). Effects of nest habitat, food,

and parental behavior on shorebird nest success. *Condor*, *109*(1), 15–31. https://doi.org/10.1650/0010-5422(2007)109[15:EONHFA]2.0.CO;2

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology and Evolution*, *3*(6), 879–885. https://doi.org/10.1038/s41559-019-0880-8

Walker, D. A., Billings, W. D., & De Molenaar, J. G. (2001). Snow-Vegetation Interactions in Tundra Environments. *Snow Ecology*, *266*, 266–324.

Williams, C. T., Klaassen, M., Barnes, B. M., Buck, C. L., Arnold, W., Giroud, S., Vetter, S. G., & Ruf, T. (2017). Seasonal reproductive tactics: annual timing and the capital-to-income breeder continuum. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1734), 20160250. https://doi.org/10.1098/rstb.2016.0250

Supporting Information for

Timing matters: phenological constraints and predation shape Arctic community structure

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1. Additional methods

1.1 Species habitat, diet and vulnerability to predation

Shorebirds and passerines (i.e. Lapland longspur (28g), snow bunting (39g), White-rumped sandpiper (45g), Baird's sandpiper (50g), American golden plover (158g)) nest in mesic to xeric tundra and feed primarily on arthropods along with seeds and berries (Baker, 1977; Leung et al., 2018; Montgomerie & Lyon, 2020). Long-tailed jaegers (281g) also nest in these habitats and, during the breeding period, mainly feed on lemmings but also on passerines and shorebirds chicks, arthropods, and berries (Andersson, 1976; Seyer et al., 2020). In contrast, water-associated species such as the cackling goose (1889g), glaucous gull (1975g), and red-throated loon (1855g) nest around lakes and wetlands. Cackling geese feed mainly on vegetation, gulls are opportunistic predators and scavengers eating fish, invertebrates and eggs of other nesting birds (Gauthier et al., 2015), and loons primarily consume fish and invertebrates (Davis, 1972). Snow geese (2450 g) are colonial nesters that occupy both mesic tundra and wetlands, often concentrating in large colonies but also nesting individually away from the colony center. Their diet consists mainly of vegetation such as grasses, sedges, and forbs. Artic fox (2500g) predation is the main terrestrial predator of all all these species (Gauthier et al., 2011; McKinnon & Bêty, 2009). Ground-nesting shorebirds and passerines are highly vulnerable to arctic fox predation, whereas larger and water-associated birds have partial defences and may benefit from nesting habitat that reduces fox foraging effort or success (Corbeil-Robitaille et al., 2024).

1.2 Delayed field work in 2024

In 2024, a helicopter crash delayed all field work activities, and sampling exceptionally occurred from July 21 to August 1, a period that overlaps brood rearing for many species. Although the scale of the analysis exceeds the typical movement range of most

952 focal species during brood rearing, snow geese often engage in long-distance
953 movements during this period (Mainguy et al., 2006) and were excluded in 2024. Data
954 for snow bunting and white-rumped sandpiper from 2024 were also excluded because
955 both species become much more detectable during brood rearing due to the presence of
956 large fledglings, and because of the conspicuous distraction displays of brood-rearing
957 white-rumped sandpipers. To further reduce potential bias on that year, we deployed
958 field teams simultaneously across the study areas and completed transects within a
959 condensed 11-day period. We also confirmed that the direction and magnitude of results
960 were similar when excluding that year from the analyses (Appendix S1, Fig. S9).

961 **1.3 Criteria to assess breeding status on transect**

962 Reproductive status of individuals detected on transects was determined from their
963 behaviour. For plovers and sandpipers, distraction displays (broken wing, rodent run)
964 and insistent calls indicated nesting individuals (Lamarre et al., 2017), with status
965 confirmed by approaching the bird. Individuals that did not react or were foraging,
966 flying by, or resting, were considered non-breeders. Jaegers observed as one or two
967 individuals along a transect were classified as nesting pair, as they typically leave their
968 territory if breeding fails, while non-incubating groups of three or more were considered
969 non-breeders (Andersson, 1976). Snow geese were considered breeders when near a
970 nest and non-breeders when in large groups or without a nest in sight. All detected
971 Lapland longspurs, horned larks, and snow buntings were assumed to be nesting, as
972 they exhibited singing, display flights, or alarm calls when approached (Drury 1961,
973 Hunt et al. 1995).

1.4 Home range analysis

The distribution of fox home range sizes was clearly bimodal with a large part of the variation explained by the presence of the goose colony (marginal R^2=0.20, conditional R^2= 0.46, n=248, from a linear mixed-effects model with home range size as the response variable, den location (inside vs outside of the colony) as fixed effect, and year as random effect). We therefore classified transects and lakes into two categories of predation risk to reflect this distribution. Using a Gaussian Mixture Model fitted with the mclust R package, we identified two distinct groups separating transects and lakes located within smaller home ranges (11 to 16.35 km²) corresponding to areas with high fox density, and larger home ranges (16.35 to 31 km²) corresponding to areas with lower fox density. In the smaller home range group, 85% of transects and lakes were within home ranges smaller than 15 km², while in the larger home range group, 85% were in home range larger than 18 km². To further validate our classification, we compared the occurrence of foraging foxes on transects in large and small home range, corresponding to low and high fox densities respectively. Occurrence of foraging foxes on transect were 4.2 times higher in areas of high fox densities compared to areas with low fox densities (Figure S1).

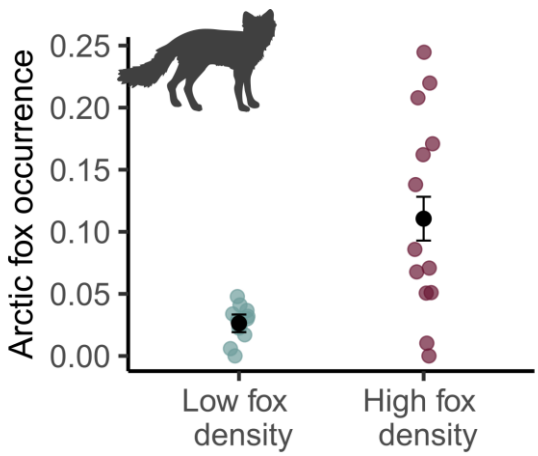

Figure S1. Arctic fox occurrence on transects in areas classified as low and high fox density on Bylot Island, Nunavut (2010–2024). Black dots and error bars represent

average occurrence with 95% confidence intervals based on a binomial model with year and transect ID as random intercepts. Colored dots represent the proportion of fox sightings based on all transects for each fox density category in each year (n=30).

1.5 Number of surveys with sighting per species

Among nesting species, we recorded 3579 transect-years with Lapland longspurs, 1585 with snow geese, 1096 with American golden plovers, 629 with glaucous gulls, 530 with long-tailed jaegers, 468 with horned larks, 303 with Baird's sandpipers, 296 with white-rumped sandpipers, 244 with snow buntings. Around lakes, we recorded 124 lake-years with cackling goose nests, 54 with red-throated loon and 37 with glaucous gulls. We recorded the presence of foraging arctic fox on 185 transects.

2. Enhanced snowmelt data from the integration of MODIS and Sentinel-2

To combine MODIS and Sentinel-2 derived products, we first extracted MODIS and Sentinel-2 data (section 2.1) and assessed the consistency of snowmelt date estimates from each method and satellite platform (section 2.2). Next, we calculated the difference in snowmelt dates between each MODIS pixel and all corresponding Sentinel-2 for the years when both datasets were available (n=5; 2018-2023) to generate a correction raster (section 2.3). We then added the median Sentinel-2-MODIS difference at each pixel to MODIS derived snowmelt rasters to generate a final 20 m resolution snowmelt map of all years. Finally, we validated our enhanced MODIS product against the original Sentinel-2 snowmelt maps for years when Sentinel-2 products were available (section 2.4).

