Timing matters: phenological constraints and predation shape Arctic community structure

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Summary

Top-down and bottom-up controls of animal populations are well-known elements of niche and coexistence theories, but there is little empirical evidence on how these forces determine species distribution and community assemblies. In Arctic ecosystems, spring snowmelt sets the timing and duration of the snow-free period, thereby controlling food availability, while predation often imposes additional control on prey species. The relative importance of abiotic and biotic filters on distribution is also susceptible to vary with body size. Using 10-years of high-resolution data on all major members of an Arctic vertebrate community and their shared predator, we tested how snowmelt timing interacts with predation to shape species occurrence and community structure. 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 important filters shaping local community structure. Building on species contrasted responses, we propose a conceptual framework for how phenological constraints and predation jointly shape community assembly in highly seasonal environments.

Key-words

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

Introduction

Niche theory is a cornerstone of community ecology and has evolved considerably since original propositions by Grinell (1917) and Elton (1927; see Chase & Liebold (2003), Gravel *et al.* (2019) for reviews). The niche is defined as the set of abiotic and biotic environmental conditions under which a species can persist (Hutchinson 1957), i.e. maintain a positive intrinsic growth rate (Holt 2009). It is a central tenet to both coexistence (Chesson 2000) and species distribution (Godsoe *et al.* 2017) theories. In this context, MacArthur's theory of limiting similarity introduced a bottom-up perspective on niche differentiation, where species coexistence depends on resource partitioning and competitive abilities (MacArthur 1972). In contrast, Holt's concept of apparent competition introduced a top-down perspective, where species sharing common predators can indirectly affect one another's abundance and persistence (Holt 1977). These contrasting forces were unified by Chesson & Kuang (2008), who established that species niche overlap and ultimately coexistence should reflect the combination of both bottom-up and top-down interactions. Chesson's integration of the niche theory has yet to be applied to species distribution theory. Understanding the relative importance of resource availability and predation on species distribution could solve long lasting questions in biogeography and community assembly (Godsoe *et al.* 2017; Kissling *et al.* 2012; Wisz *et al.* 2013).

Energy availability is one of the most fundamental drivers of species community assembly (Lindeman 1942). In most ecosystems, plants absorb energy from sun radiation, which is then transferred through trophic levels by consumptive interactions. Herbivores can establish and persist in a system only if the available energy is sufficient to support their growth and reproduction (Lindeman 1942). Yet, while the total energy available may set an upper limit on species abundance and diversity across trophic levels, the timing of resource availability is also critical. 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

87 the restricted time available (Durant *et al.* 2007; McNamara & Houston 2008). The
88 timing and duration of phenological windows thus filter which species can locally
89 complete their lifecycle and persist (Godsoe *et al.* 2017; Schneider & Frost 1996;
90 Williams *et al.* 2017).

91 Species vary in how they navigate constraints imposed by phenological windows due
92 to differences in functional traits (Humphries *et al.* 2017). Body mass is a fundamental
93 trait shaping both energetic demands and trophic relationships (Brose 2010; Gravel *et*
94 *al.* 2013; Riede *et al.* 2011). Because metabolic rate scales with body mass (Brown *et*
95 *al.* 2004; Kleiber 1932), it is a strong indicator of energy requirements and can serve as
96 a proxy for several other traits (Peters 1986). For example, larger bird species
97 consistently have heavier eggs and longer incubation and chick-rearing periods (Sæther
98 1987). Thus, a species' body mass should be intimately linked to the phenological
99 window it needs to persist and reproduce.

100 Phenological constraints on resource availability can also propagate to higher trophic
101 levels, as areas with longer productive periods may support more consumers, in turn
102 altering top-down dynamics (Fretwell & Barach 1977; Hopcraft *et al.* 2012; Oksanen
103 *et al.* 1981). For example, in ephemeral ponds, the short availability of suitable habitats
104 can exclude prey species that need long windows to reproduce and therefore prevent
105 the establishment of predators (Schneider & Frost 1996). Therefore, longer growing
106 periods tend to support greater prey biomass, which in turn can sustain higher predator
107 abundance (Oksanen *et al.* 1981). Predator density may change nonlinearly and can
108 increase sharply once the growing season is long enough to allow new prey species.
109 This is particularly striking in the case of large colonial prey, such as waterfowl in arctic
110 ecosystems, which can drastically increase predator densities (Dulude-de Broin *et al.*
111 2023; Giroux *et al.* 2012). The ability of species to withstand predation should also be
112 influenced by their body mass. For instance, the body mass ratio between consumers
113 and their prey affects both the rate and success of attacks, as larger prey are generally
114 more difficult to subdue and consume (Brose 2010; Portalier *et al.* 2019). Consequently,
115 phenological constraints not only shape resource availability for primary consumers but
116 may also alter biotic interactions within food webs.

117 Although the interplay between top-down and bottom-up processes is well recognized
118 in the context of population abundance (Hopcraft *et al.* 2010; Hunter & Price 1992),

119 their joint influence on vertebrate community structure and distributions remains much
120 less studied (Godsoe *et al.* 2017; Tylianakis & Morris 2017). In particular, the combined
121 effects of food resource phenology and predation on community structure are rarely
122 integrated (Ponti & Sannolo 2023), likely due to the challenge of obtaining detailed and
123 concurrent information on phenological windows, predation risk and multi-species
124 distribution. Arctic terrestrial ecosystems offer a unique opportunity to tackle these
125 questions as seasonal changes impose severe phenological constraints on ecological
126 processes (Humphries *et al.* 2017; Saulnier-Talbot *et al.* 2024). Snow cover creates
127 strong heterogeneity in the length of the growing season, leading to abrupt changes in
128 primary production (Niittynen & Luoto 2018). In particular, the spring snowmelt
129 unlocks the window of opportunity for plant growth, making it the primary
130 phenological driver of primary production (Walker *et al.* 2001). Snowmelt timing is
131 also intimately linked to the duration of the snow free period, which can constrain
132 access to terrestrial food resources for consumers (Rixen *et al.* 2022). Moreover,
133 predation could affect the ability of prey species to persist in the arctic tundra landscape
134 (Beardsell *et al.* 2023).

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

abiotic (snowmelt) and biotic (predation) drivers on the structure of Arctic vertebrate communities and set the stage for a trait-based examination of species responses across environmental gradients.

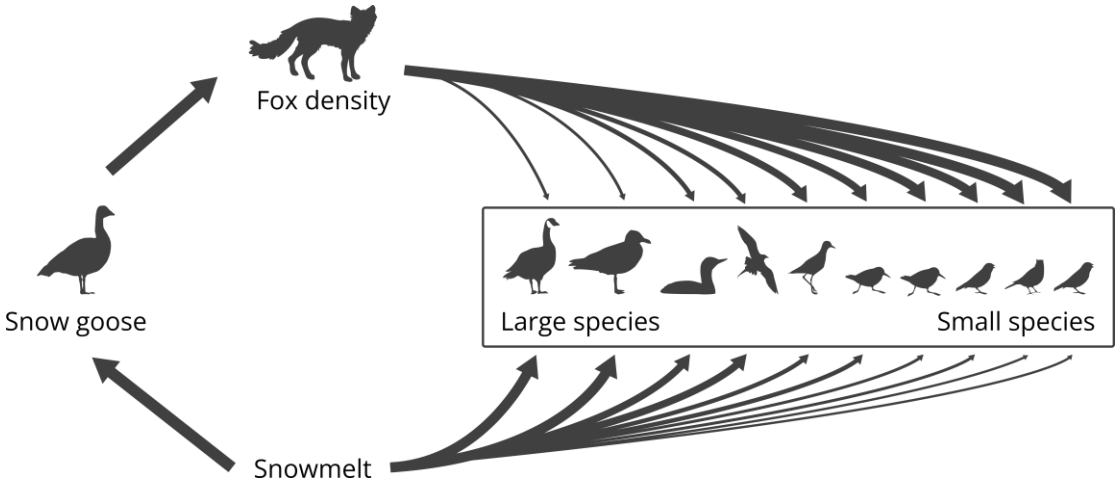

Figure 1. Combined influence of abiotic (snowmelt) and biotic (predation) drivers on Arctic community structure. We hypothesize that snowmelt timing sets the temporal window for reproduction, influencing species occurrence, while predator density further modulates these patterns. Body mass is expected to mediate species responses, with larger-bodied species more sensitive (wider arrow) to snowmelt timing but less affected (narrower arrow) by predation. Note that the abundance of all prey species can influence predator density, but the presence of large colonial prey, such as snow geese, can have a dominant effect.

