Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice

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Abstract

Predator use of resource subsidies can strengthen top-down effects on prey when predators respond numerically to subsidies. Although allochthonous subsidies are generally transported along natural gradients, consumers can cross ecosystem boundaries to acquire subsidies, thereby linking disparate ecosystems. In coastal Arctic ecosystems, terrestrial predators can easily cross into the marine environment (sea ice) during winter, which is a foraging strategy that Arctic foxes (*Vulpes lagopus*) use to access marine subsidies – largely seal carrion leftover from polar bear (*Ursus maritimus*) kills – especially when rodent abundance is low. Terrestrial predator use of marine subsidies may strengthen the top-down control of tundra food webs, but this hypothesis had remained untested. We took an ecosystem-level approach towards evaluating tundra food web dynamics at the terrestrial–marine interface by assessing: (i) how winter environmental conditions affect rodent abundance and marine subsidy availability, (ii) the responses of the Arctic fox population to this winter food variability, and (iii) the subsequent effects of Arctic foxes on the reproductive success of other tundra prey (Canada geese [*Branta canadensis interior*]). Arctic foxes responded numerically to rodent abundance and marine subsidy availability, which were positively related to greater snow and sea ice persistence, respectively. Canada goose reproductive success, in turn, was negatively related to Arctic fox abundance. Long-term trends in Canada goose reproduction and snow persistence on the tundra also indicate an ongoing phenological mismatch between nesting initiation and the onset of spring. Our results reveal short-term apparent competition between rodents and geese through a shared predator, Arctic foxes, which contrasts with prior studies evaluating rodent–goose–predator relationships. Moreover, we establish a link between tundra and sea ice food webs by demonstrating seal availability has a negative indirect effect on goose reproduction via carrion provisioning from polar bears to Arctic foxes, both of which are undergoing long-term population declines evidently driven by climate-related changes in prey abundance and availability. Given the importance of the winter environment in mediating these trophic interactions, we contextualize our study within ongoing climate change and highlight the vulnerability of this likely widespread terrestrial–marine linkage in a warming Arctic.

Keywords: allochthonous resources, apparent competition, Arctic fox, Canada goose, carrion provisioning, climate change, indirect effects, lemmings, phenological mismatch, polar bear, predator-prey dynamics, resource subsidy

Introduction

The flow of allochthonous resources from one ecosystem to another is ubiquitous and can have powerful effects on food webs within recipient ecosystems (Polis et al., 1997). In general, the effects of allochthonous subsidies on recipient food webs are higher when they subsidize low-productivity systems (Marczak et al., 2007). Resource subsidies can also have context-dependent effects on consumers depending on the timing, duration, or nutritional content of the subsidies (Subalusky & Post, 2019). For instance, predators may only show a numerical response to resource subsidies when they are available at particular times of year (Sato et al., 2016). Subsidies that are available to predators at irregular intervals or only for short periods of time can have short-term positive indirect effects on other prey by reducing predation pressure through consumer diet switching (Spiller et al., 2010). In contrast, spatial subsidies that are regularly available tend to elicit a numerical response in predator populations (Rose & Polis, 1998; Eide et al., 2012; Eriksson et al., 2022), which, in turn, may strengthen top-down effects on other prey through increased predator abundance (i.e., apparent competition; Holt, 1977; Polis et al., 1997).

Generally, allochthonous resources are transported *with* natural gradients (e.g., wind, current, gravity), but mobile consumers can cross ecosystem boundaries *against* natural gradients to consume resources, effectively linking disparate ecosystems through their movement (Lundberg & Moberg, 2003; McInturf et al., 2019). Resource dynamics in one ecosystem can have influential, indirect effects on another ecosystem via these mobile consumers, including modifying trophic interactions with other prey species. Notable examples of this phenomenon come from the North American Pacific Northwest: wolf (*Canis lupus*) consumption of sea otters (*Enhydra lutris*) and spawning salmon in aquatic ecosystems can subsidize wolf populations and lead to top-down limitation of ungulates through the wolves' numerical response to marine subsidies (Adams et al., 2010; Roffler et al., 2023). Despite the recognition that (i) allochthonous subsidies can have strong effects on predator populations, and (ii) predators regularly cross ecosystem boundaries to acquire resources, examples that demonstrate resource subsidies from a donor ecosystem can indirectly affect food web dynamics in a recipient ecosystem via mobile predators crossing ecosystem boundaries are lacking, in large part due to the challenges of studying these trophic relationships at relevant spatial and temporal scales.