2.1. Sentinel-2 and MODIS derived snow products

We obtained Sentinel-2 derived snowmelt dates (years 2017-2023) from the Sentinel-2 Level 3A snow product developed by THEIA (https://www.theia-land.fr/ces-cryosphere/neige/). This product uses all available Sentinel-2 images to track snow

cover at a 20 m resolution and fills gaps caused by clouds or missing images using temporal interpolation (Barrou Dumont et al., 2025). Each image is analyzed to classify every pixel as either snow-covered or snow-free based on the Normalized Difference Snow Index (NDSI). The interpolated time series of these classifications is then used to estimate the snowmelt date, defined as the last day of the longest uninterrupted snow-covered period within the hydrological year. Compared to in situ measurements in the Alps and the Pyrenees, the method yielded a mean absolute error of 8 days, an root mean square error (RMSE) of 23 days, and a bias of -1 day (Barrou Dumont et al., 2025). Given the shorter Sentinel-2 revisit time in the high arctic (1 day) compared to these mid-latitude regions (5 days), errors are expected to be lower within our study area.

We obtained MODIS derived snowmelt dates (years 2010-2024) using MOD10A1 snow cover product Version 61 (Hall & Riggs, 2021). To determine snowmelt dates for each year, we analyzed the snow cover time series for each pixel from March 1 to August 31. A pixel was considered snow-free for values <50, and the snowmelt date was defined as the first snow-free day followed by at least five consecutive snow-free days. To account for brief spring snowfall events that melt shortly after precipitation, we allowed a single day within this five-day period to exceed 50. Gaps in the time series, caused by clouds or missing imagery, were filled using linear interpolation. Detailed information on the MOD10A1 Snow Cover Product, Version 61, is provided in Hall et al. (2019).

2.2 Validation of consistency between Sentinel-2 and MODIS derived snowmelt dates

We evaluated the relationship between snowmelt dates derived from MODIS (lower spatial, higher temporal resolution) and Sentinel-2 imagery (higher spatial, lower temporal resolution). Sentinel-2 maps were first aggregated to MODIS resolution (500 × 500 m) by averaging all corresponding high-resolution (20 × 20 m) Sentinel-2 pixels within each coarser pixel (Figure S2). This created a new 500 m x 500 m raster where each pixel reflects the aggregated value of the finer-scale data.

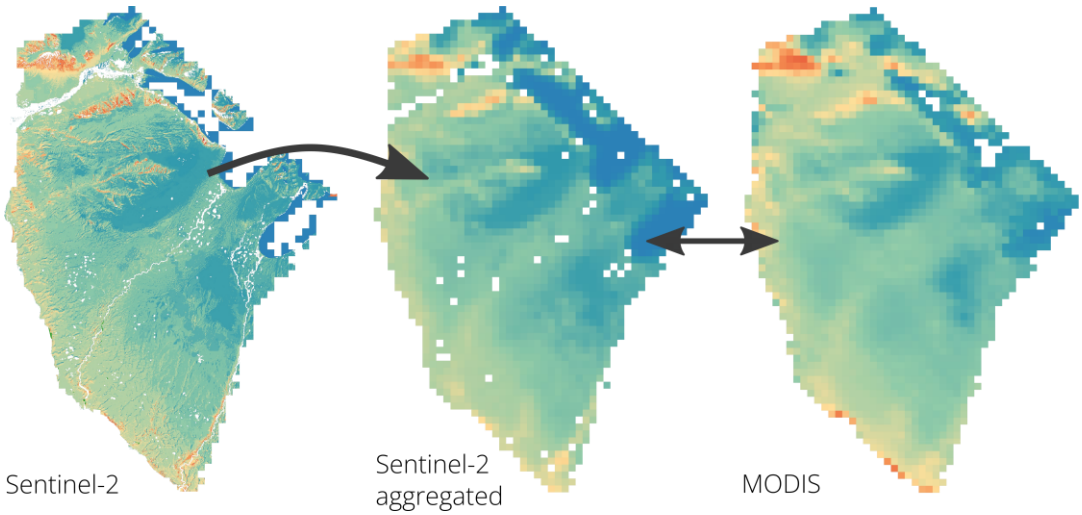

Figure S2 Comparison of Sentinel-2 and MODIS snow products for 2020. The Sentinel-2 map was aggregated to match MODIS spatial resolution (500 × 500 m) by averaging all corresponding high-resolution (20 × 20 m) Sentinel-2 pixels within each coarser pixel.

We then performed a pixel-by-pixel comparison of snowmelt dates at the 500 x 500 m resolution across five years (2018–2023) where both datasets were available. Snowmelt dates derived from Sentinel-2 and MODIS were highly correlated for all years with overlapping data (Figure S3; all slopes = 1.0, $R^2 > 0.89$, n=1618). The strong agreement between the two datasets, derived from different satellite platforms and analytical methods, suggests that snowmelt date estimates are consistent and support the combination of these snow products.

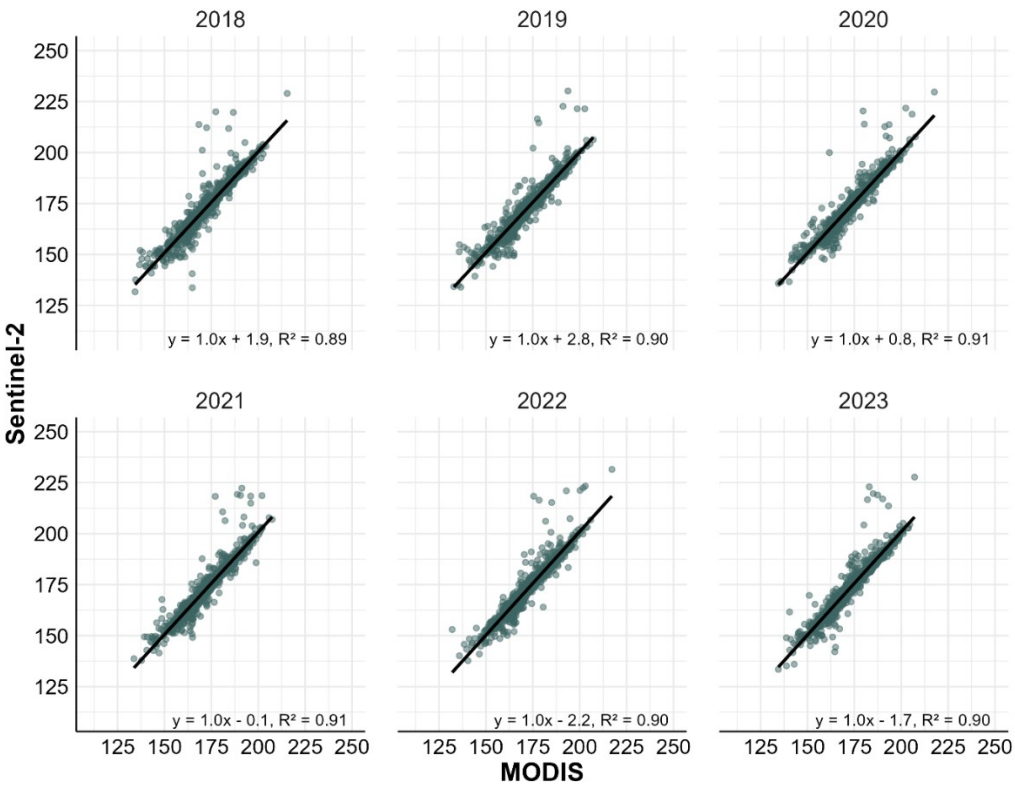

Figure S3 Relationship between snowmelt dates derived from Sentinel-2 and MODIS snow products. Snowmelt dates were compared on a pixel-by-pixel basis after aggregation of Sentinel-2 snowmelt data to match MODIS resolution. Linear model sample size: n=1618.