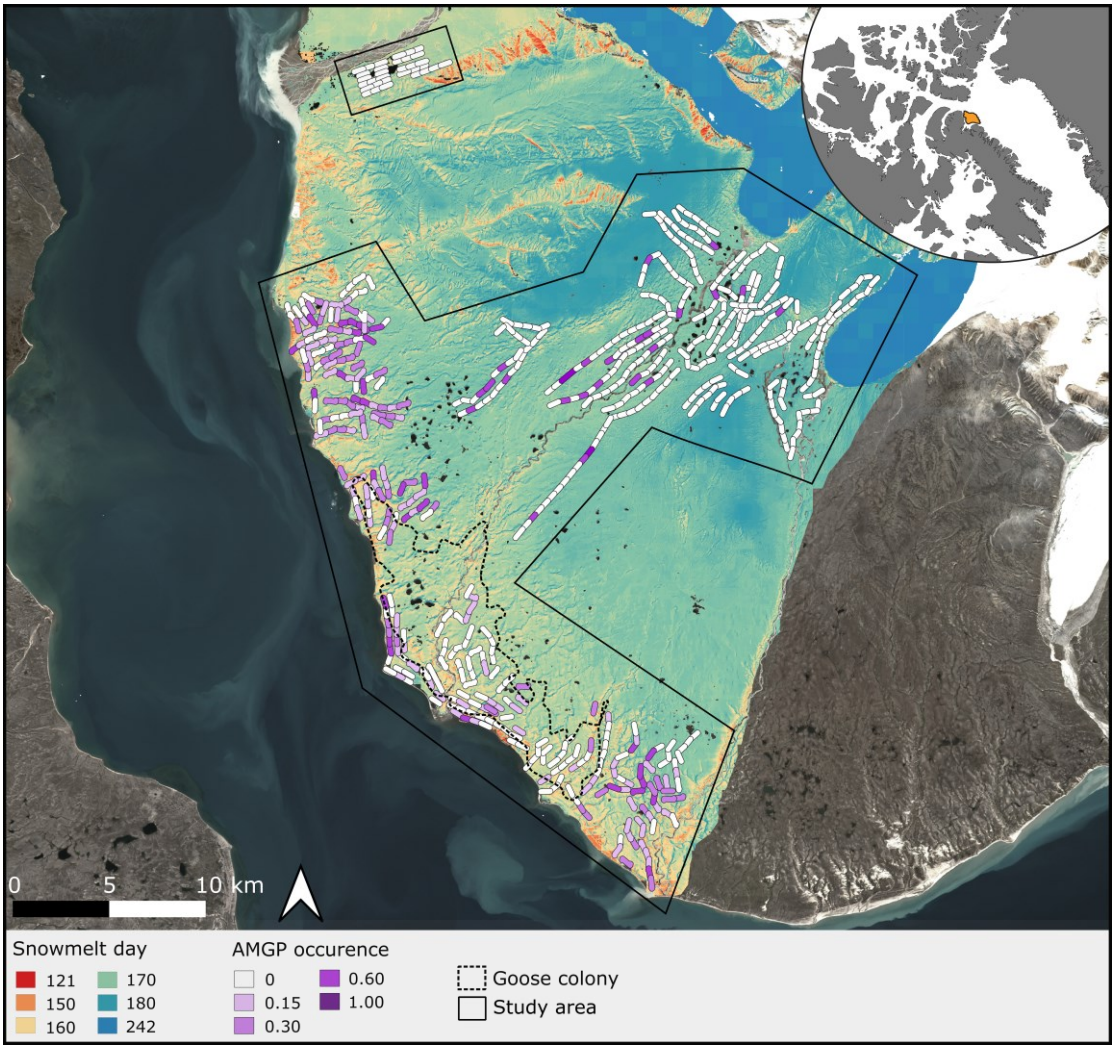

Figure 2. Map of the study area (inside solid black lines) on Bylot Island (Nunavut, Canada) showing the location of sampling transects (coloured lines), the greater snow goose colony boundary (black dashed line), and the average snowmelt day. The occurrence of each species was recorded within 150 m 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 (Figure 2). The ~600 km² area consists of rolling hills, plateaus, and lowlands separated by glacial valleys (Gauthier *et al.* 2011). It includes a large snow goose (*Anser caerulescens*) colony, occupying ca. 70 km^2 where around 5,000 to 20,000 pairs nest each year (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).

Nesting bird occurrence

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

Transects

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

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

For analyses, we used the occurrences of breeding individuals along transects for plovers, jaegers, and passerines, and both breeding and unknown-status individuals for other species, excluding non-breeders. Only high lemming years (see below) were 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 large samples 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 (see Statistical Analyses).

Snowmelt phenology

To assess the influence of snowmelt patterns on spatiotemporal variation in species occurrence, we mapped the date of spring 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 produced 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.

335 Our analysis followed a two-step approach. First, because we expected non-linear
336 relationships between snowmelt dates and the probability of occurrence, we fitted the
337 full model (see below) using natural cubic splines with degrees of freedom ranging
338 from 1 to 5. The most parsimonious model was selected based on AICc. Second, we
339 compared a set of models with different combinations of snowmelt dates (fitted with
340 the selected spline), predator and lemming density (both, high vs. low), and the
341 interaction between predator density and lemming density. All models included year as
342 a random intercept. Models based on transect data also included transect ID as a random
343 intercept to account for repeated surveys over the years. For lake data, lake ID was not
344 included because nearly half the lakes (42%) were surveyed only once. We considered
345 models with ΔAICc< 2 to be equally supported (Burnham & Anderson 2002) and
346 discussed all variables included in these models. To illustrate the effect, or lack of
347 effect, of the main variable of interests (i.e. snowmelt date and fox density), we present
348 predictions and model summary from the most parsimonious model that includes both
349 variables, rather than from the single best-fitting model overall. All predictions are
350 shown for high lemming density.

351 To assess the relative influence of snowmelt timing across species with different body
352 masses, we fitted a weighted linear model relating snowmelt thresholds to body mass,
353 using the inverse of the thresholds' standard error as weights to account for estimates
354 uncertainty. This snowmelt-threshold approach was well suited to our analysis, as it
355 captured the influence of snowmelt timing irrespective of the specific form of the non-
356 linear snow-occurrence relationships, minimizing sensitivity to subtle variations in
357 model fit. We examined how the impact of predation on species occurrence varied with
358 body mass by comparing the effect sizes of fox density extracted from the full models,
359 which controlled for snowmelt timing, across species.

Results

We monitored 637 unique transects and 444 lakes resulting in 4097 transect-year and 804 lake-year (number of sightings 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 [4, 16] for the same lake. Within a given year, snowmelt timing varied on average by 24 days [14, 43] among transects and 29 days [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 3-4, see Appendix S1, Table S1 for threshold values). Waterfowls had the earliest snowmelt thresholds and did not nest in areas still covered by snow in late June, 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 3-4). 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 4). As expected, larger-bodied species were most affected by a late snowmelt and had the earliest thresholds (Figure 5).

Snowmelt date was an important predictor of occurrence in all species except glaucous gulls and red-throated loons (Figure 3-4) 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, and snow geese had high and consistent occurrence probability in early snowmelt areas followed by a steep decline in late snowmelt areas, while the decline was more gradual for horned larks and

Baird's sandpipers (Figures 3-4). White-rumped sandpipers showed a humped shaped relationship, with low occurrence in early and late snowmelt sites. Notably, snow buntings were largely absent from early snowmelt areas, occurring mainly in sites where snowmelt happened after day 180 (June 29), before declining again.