2.3 Creation of an adjustment raster to upscale MODIS product

To enhance the spatial resolution of MODIS snow products, we generated a correction raster from the difference between MODIS and Sentinel-2 derived snow rasters (Figure S4). For each 20 x 20 m pixel in the study area, we subtracted the value of the MODIS derived snowmelt date to the Sentinel-2 derived snowmelt date. As an illustration, if a large MODIS pixel indicated snowmelt on day 180, corresponding higher-resolution Sentinel-2 pixels within that area might show snowmelt occurring slightly earlier or later such as day 178, 184, or 174, resulting in difference values of –2, +4, and –6 days, respectively. These values were calculated for all 20 x 20 m pixels every year to generate the correction raster for all years when both data sources were available. Most annual differences in snowmelt dates at the 20 x 20 m resolution ranged between -20

and +20 days (figure S5), and interannual repeatability in adjustment values was high (Figure S6). We took the median value across years for each pixel to build the final adjustment raster. Median adjustment values ranged between -10 and + 10 days (Figure S5).

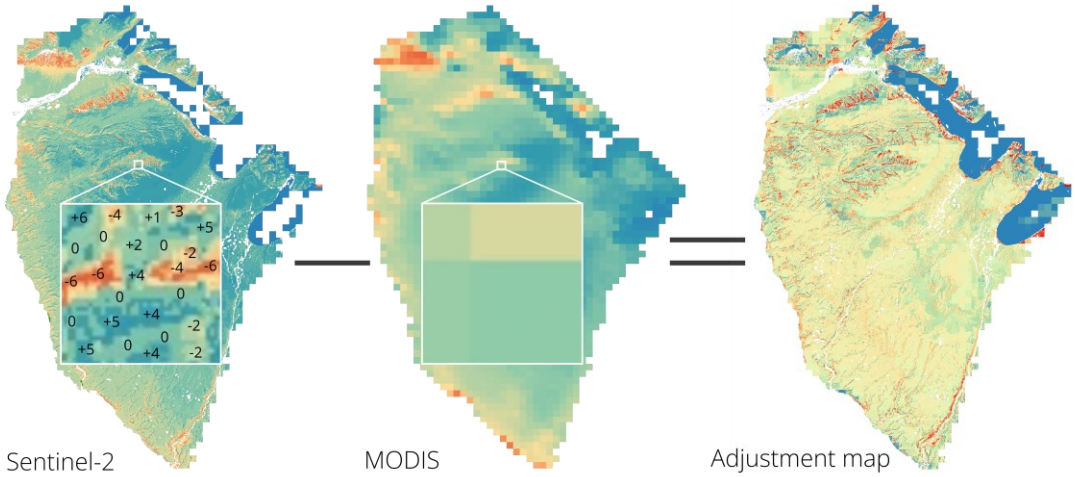

Figure S4 Difference between MODIS snowmelt dates and Sentinel-2 snowmelt dates to create the adjustment raster. The inset illustrates how high-resolution Sentinel-2 pixels differ from the corresponding coarser MODIS pixels. These differences constitute the values of the adjustment map.

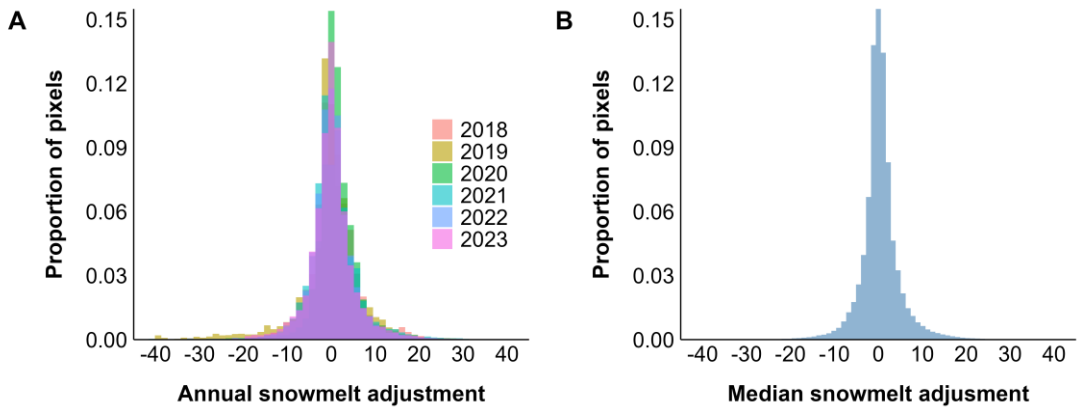

Figure S5 Distribution of snowmelt date adjustment values used to increase the spatial resolution of MODIS-derived snowmelt dates. Adjustment values correspond to the number of days difference between snowmelt estimates from each small Sentinel-2 pixel and coarser overlapping MODIS pixel. Annual adjustment values (A) were calculated for every 20 x 20 m pixel of the study area across all years where both data sources were available. The median difference per pixel (B) was used to create the final adjustment raster.

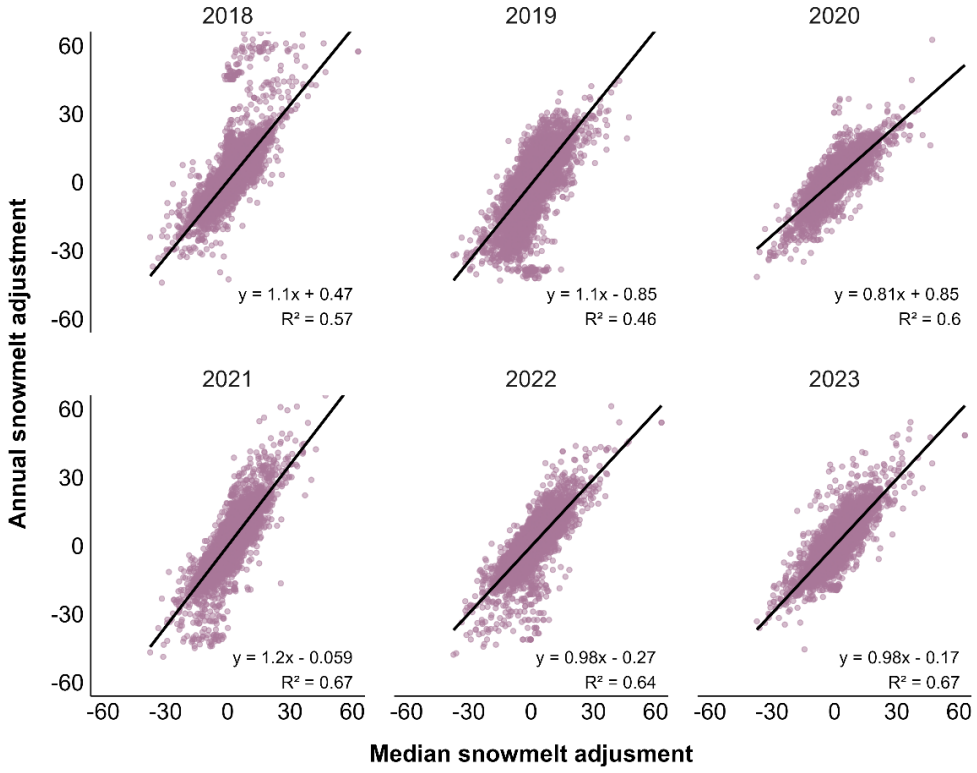

Figure S6 Repeatability in snowmelt adjustment values at the pixel level between Sentinel-2 and MODIS derived snow products. Adjustment values correspond to the number of days difference between snowmelt estimates from each small Sentinel-2 pixel and coarser overlapping MODIS pixel. Individual graphs relate the annual adjustment value to the median adjustment value across all years for the same pixel.

2.4 Adjustment of MODIS-derived snowmelt maps and validation against Sentinel-2

We produced the final snowmelt date maps by adding the adjustment layer to the MODIS-derived product (Figure S7), resulting in 20 m resolution snowmelt maps for all years from 2010 to 2024. To evaluate the accuracy of this hybrid product, we compared it against Sentinel-2 snowmelt maps for the years when both datasets were available (2018–2023). For both layers, we extracted the median snowmelt date within a 150 m buffer on each side of our transects (same as the main analysis). We then assessed the relationship between the enhanced MODIS and Sentinel-2 maps using a linear model (Figure S8-S9). The two products were highly related (Estimate [95% CI] = 0.99 [0.98, 1.00], n = 3298, R^2 = 0.93). The strong agreement is notable given that the adjustment map is the same for all years as it was obtained from median adjustment values. This further suggests that fine-scale spatial patterns in snowmelt timing were consistent across years (as previously shown in section 2.3, Figure S6), allowing accurate adjustment of MODIS data. The approach allowed us to obtain high-resolution and reliable snowmelt date maps for the entire study area across all years.

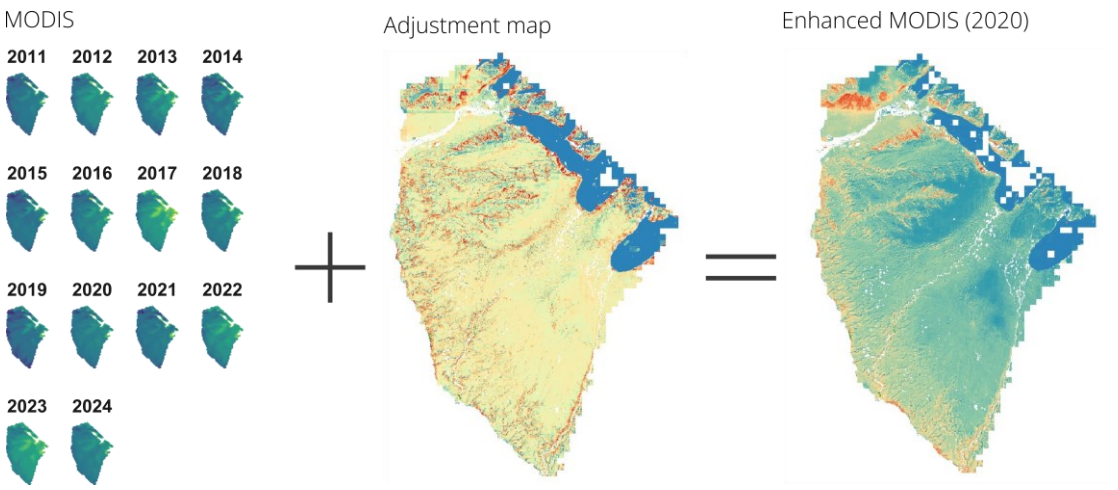

Figure S7 Method used to generate the final snow product used in the study. For each year, we adjusted the MODIS-derived snowmelt map using the adjustment map derived from Sentinel-2 data to obtain a product with a 20-m resolution.

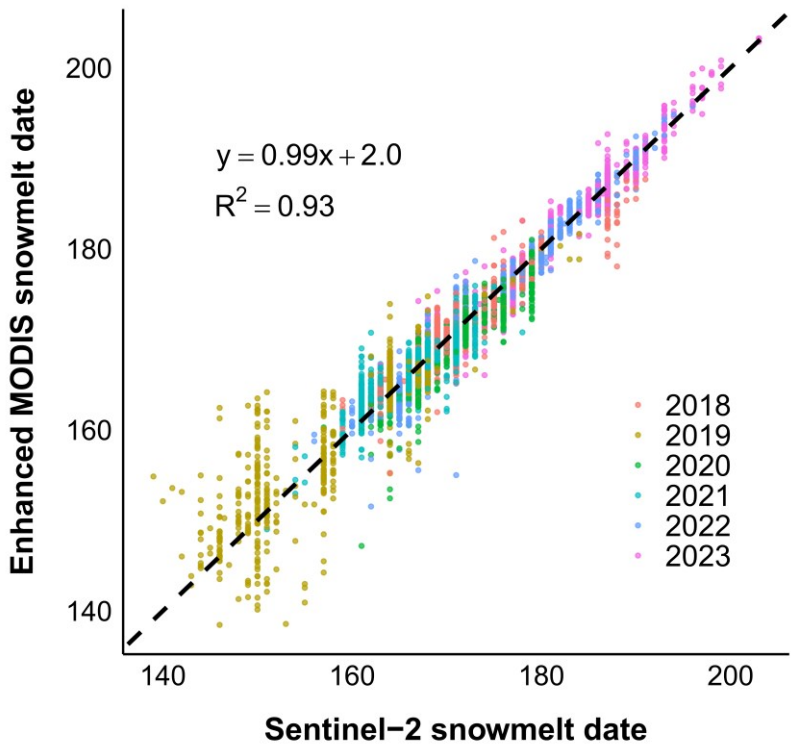

Figure S8 Validation of the snowmelt date derived from the enhanced MODIS snowmelt map against Sentinel-2 data for years with available Sentinel-2 coverage. Each point represents the median snowmelt date for each transect surveyed in the study area every year. The dashed line shows the 1:1 reference line. Dates are day of the year. Linear model sample size: n=3956.

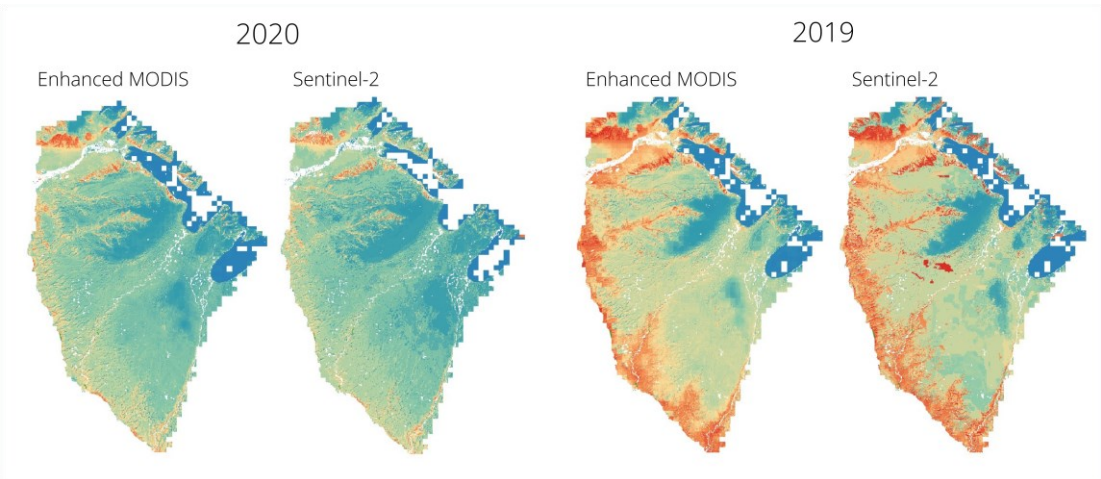

Figure S9 Visual comparison of enhanced MODIS and Sentinel-2–derived snowmelt products for two years with contrasting snowmelt timing, illustrating their consistency.