Predator density was an important predictor of occurrence probability, although associations were either positive or negative depending on species (Figures 3-4). As expected, snow geese occurrence and areas of high fox density were strongly positively associated (Odds ratio (OR)=140.85 [72.74, 272.73], 95% CI). Fox density was included in the most parsimonious model for all species except Lapland longspur, snow bunting, and white-rumped sandpiper, where it appeared among the top-ranked models, but not in the most parsimonious (Appendix S1, Tables S2). Horned larks (OR=0.70 [0.55, 0.90]), Baird's sandpipers (OR=0.25 [0.13, 0.46]), American golden plovers (OR=0.28 [0.21–0.37]), and long-tailed jaegers (OR=0.68 [0.51, 0.91]) were less likely to occur in areas of high fox density, with reductions in the probability of occurrence ranging from 26% to 74%. Lapland longspurs showed a similar trend (22% reduction in high fox density areas, OR=0.78 [0.60, 1.01]). In contrast, cackling geese (OR=2.47 [1.57, 3.87]), glaucous gulls (OR=3.99 [1.67, 9.53]), and red-throated loons (OR=3.62 [1.69, 7.74]) were more likely to occur in high fox density areas. Fox density did not affect the occurrence of white-rumped sandpipers and snow buntings (Tables S2 and S3). Lemming density had a lesser effect on species occurrence than fox density as it was in the most parsimonious model only for snow goose and Baird's sandpiper (Appendix S1, Table S2).

Larger bodied species (≥1855 g) were generally less sensitive to predation than smaller ones (Figure 6), even showing positive associations with areas of high fox densities. Interestingly, although smaller species were generally negatively affected by fox densities, the strongest negative associations occurred among species of intermediate body size (50-150 g; Figure 6).

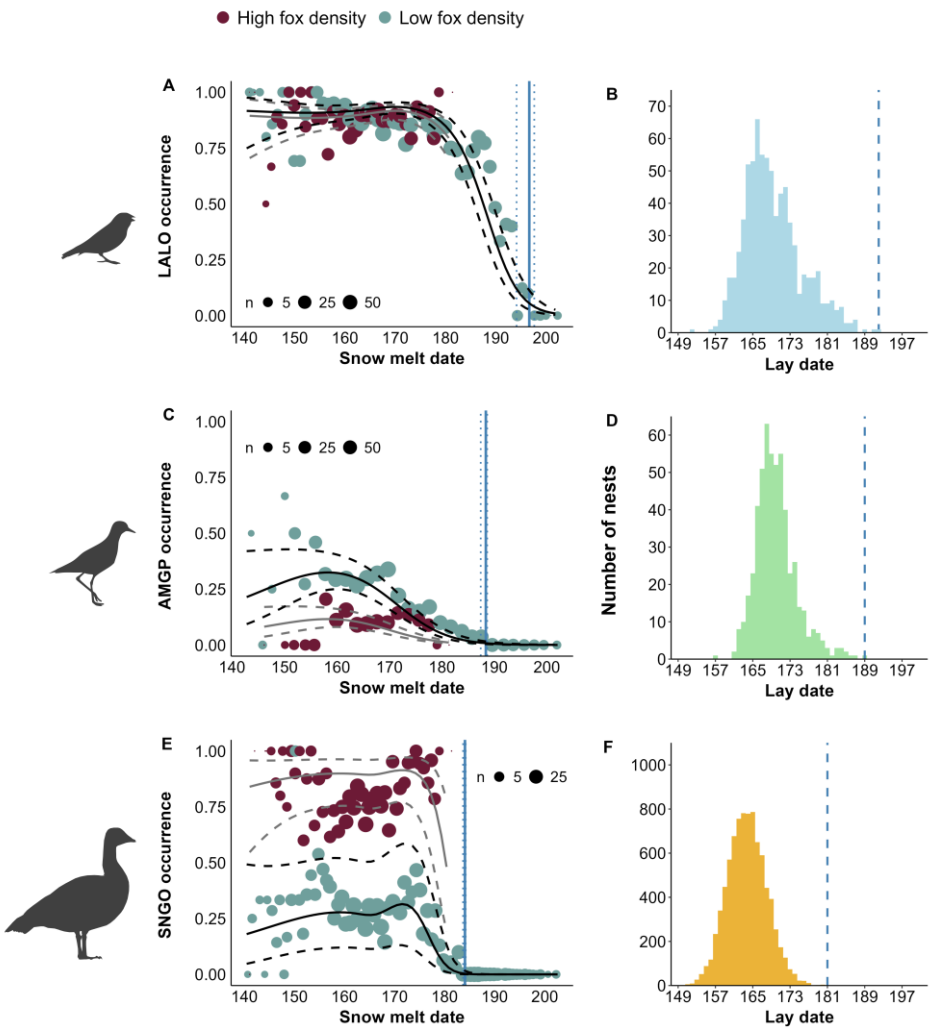

Figure 3. Influence of snowmelt date on occurrence probability of breeding (A) Lapland longspur (LALO), (B) American golden plover (AMGP), and (C) greater snow goose (SNGO) on Bylot Island, Nunavut (2010–2024). The full and dotted lines show model predictions along with their 95% confidence intervals 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).

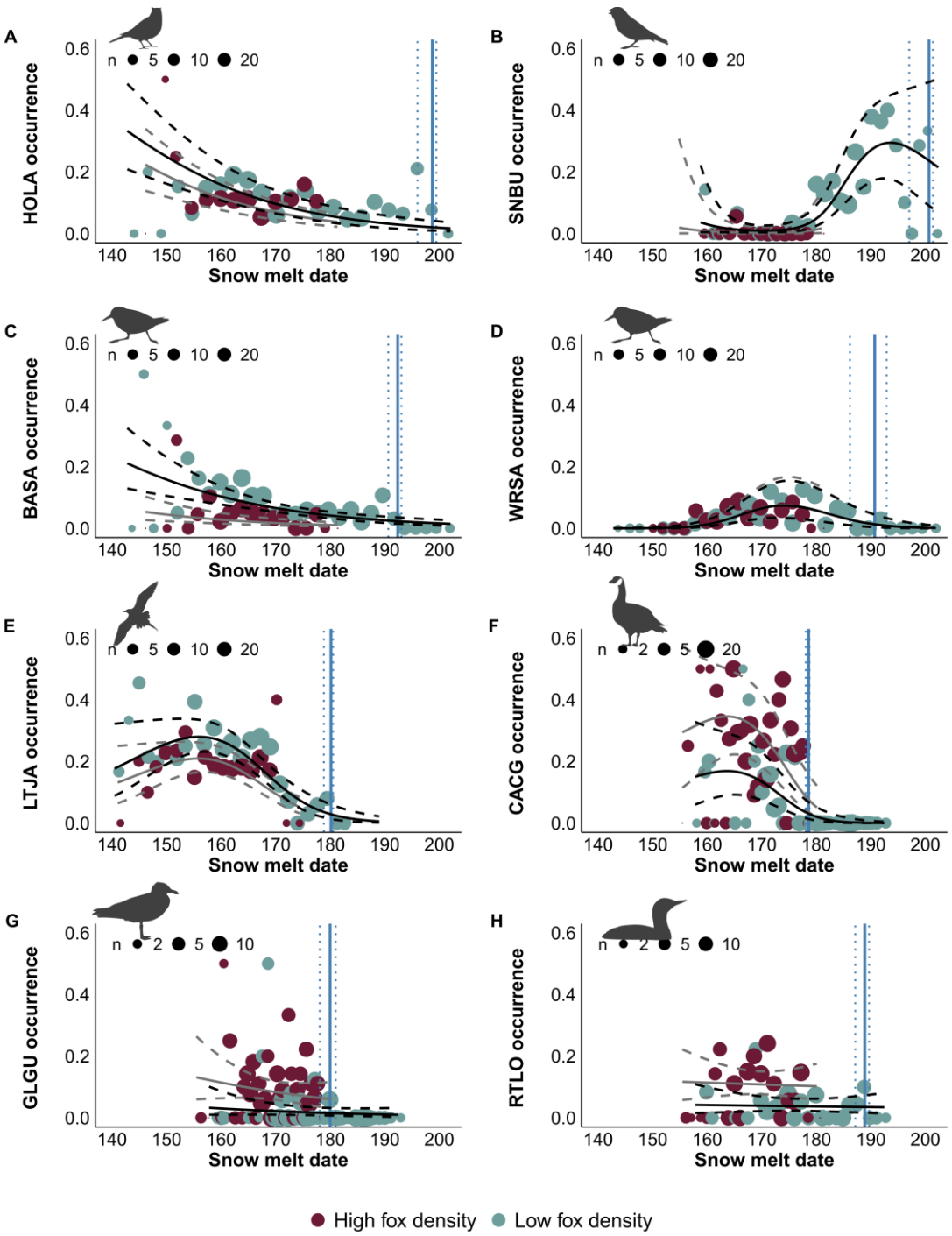

Figure 4. Influence of snowmelt date on occurrence probability of breeding (A) horned lark (HOLA), (B) snow bunting (SNBU), (C) Baird's sandpiper (BASA), (D) white-rumped sandpiper (WRSA), (E) long-tailed jaeger (LTJA), (F) cackling goose (CACG), (G) glaucous gull (GLGU), and (H) red-throated loon (RTLO) 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.