3. Relationship between the number of snow-free days and snowmelt date

We assessed the relationship between the number of snow-free days and snowmelt date using Sentinel-2 derived products from THEIA between 2018 and 2023. We extracted the median snow-free period (number of days between snowmelt and snow onset) and the median snowmelt date within a 150 m buffer (same as the main analysis) on each side of our 500 m transects. We then used a linear model to evaluate the relationship between the length of the snow-free period and snowmelt date. Snowmelt date was a strong predictor of the number of days without snow (Estimate [95%CI] = –1.05 [–1.08, –1.03], n = 3298, R^2 = 0.65, Figure S10), indicating that in addition to being the primary driver of primary production, snowmelt date is a good indicator of the duration of the snow-free window.

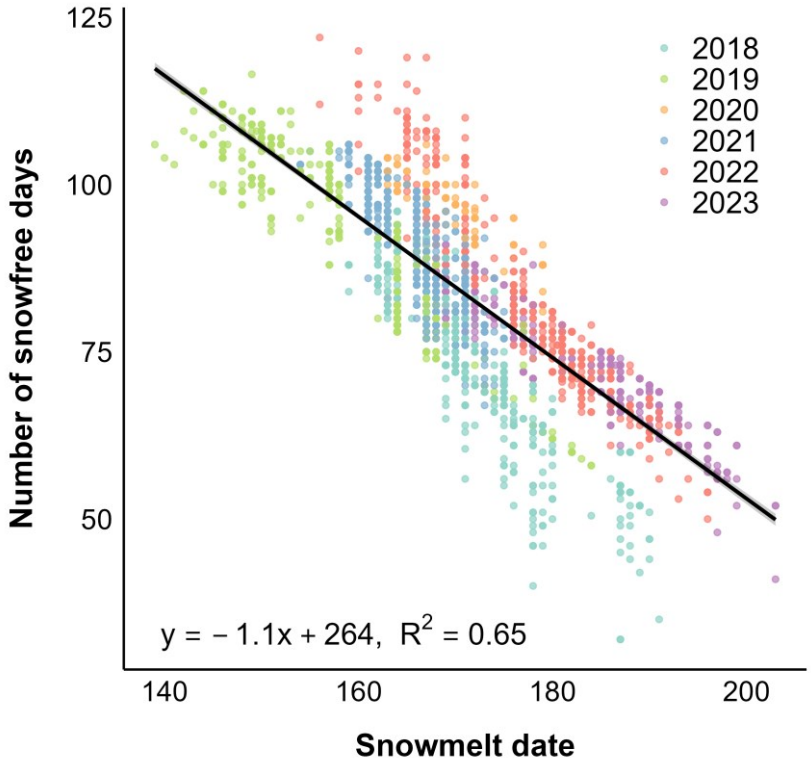

Figure S10 Relationship between snowmelt date and the number of snow-free days around individual transects every year, based on Sentinel-2 derived snow products from THEIA (2018–2023). Linear model sample size: n=3298.

1149 **4. Snowmelt threshold values by species**

Species	Day of year	95% CI	Calendar date (non-leap year)
Greater snow goose	184	183–184	July 3
Cackling goose	179	178–179	June 28
Glaucous gull	180	178–181	June 29
Long-tailed jaeger	180	179–181	June 29
Red-throated loon	189	187–190	July 8
American golden plover	188	187–189	July 7
White-rumped sandpiper	191	186–193	July 10
Baird's sandpiper	192	191–193	July 11
Lapland longspur	197	194–198	July 16
Horned lark	199	196–199	July 18
Snow bunting	201	197–201	July 20

1150

1151 **Table S1.** Snowmelt threshold values for nesting birds on Bylot Island, Nunavut (2010–
1152 2024). Snowmelt threshold corresponds to the last date at which a breeding individual
1153 was sighted. Confidence intervals were obtained through non-parametric bootstrap.
1154
1155

5. Model selection results for all species

A) Lapland longspur

Model	K	LL	ΔAICc	w
Snow + Fox	**7**	**-1531.9**	**0.00**	**0.43**
Snow	**6**	**-1533.6**	**1.37**	**0.22**
Snow + Fox + Lemming	**8**	**-1531.7**	**1.72**	**0.18**
Snow + Lemming	7	-1533.5	3.16	0.09
Snow + Fox*Lemming	9	-1531.7	3.58	0.07
Fox	4	-1670.4	270.96	0.00
Null	3	-1672.3	272.78	0.00

B) Snow bunting

Model	K	LL	ΔAICc	w
Snow + Fox	**7**	**-307.7**	**0.00**	**0.50**
Snow	**6**	**-308.7**	**0.01**	**0.50**
Fox	4	-337.6	53.82	0.00
Null	3	-341.4	59.45	0.00

C) Horned lark

Model	K	LL	ΔAICc	w
Snow + Fox + Lemming	**6**	**-1325.7**	**0.00**	**0.44**
Snow + Fox	**5**	**-1326.9**	**0.49**	**0.34**
Snow + Fox*Lemming	**7**	**-1325.6**	**1.86**	**0.17**
Snow + Lemming	5	-1329.6	5.86	0.02
Snow	4	-1330.8	6.19	0.02
Fox	4	-1344.3	33.18	0.00
Null	3	-1345.4	33.42	0.00

D) White-rumped sandpiper

Model	K	LL	ΔAICc	w
Snow	**5**	**-618.9**	**0.00**	**0.50**
Snow + Lemming	**6**	**-618.8**	**1.76**	**0.21**
Snow + Fox	**6**	**-618.9**	**1.99**	**0.19**
Snow + Fox + Lemming	7	-618.8	3.76	0.08
Snow + Fox*Lemming	8	-618.8	5.74	0.03
Null	3	-637.8	33.74	0.00
Fox	4	-637.8	35.66	0.00

E) Baird's sandpiper

Model	K	LL	ΔAICc	w
Snow + Fox*Lemming	**7**	**-963.9**	**0.00**	**0.74**
Snow + Fox + Lemming	6	-966.2	2.50	0.21
Snow + Fox	5	-968.8	5.68	0.04
Fox	4	-974.9	16.00	0.00
Snow + Lemming	5	-979.6	27.45	0.00
Snow	4	-983.0	32.07	0.00
Null	3	-987.4	39.00	0.00

F) American golden plover

Model	K	LL	ΔAICc	w
Snow + Fox	**6**	**-1645.2**	**0.00**	**0.63**
Snow + Fox + Lemming	7	-1645.0	1.68	0.27
Snow + Fox*Lemming	8	-1645.0	3.60	0.10
Snow	5	-1682.0	71.61	0.00
Snow + Lemming	6	-1681.6	72.81	0.00
Fox	4	-1730.0	165.77	0.00
Null	3	-1742.7	189.05	0.00