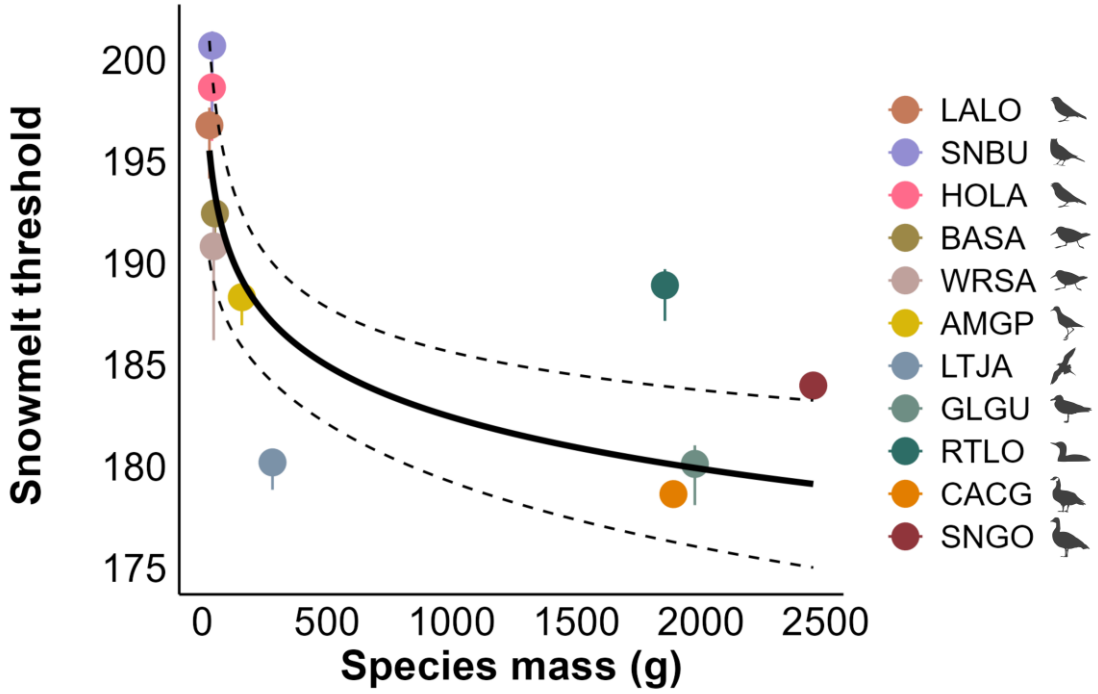

Figure 5. Relationship between the snowmelt threshold date for reproduction and body mass of individual species. Snowmelt threshold corresponds to the last date at which a breeding individual was sighted. Dots represent the threshold for each species shown with 95% confidence intervals obtained through non-parametric bootstrap. Solid and dashed curves are predictions from a simple linear model relating snowmelt threshold to body mass (intercept = 207.75 [95% CI: 197.15, 218.35]; slope = –3.67 [–5.36, -1.98]; $R^2 = 0.72$).

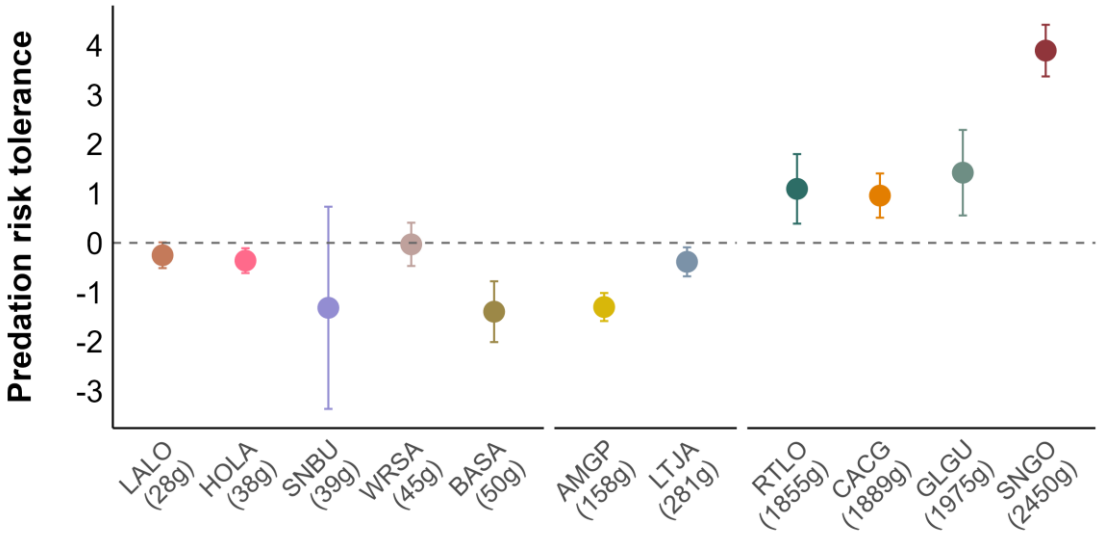

Figure 6. Predation risk tolerance of species ordered by body mass. Predation risk tolerance is the coefficient for the relationship between fox density and species occurrence probability (values in Appendix S1, Table S3). Dots represent effect size shown with 95% confidence intervals. A positive value indicates a higher probability of occurrence in high fox density area.

Discussion

Benefiting from a 10-year dataset on the relative occurrence of 11 bird species and their common predator across 600 km^2 in the Arctic tundra, we found that species occurrence 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 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

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

494 Species had a clear snowmelt threshold for reproduction as observed in other systems
495 (Smith *et al.* 2010), and larger-bodied species were generally more sensitive to a late
496 snowmelt. The inverse association between the snowmelt threshold and body mass
497 supports the hypothesis that species with higher energetic demands and especially
498 longer developmental periods are more constrained by the duration and timing of
499 resource availability as they require more time to complete their vital cycle. However,
500 other traits such as diet and energy storage capacity may also shape species-specific
501 responses to the duration of phenological windows. Some species such as the red-
502 throated loon had thresholds that did not align well with their mass. Species
503 phenological tolerance should be closely tied to and overlap with that of their food
504 resources (Altermatt 2010; Diamond *et al.* 2011). As such, species such as loons (Davis
505 1972) and gulls (Gauthier *et al.* 2015) that can forage at sea might be less affected by
506 terrestrial snowmelt than herbivores or terrestrial insectivores. The accumulation of
507 energy stores or ability to forage in presence of snow can also extend a species
508 phenological window by providing access to resources during less productive periods
509 (Kerby & Post 2013; Williams *et al.* 2017). For instance, snow geese and cackling geese
510 would likely need a much longer pre-breeding foraging period without body stores.
511 Similarly, species such as the snowy owl (*Bubo scandiacus*) that can forage effectively
512 despite snow cover should be less constrained by snowmelt timing.

513 To minimize potential biases associated with imperfect detection and nest failure, we
514 focused on presence/absence data over broad areas (transect: 500 m x 300 m and 150
515 m buffer around lakes) and alternated surveys across gradients of snowmelt timing and
516 predator densities. However, differences in detectability across species are likely and
517 the raw occurrence probabilities we report should not be compared between species.
518 Importantly, such cross-species differences in detectability are unlikely to have biased
519 estimated snowmelt thresholds, as the larger, more easily detected species showed
520 earlier thresholds than the smaller, more cryptic ones. The pattern is thus conservative,
521 as imperfect detection would be expected to advance threshold estimates rather than
522 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 occurrence from annual snowmelt dynamics. Comparing the explanatory power of annual and long-term averaged snowmelt dates could help clarify the timescale over which vertebrate communities respond to these snowmelt gradients. Overall, 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; 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 that could shape breeding birds distribution. Within our study area, early snowmelt sites host abundant food resources for predators provided in large part by the presence of a goose colony, which allows foxes to maintain smaller home ranges at high density, thereby increasing predation risk for prey (Dulude-de Broin *et al.* 2023). American golden plovers and Baird's sandpipers were the species most affected by high fox density, likely because they are large enough to facilitate detection, but cannot efficiently defend their nest (Beardsell et al. 2021). The negative effect of predation was also clear for long-tailed jaegers, which are highly detectable and have limited defences against foxes. Smaller

passerines cannot defend their nests either, but they may be harder to detect (Beardsell *et al.* 2021) and their shorter breeding cycles (20-25 days) than shorebirds (36-55 days) could lead to a steep reduction in exposure to predation. We found no effect of predation risk on white-rumped sandpiper. White-rumped sandpipers may lower detectability by using microhabitats with dense lateral cover (Smith *et al.* 2007), yet the lack of effect remains puzzling given their overall similarity to Baird's sandpipers.