G) Long-tailed jaeger

Model	K	LL	ΔAICc	w
Snow + Fox	**7**	**-944.1**	**0.00**	**0.90**
Snow	6	-947.3	4.46	0.10
Null	3	-966.0	37.83	0.00
Fox	4	-965.1	38.09	0.00

H) Red-throated loon

Model	K	LL	ΔAICc	w
Fox	**3**	**-189.9**	**0.00**	**0.62**
Snow + Fox	**4**	**-189.9**	**1.98**	**0.23**
Snow + Fox + Lemming	5	-189.7	3.66	0.10
Snow + Fox*Lemming	6	-189.7	5.63	0.04
Snow	3	-195.2	10.62	0.00
Snow + Lemming	4	-194.9	12.05	0.00
Null	2	-197.3	12.80	0.00

I) Glaucous gull

Model	K	LL	ΔAICc	w
Fox	**3**	**-139.7**	**0.00**	**0.40**
Snow + Fox	**4**	**-139.0**	**0.56**	**0.30**
Snow + Fox + Lemming	**5**	**-138.4**	**1.37**	**0.20**
Snow + Fox*Lemming	6	-138.2	2.90	0.09
Snow	3	-145.2	10.93	0.00
Snow + Lemming	4	-144.9	12.35	0.00
Null	2	-150.1	18.59	0.00

J) Cackling goose

Model	K	LL	ΔAICc	w
Snow + Fox*Lemming	**9**	**-291.5**	**0.00**	**0.43**
Snow + Fox + Lemming	**8**	**-292.8**	**0.62**	**0.31**
Snow + Fox	**7**	**-294.0**	**0.98**	**0.26**
Snow + Lemming	7	-299.4	11.81	0.00
Snow	6	-300.5	11.95	0.00
Fox	3	-318.8	42.37	0.00
Null	2	-345.7	94.23	0.00

K) Snow goose

Model	K	LL	ΔAICc	w
Snow + Fox*Lemming	**10**	**-1348.4**	**0.00**	**0.92**
Snow + Fox	8	-1353.2	5.69	0.05
Snow + Fox + Lemming	9	-1352.9	7.14	0.03
Snow	7	-1469.9	237.13	0.00
Snow + Lemming	8	-1469.8	238.91	0.00
Fox	4	-1504.3	299.93	0.00
Null	3	-1711.8	712.85	0.00

Table S2. Model selection results for breeding species occurrence in relation to snowmelt date, fox density, and lemming density. All models are generalized linear mixed models with a binomial distribution and include year as a random intercept. Models for tundra-nesting birds (species A–G and K) are based on presence/absence data from 500 m transects and include transect ID as a random intercept. Models for lake-associated birds (species H–I) are based on presence/absence data around lakes. Models are ranked by Akaike Information Criterion (AICc). The table shows the number of parameters (K), log-likelihood (LL), delta AICc (ΔAICc), and AICc weight (w). Models in bold are considered competitive (delta AICc < 2).

6. Model results for all species

A) Lapland longspur

	Estimate	95%CI
(Intercept)	**2.40**	**[1.12, 3.68]**
Snow	**0.93**	**[0.04, 1.82]**
Snow²	**-3.87**	**[-6.46, -1.28]**
Snow³	**-7.21**	**[-8.42, -6.00]**
Fox [High]	-0.25	[-0.51, 0.01]

σ transect = 0.28		
σ year = 0.4		
n = 4077		

B) Snow bunting

	Estimate	95%CI
(Intercept)	**-3.28**	**[-5.25, -1.31]**
Snow	**3.92**	**[2.51, 5.34]**
Snow²	0.32	[-3.77, 4.40]
Snow³	**3.22**	**[1.72, 4.73]**
Fox [High]	-1.32	[-3.36, 0.73]

σ transect = 0.22		
σ year = 0.15		
n = 1167		

C) Horned lark

(Intercept)	**-0.69**	**[-1.34, -0.05]**
Snow	**-4.24**	**[-5.67, -2.80]**
Fox [High]	**-0.36**	**[-0.61, -0.11]**

σ transect = 0.18		
σ year = 0.49		
n = 3864		

D) White-rumped sandpiper

(Intercept)	**-10.31**	**[-12.76, -7.41]**
Snow	**12.60**	**[7.43, 17.67]**
Snow²	-1.20	[-3.08, 0.67]
Fox [High]	-0.03	[-0.47, 0.41]

σ transect = 0.80		
σ year = 0.39		
n = 3343		

E) Baird's sandpiper

(Intercept)	**-1.32**	**[-2.15, -0.48]**
Snow	**-3.65**	**[-5.68, -1.62]**
Fox [High]	**-1.39**	**[-2.01, -0.78]**
Lem [High]	0.19	[-0.20, 0.57]
Fox : Lem	**0.75**	**[0.04, 1.46]**

σ transect = 0.36		
σ year = 0		
n = 3864		

F) American golden plover

(Intercept)	**-1.30**	**[-2.28, -0.32]**
Snow	**-3.07**	**[-4.92, -1.22]**
Snow²	**-8.01**	**[-9.44, -6.59]**
Fox [High]	**-1.30**	**[-1.58, -1.02]**

σ transect = 0.57		
σ year = 0.25		
n = 3864		

G) Long-tailed jaeger

(Intercept)	**-1.54**	**[-2.42, -0.66]**
Snow	-0.54	[-2.28, 1.21]
Snow²	**-3.25**	**[-4.43, -2.06]**
Fox [High]	**-0.38**	**[-0.68, -0.09]**

σ transect = 0.41		
σ year = 0.02		
n = 1928		

H) Red-throated loon

(Intercept)	**-3.12**	**[-4.43, -1.80]**
Snow	-0.28	[-3.05, 2.48]
Fox [High]	**1.09**	**[0.39, 1.80]**

σ year = 0.02		
n = 804		

I) Glaucous gull

(Intercept)	**-3.31**	**[-4.63, -1.99]**
Snow	-1.62	[-4.24, 1.00]
Fox [High]	**1.42**	**[0.56, 2.29]**

σ year = 0		
n = 804		

J) Cackling goose

(Intercept)	**-1.83**	**[-3.06, -0.60]**
Snow	**-3.67**	**[-6.06, -1.29]**
Snow²	**-7.16**	**[-10.39, -3.92]**
Fox [High]	**0.96**	**[0.51, 1.41]**

σ year = 0.2		
n = 804		

K) Snow goose

(Intercept)	**-2.32**	**[-3.93, -0.7]**
Snow	0.39	[-0.81, 1.6]
Snow²	**2.06**	**[0.18, 3.94]**
Snow³	**-12.77**	**[-16.48, -9.06]**
Snow⁴	**-25.75**	**[-31.93, -19.58]**
Fox [High]	**3.89**	**[3.37, 4.42]**
Lem [High]	0.80	[-0.64, 2.25]
Fox : Lem	**-0.75**	**[-1.24, -0.26]**

σ transect = 1.97		
σ year = 1.51		
n = 3556		

Table S3 Parameter values for selected models relating breeding species occurrence to snowmelt date (Snow), fox density (Fox), and lemming density (Lem) in Table S2. Models for tundra-nesting birds (species A–G and K) and wetland-associated birds (species H–I) are based on transects and lakes survey respectively. To illustrate the effect, or lack of effect, of snowmelt date and fox density, we present results from the most parsimonious model including both variables.

7. Results obtained when excluding data from 2024

Results were unaffected when excluding data from 2024 (Table S4 and Figures S11, S12, S13), a year in which surveys were delayed due to helicopter availability. The only notable difference was the long-tailed jaeger for which we no longer had data in late snowmelt areas. This species nest only in years of high lemming density, which substantially reduces sample size, particularly in late snowmelt areas for which 2024 was our only year of high lemming abundance. In the range for which we had data with and without 2024, patterns for jaeger were unaffected by the removal of 2024 data. Results for all other species were highly consistent with and without 2024 data.

A) Lapland longspur

	Estimate	95%CI
(Intercept)	**2.54**	**[1.31, 3.77]**
Snow	0.75	[-0.17, 1.68]
Snow²	**-3.65**	**[-6.17, -1.13]**
Snow³	**-6.86**	**[-8.04, -5.68]**
Fox [High]	-0.23	[-0.52, 0.05]

σ transect = 0.28		
σ year = 0.19		
n = 3556		

B) Snow bunting

	Estimate	95%CI
(Intercept)	**-3.28**	**[-5.25, -1.31]**
Snow	**3.92**	**[2.51, 5.34]**
Snow²	0.32	[-3.77, 4.40]
Snow³	**3.22**	**[1.72, 4.73]**
Fox [High]	-1.32	[-3.36, 0.73]

σ transect = 0.22		
σ year = 0.15		
n = 1167		

C) Horned lark

(Intercept)	-0.59	[-1.24, 0.06]
Snow	**-4.31**	**[-5.79, -2.83]**
Fox [High]	**-0.32**	**[-0.57, -0.07]**

σ transect = 0.15		
σ year = 0.46		
n = 3343		

D) White-rumped sandpiper

(Intercept)	**-10.31**	**[-12.76, -7.41]**
Snow	**12.60**	**[7.43, 17.67]**
Snow²	-1.20	[-3.08, 0.67]
Fox [High]	-0.03	[-0.47, 0.41]

σ transect = 0.80		
σ year = 0.39		
n = 3343		

E) Baird's sandpiper

(Intercept)	**-1.37**	**[-2.18, -0.57]**
Snow	**-3.55**	**[-5.49, -1.6]**
Fox [High]	**-1.4**	**[-2.02, -0.78]**
Lem [High]	0.30	[-0.12, 0.72]
Fox : Lem	0.57	[-0.17, 1.32]

σ transect = 0.40		
σ year = 0.01		
n = 3343		

F) American golden plover

(Intercept)	**-1.86**	**[-2.85, -0.87]**
Snow	-1.23	[-3.14, 0.68]
Snow²	**-6.54**	**[-7.88, -5.19]**
Fox [High]	**-1.51**	**[-1.82, -1.21]**

σ transect = 0.50		
σ year = 0.18		
n = 3343		

G) Long-tailed jaeger

(Intercept)	-0.88	[-1.78, 0.02]
Snow	-0.60	[-2.25, 1.05]
Snow²	-0.41	[-1.6, 0.78]
Fox [High]	**-0.56**	**[-0.88, -0.25]**

σ transect = 0.35		
σ year = 0.02		
n = 1407		

H) Red-throated loon

(Intercept)	**-3.30**	**[-4.8, -1.8]**
Snow	0.00	[-2.9, 2.9]
Fox [High]	**1.13**	**[0.36, 1.9]**

σ year = 0.05		
n = 687		

I) Glaucus gull

(Intercept)	**-2.98**	**[-4.36, -1.6]**
Snow	-2.48	[-5.3, 0.33]
Fox [High]	**1.50**	**[0.6, 2.39]**

σ year = 0		
n = 687		

J) Cackling goose

(Intercept)	**-2.14**	**[-3.61, -0.68]**
Snow	**-3.10**	**[-5.89, -0.31]**
Snow²	**-8.36**	**[-12.14, -4.58]**
Fox [High]	**0.85**	**[0.38, 1.32]**

σ year = 0.10		
n = 687		

K) Snow goose

(Intercept)	**-2.32**	**[-3.93, -0.7]**
Snow	0.39	[-0.81, 1.6]
Snow²	**2.06**	**[0.18, 3.94]**
Snow³	**-12.77**	**[-16.48, -9.06]**
Snow⁴	**-25.75**	**[-31.93, -19.58]**
Fox [High]	**3.89**	**[3.37, 4.42]**
Lem [High]	0.80	[-0.64, 2.25]
Fox : Lem	**-0.75**	**[-1.24, -0.26]**

σ transect = 1.97		
σ year = 1.51		
n = 3556		

Table S4 Model results for nesting species occurrence in relation to snowmelt date (Snow), fox density (Fox), and lemming density (Lem) when excluding data from 2024.

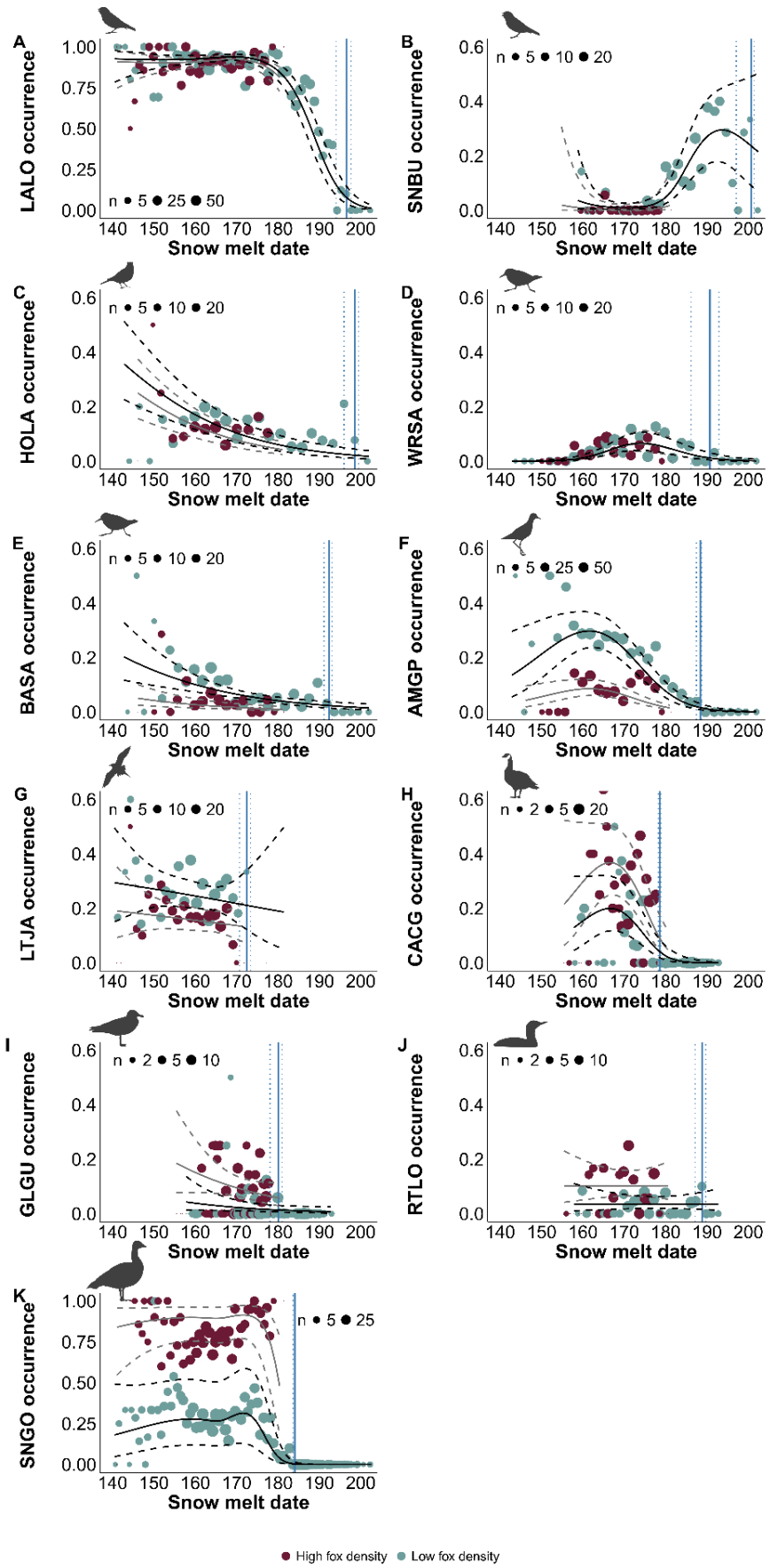

Figure S11 Influence of snowmelt date on occurrence probability of breeding species on Bylot Island, Nunavut when excluding data from 2024 (2010–2023).