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

We found limited effect of lemming density on species occurrence. While nest predation release at high lemming densities is well known (Beardsell *et al.* 2022; Bety *et al.* 2002; McKinnon *et al.* 2014), the reduction in predation rates it induces (0.5-1 fold reduction; Beardsell et al., 2022; McKinnon et al., 2014) is small compared to the sharp increase driven by fox numerical response near the goose colony (up to six-fold; Dulude-de Broin et al., 2023). Our monitoring was based on species presence-absence along transects or 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 predator density 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 predation 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 7). 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 and less vulnerable species, while late snowmelt areas would host species that are more vulnerable to predation but less affected by the timing and duration of food resources

availability. This framework offers opportunities for hypothesis testing in arctic and other seasonal study systems.

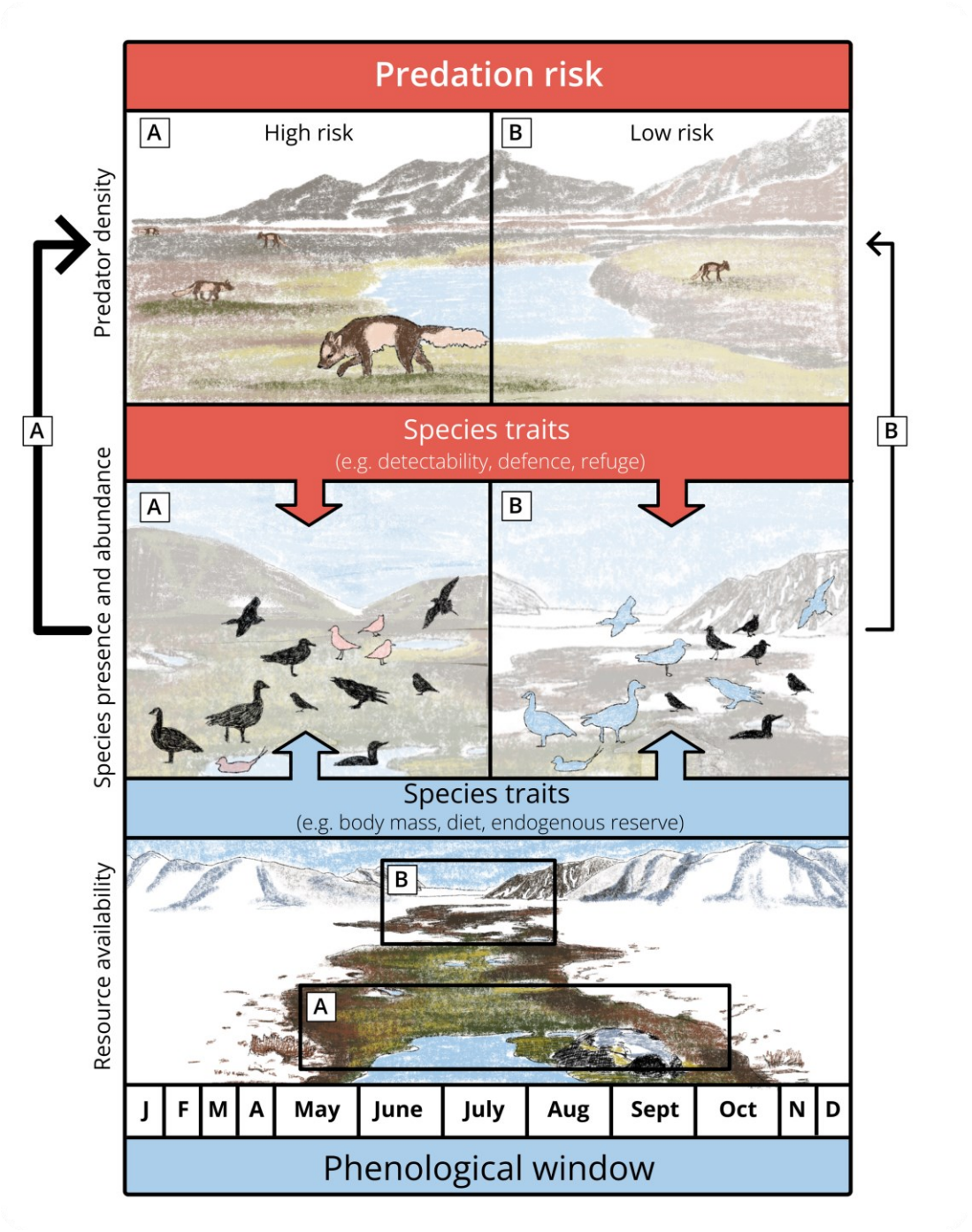

Figure 7. Conceptual model illustrating how phenological constraints and predation shape community composition. Early snowmelt sites (A) allow a longer period of resource availability that can support a broad range of breeding species including those with large body size. This results in higher overall 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.

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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

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

1.3 Criteria to assess breeding status on transect

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

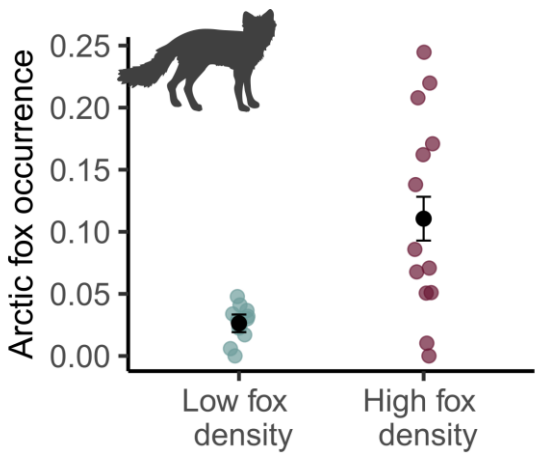

Figure S1. Arctic fox occurrence on transects in areas classified as low and high fox density on Bylot Island, Nunavut (2010–2024). Black dots and error bars represent

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.

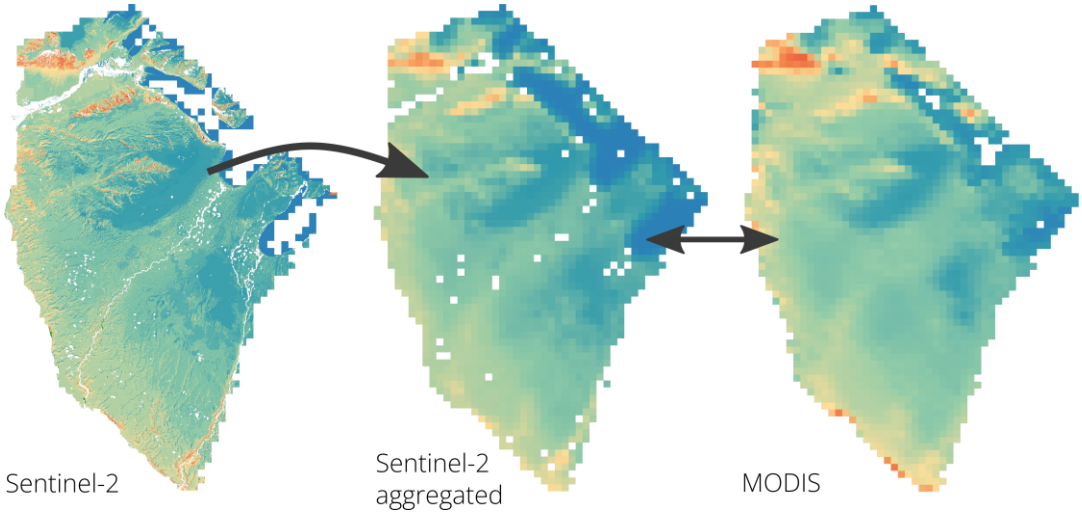

Figure S2 Comparison of Sentinel-2 and MODIS snow products for 2020. The Sentinel-2 map was aggregated to match MODIS spatial resolution (500 × 500 m) by averaging all corresponding high-resolution (20 × 20 m) Sentinel-2 pixels within each coarser pixel.

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.

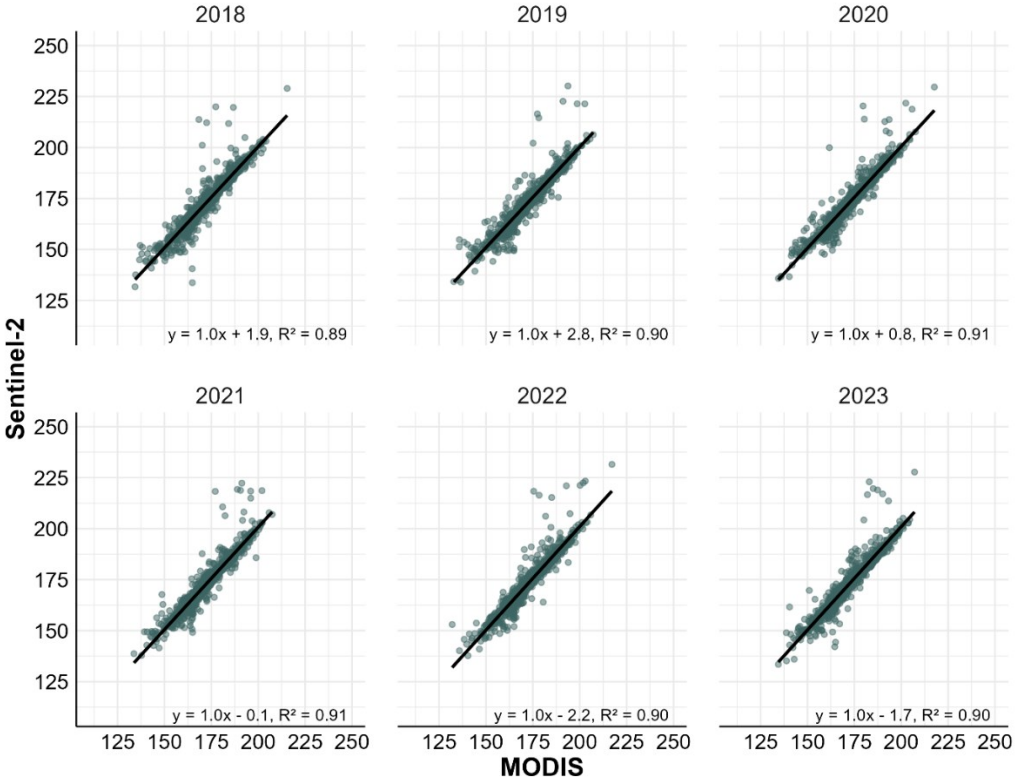

Figure S3 Relationship between snowmelt dates derived from Sentinel-2 and MODIS snow products. Snowmelt dates were compared on a pixel-by-pixel basis after aggregation of Sentinel-2 snowmelt data to match MODIS resolution. Linear model sample size: n=1618.

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).

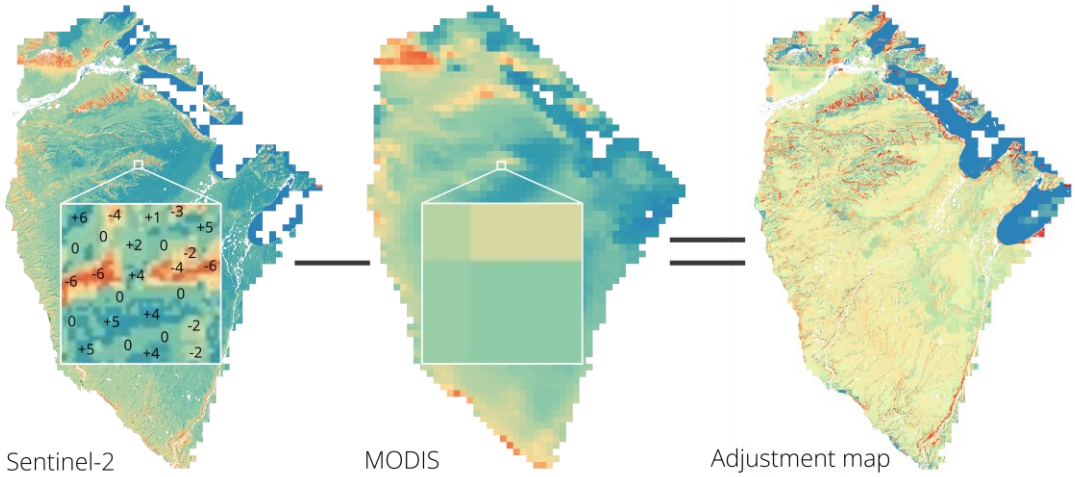

Figure S4 Difference between MODIS snowmelt dates and Sentinel-2 snowmelt dates to create the adjustment raster. The inset illustrates how high-resolution Sentinel-2 pixels differ from the corresponding coarser MODIS pixels. These differences constitute the values of the adjustment map.

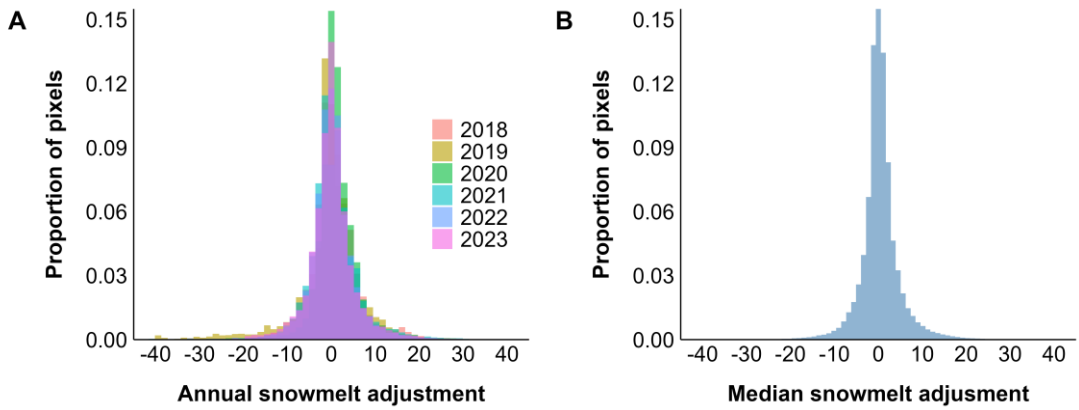

Figure S5 Distribution of snowmelt date adjustment values used to increase the spatial resolution of MODIS-derived snowmelt dates. Adjustment values correspond to the number of days difference between snowmelt estimates from each small Sentinel-2 pixel and coarser overlapping MODIS pixel. Annual adjustment 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.

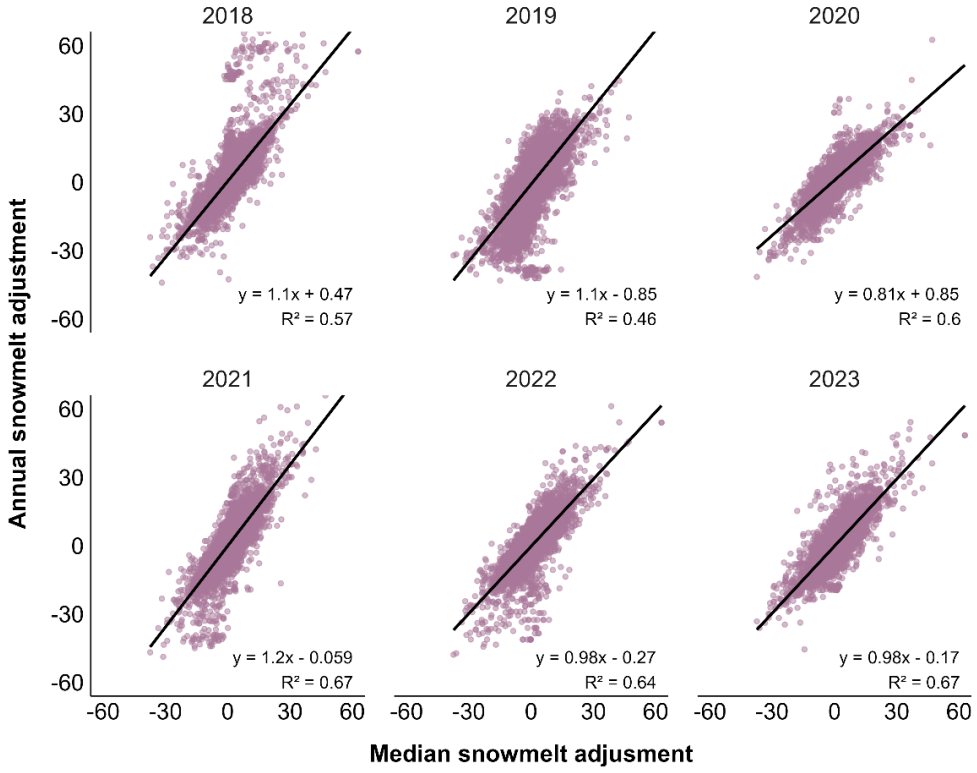

Figure S6 Repeatability in snowmelt adjustment values at the pixel level between Sentinel-2 and MODIS derived snow products. Adjustment values correspond to the number of days difference between snowmelt estimates from each small Sentinel-2 pixel and coarser overlapping MODIS pixel. Individual graphs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