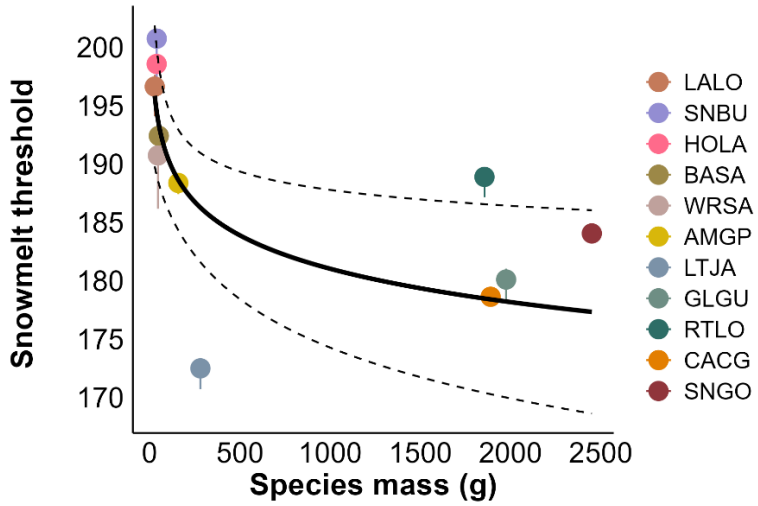

Figure S12 Relationship between the snowmelt threshold date for reproduction and body mass of individual species when excluding data from 2024. Snowmelt threshold corresponds to the last date at which a breeding individual was sighted. Dots represent the threshold for each species shown with 95% confidence intervals obtained through non-parametric bootstrap. Solid and dashed curves are predictions from a simple linear model relating snowmelt threshold to body mass (intercept = 209.84 [95% CI: 196.24, 223.44], slope = –4.18 [–6.80, –1.57], R^2 = 0.58).

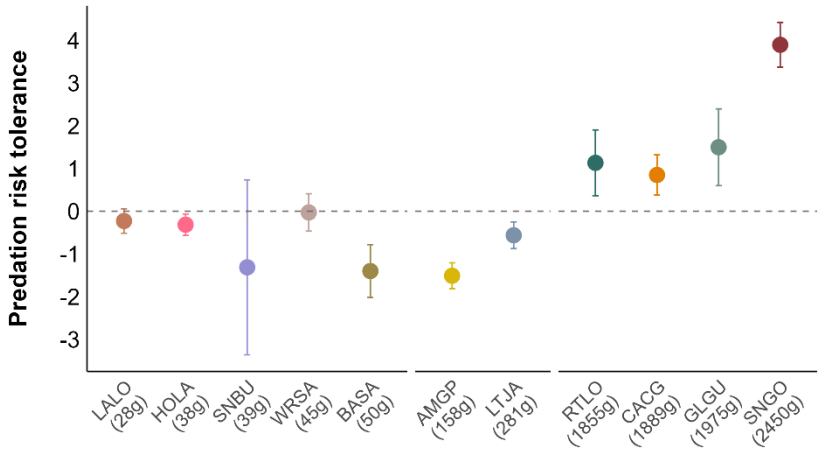

Figure S13 Predation risk tolerance of species ordered by body mass when excluding data from 2024. Predation risk tolerance is the coefficient for the effect of fox density on species occurrence probability (values in Table S4). Dots represent effect size shown with 95% confidence intervals.

7. Supplementary Material References

Andersson, M. (1976). Population Ecology of the Long-Tailed Skua. *Journal of Animal Ecology*, *45*(2), 537–559.

Baker, M. C. (1977). Shorebird food habits in the eastern Canadian Arctic. *The Condor*, *79*(1), 56–62.

Barrou Dumont, Z., Gascoin, S., Inglada, J., Dietz, A., Köhler, J., Lafaysse, M., Monteiro, D., Carmagnola, C., Bayle, A., Dedieu, J.-P., Hagolle, O., & Choler, P. (2025). Trends in the annual snow melt-out day over the French Alps and the Pyrenees from 38 years of high resolution satellite data (1986–2023). *The Cryosphere*, *19*, 2407–2429.

Corbeil-Robitaille, M.-Z., Duchesne, É., Fortier, D., Kinnard, C., & Bêty, J. (2024). Linking geomorphological processes and wildlife microhabitat selection : nesting birds select refuges generated by permafrost degradation in the Arctic. *Biogeosciences*, *21*, 3401–3423.

Davis, R. A. (1972). A comparative study of the use of habitat by Arctic loons and Red-throated Loons. *Digitized Thesis*, 288.

Gauthier, G., Legagneux, P., Valiquette, M. A., Cadieux, M. C., & Therrien, J. F. (2015). Diet and reproductive success of an Arctic generalist predator: Interplay between variations in prey abundance, nest site location, and intraguild predation. *Auk*, *132*(3), 735–747. https://doi.org/10.1642/AUK-14-273.1

Hall, D. K., & Riggs, G. A. (2021). *MODIS/Terra Snow Cover Daily L3 Global 500m SIN Grid, Version 61*. NASA National Snow and Ice Data Center Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MOD10A1.061

Lamarre, J.-F., Legagneux, P., Gauthier, G., Reed, E. T., & Bêty, J. (2017). Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. *Ecosphere*, *8*(5), e01788. https://doi.org/10.1002/ecs2.1788

Leung, M. C.-Y., Bolduc, E., Doyle, F. I., Reid, D. G., Gilbert, B. S., Kenney, A. J., Krebs, C. J., & Bêty, J. (2018). Phenology of hatching and food in low Arctic passerines and shorebirds: is there a mismatch? *Arctic Science*, *4*(4), 538–556. https://doi.org/10.1139/as-2017-0054

Mainguy, J., Gauthier, G., Giroux, J. F., & Duclos, I. (2006). Habitat use and behaviour of Greater Snow Geese during movements from nesting to brood-rearing areas. *Canadian Journal of Zoology*, *84*(8), 1096–1103. https://doi.org/10.1139/Z06-096

Montgomerie, R., & Lyon, B. (2020). Snow Bunting (Plectrophenax nivalis). In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), *Birds of the World*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.snobun.01

Seyer, Y., Gauthier, G., Fauteux, D., & Therrien, J. F. (2020). Resource partitioning among avian predators of the Arctic tundra. *Journal of Animal Ecology*, *89*(12), 2934–2945. https://doi.org/10.1111/1365-2656.13346