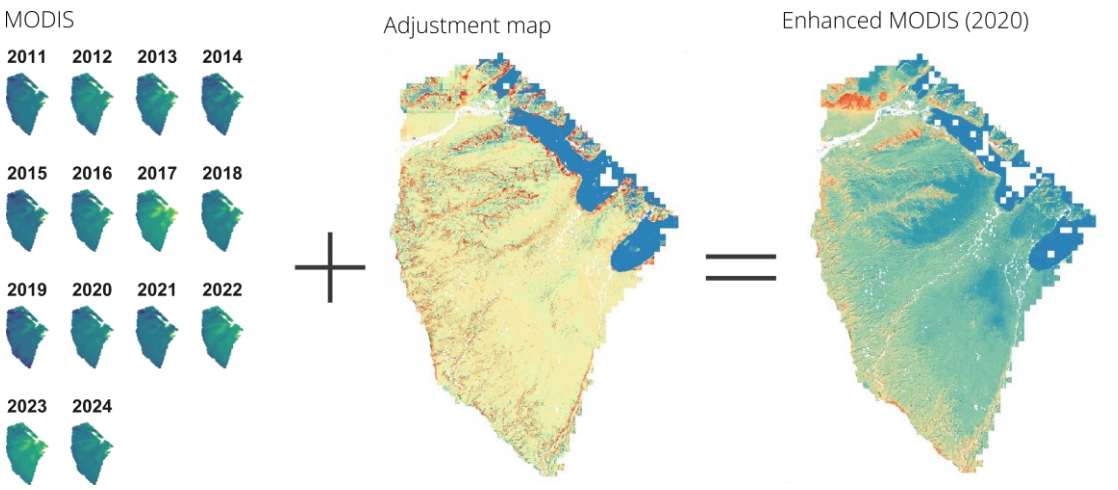

Figure S7 Method used to generate the final snow product used in the study. For each year, we adjusted the MODIS-derived snowmelt map using the adjustment map derived from Sentinel-2 data to obtain a product with a 20-m resolution.

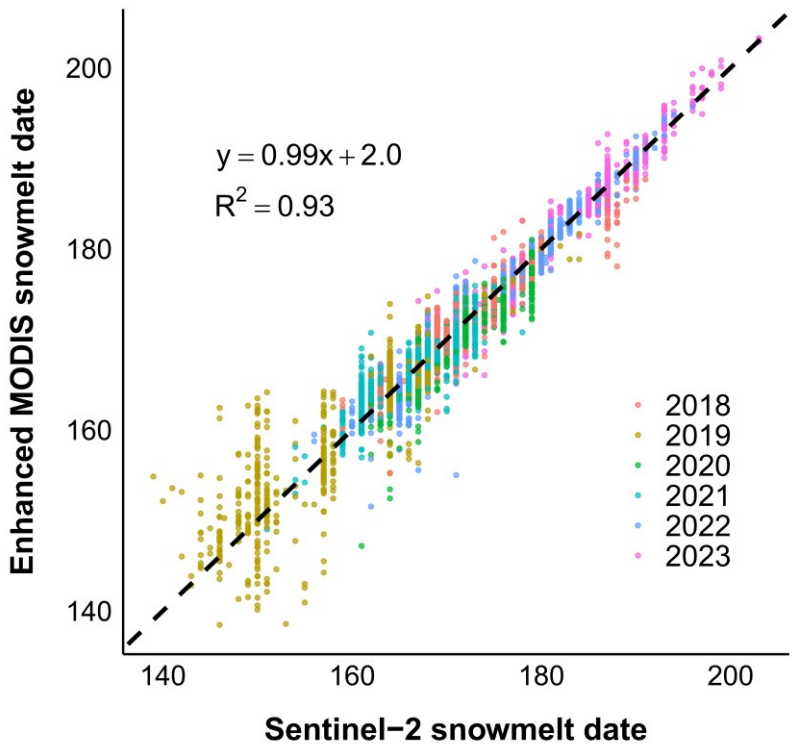

Figure S8 Validation of the snowmelt date derived from the enhanced MODIS snowmelt map against Sentinel-2 data for years with available Sentinel-2 coverage. Each point represents the median snowmelt date for each transect surveyed in the study area every year. The dashed line shows the 1:1 reference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

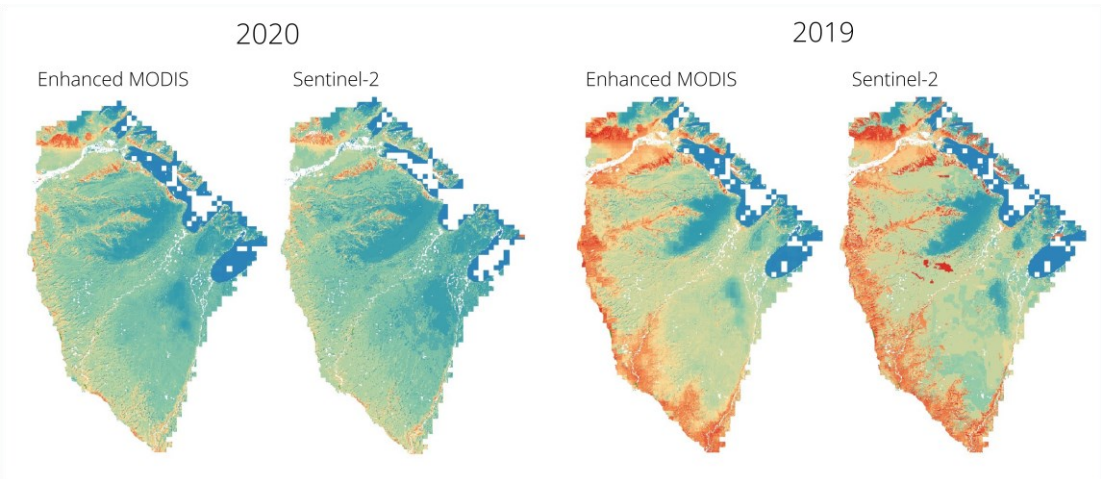

Figure S9 Visual comparison of enhanced MODIS and Sentinel-2–derived snowmelt products for two years with contrasting snowmelt timing, illustrating their consistency.

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.

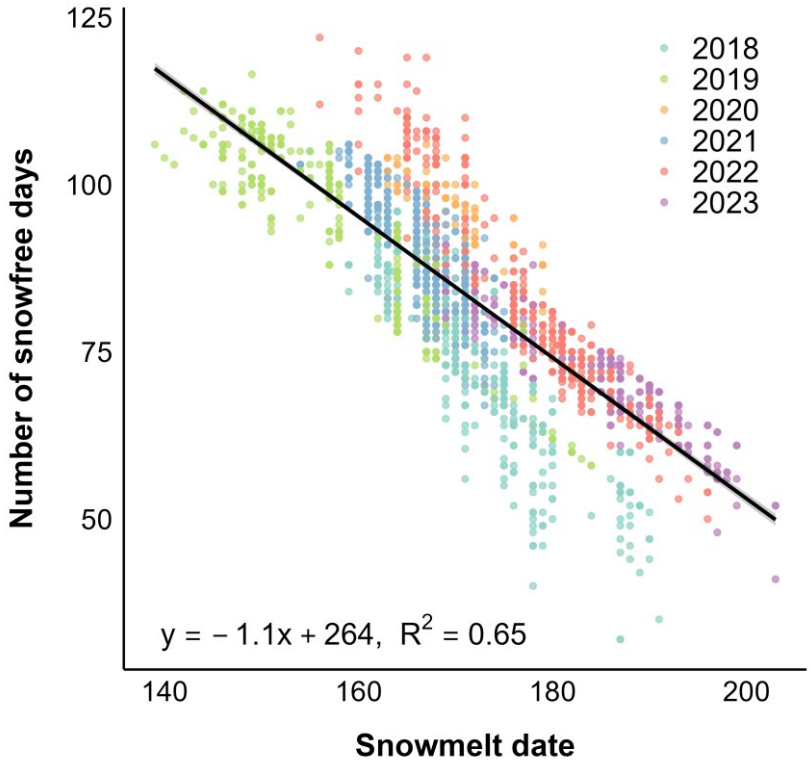

Figure S10 Relationship between snowmelt date and the number of snow-free days around individual transects every year, based on Sentinel-2 derived snow products from THEIA (2018–2023). Linear model sample size: n=3298.

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

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

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.

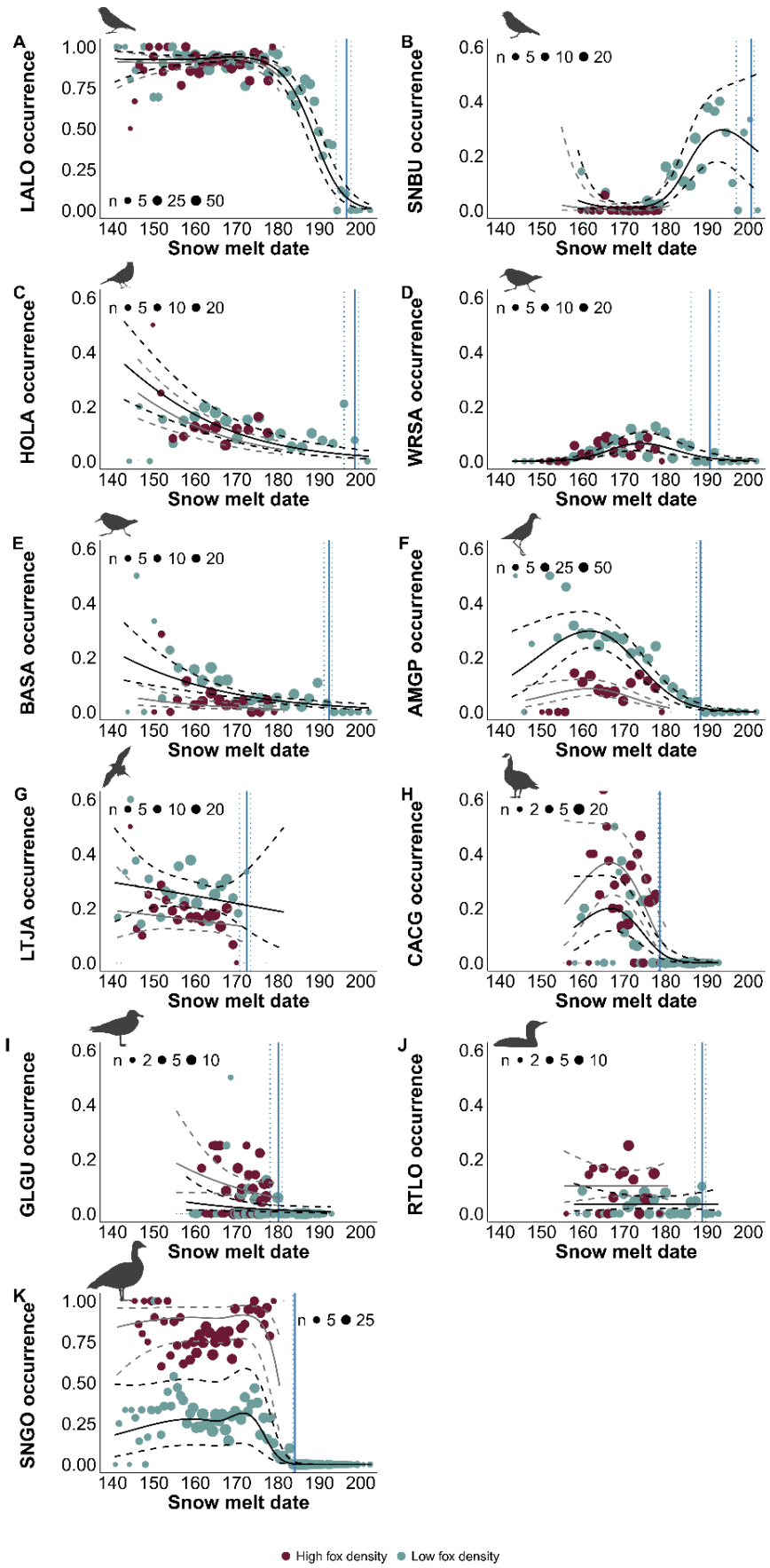

Figure S11 Influence of snowmelt date on occurrence probability of breeding species on Bylot Island, Nunavut when excluding data from 2024 (2010–2023).

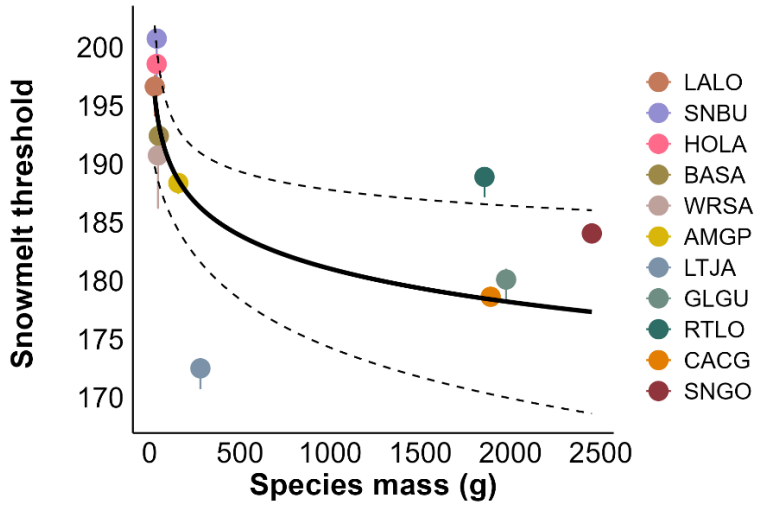

Figure S12 Relationship between the snowmelt threshold date for reproduction and body mass of individual species when excluding data from 2024. Snowmelt threshold corresponds to the last date at which a breeding individual was sighted. Dots represent the threshold for each species shown with 95% confidence 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).

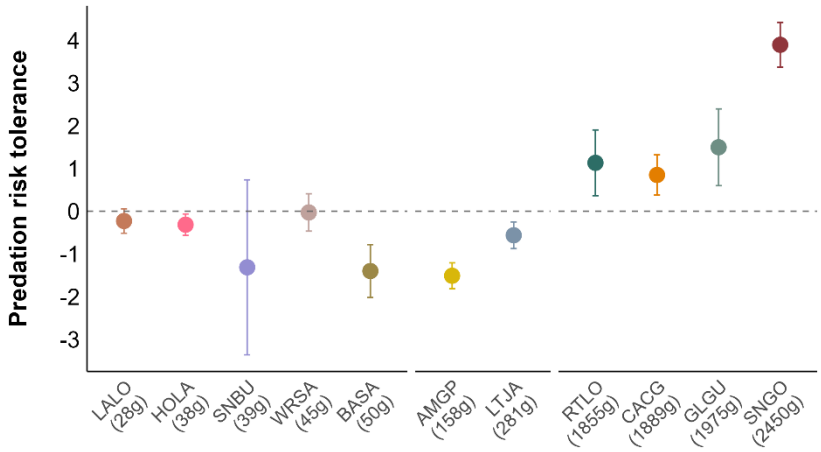

Figure S13 Predation risk tolerance of species ordered by body mass when excluding data from 2024. Predation risk tolerance is the coefficient for the effect of fox density on species occurrence probability (values in Table S4). Dots represent effect size shown with 95% confidence intervals.

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