Although tundra ecosystems have generally simple food web structures, complex indirect trophic interactions can arise through fluctuating prey populations and resource availability. Tundra rodents (namely lemmings [*Lemmus* spp. and *Dicrostonyx* spp.]) are widely known for exhibiting 3–5 yr cycles in abundance (Stenseth, 1999), and their irruptive population dynamics can have strong effects on tundra food webs (Gilg et al., 2003; Gilg et al., 2006; Schmidt et al., 2012). However, recent work found high variation in the presence, strength, and regularity of lemming cycles (Gauthier et al., 2024), suggesting lemming irruptions are likely driven by complex interactions of intrinsic (density dependence) and extrinsic factors (food supply, environmental conditions, predator abundance) (Oli, 2019). Relevant to this study is the observation that winter snow conditions can affect lemming abundance in some systems

(Kausrud et al., 2008; Bilodeau et al., 2013), with winter reproduction playing a major role in lemming population changes (Duchesne et al., 2011; Fauteux et al., 2015). Predators such as Arctic foxes (*Vulpes lagopus*) benefit from high lemming abundance, leading to population changes strongly linked to lemming dynamics (e.g., Angerbjörn et al., 1999; Gilg et al., 2006). However, as opportunistic predators, Arctic foxes readily switch to other foods when rodent abundance is low, which may generate indirect trophic interactions between rodents and other prey via their shared predator (foxes) (e.g., Bêty et al., 2001; Bêty et al., 2002; Juhasz et al., 2020). For nesting birds on the tundra, predation rates by foxes tend to increase during years of low lemming abundance (McKinnon et al., 2013; Dulude-de Broin et al., 2023).

Ecological theory suggests that ecosystems with a high perimeter to area ratio – like most coastal tundra ecosystems – are more likely to be affected by allochthonous subsidies (Polis et al., 1997), and indeed researchers have found many tundra predator diets are highly influenced by marine resources (e.g., Therrien et al., 2011; Tarroux et al., 2012; Carbonell Ellgutter et al., 2020). During winter, mobile tundra predators like Arctic foxes can easily venture onto the sea ice to access marine subsidies (Roth, 2002; Lai et al., 2017; Warret Rodrigues & Roth, 2023): Arctic foxes frequently scavenge seal carrion provisioned by polar bears (*Ursus maritimus*), which often only consume seal blubber and abandon the rest of the carcass, and foxes are also capable of killing seal pups within their lairs (Smith, 1976; Stirling & Archibald, 1977). Arctic fox use of marine resources helps stabilize their population (Nater et al., 2021), particularly when other foods (e.g., rodents) are scarce (Roth, 2003). Yet, with the Arctic warming four times faster than the rest of the world (Rantanen et al., 2022), changing climatic conditions may influence the availability of resource subsidies to predators. On one hand, rain-on-snow events, which are occurring more frequently in many Arctic ecosystems, can facilitate the availability of resource subsidies to tundra predators in the form of reindeer (*Rangifer tarandus*) carrion (Hansen et al., 2013; Ehrich et al., 2017). On the other hand, degrading sea ice regimes may reduce tundra predator access to marine subsidies in winter (Nater et al., 2021). Terrestrial predator use of marine subsidies is thought to play a role in the top-down control of tundra food webs (Gauthier et al., 2011; Legagneux et al., 2012) but little empirical support exists for this hypothesis to date. It is also unclear how environmental conditions may influence the indirect effects of marine resources on tundra food webs by affecting terrestrial predator access to these resource subsidies.

In this study, we take an ecosystem-level approach towards evaluating how abiotic and biotic factors influence coastal tundra food web dynamics via direct and indirect pathways in a warming Arctic (Fig. 1). We first investigated how environmental conditions affect the abundance of primary terrestrial prey (rodents) and the availability of marine subsidies (largely seal carrion provisioned by polar bears) to a tundra predator, Arctic foxes, during winter, and the response of the Arctic fox population to these food resources. We then evaluated how the fox population response to rodents and marine subsidies, in turn, influenced the reproductive success of Canada geese (*Branta canadensis interior*) during summer, while accounting for environmental conditions previously shown to affect goose reproduction (snow persistence, temperature, precipitation). We hypothesized that the availability of Arctic fox foods would be greater under deep winter conditions, with greater snow persistence positively affecting rodent abundance and longer sea ice duration facilitating fox access to more seals. Nests initiated later have lower rates of success in this system (Johnson-Bice et al., 2024), and we hypothesized that snow persistence on the tundra drives goose nesting phenology; we thus predicted a positive relationship between snow persistence and incubation initiation date. We also predicted lower goose nest success during years when fox den occupancy is higher; if rodent abundance and/or marine subsidy availability affect the Arctic fox population, then support for this latter prediction would demonstrate indirect effects of rodents and/or marine resources on geese via the response of a shared predator (foxes). Thus, this study also tests the hypothesis that terrestrial predator use of allochthonous subsidies may contribute to the top-down control of tundra food webs.

Methods

Study area

We conducted our study in Wapusk National Park in Manitoba, Canada, along the western coast of Hudson Bay (Roth, 2003; Johnson-Bice et al., 2023). Arctic foxes are the main fox species and predator of goose nests in the area, and we have located 88 natal fox dens within Wapusk. In this study, we focused on the closest 21 dens to the goose nesting study area, which we monitor by foot in June. Although red fox occurrence has increased in recent years (Moizan et al., 2023), the 21 dens around the goose study area are still primarily occupied by Arctic foxes and we focus our hypotheses and framing of our study on Arctic foxes.

This study uses individual Canada goose nest data from 2014–2023, though population-level data on average nest success and incubation date are available from 1976–2010. The most common goose species in our core study area is the Canada goose, but ~12 km west there has historically been a lesser snow goose (*Chen caerulescens caerulescens*) colony. For simplicity, we limit our analysis to only Canada goose nests, which comprised ~95% of nests detected. While Arctic fox diets are influenced by goose presence during summer, changes in fox abundance are driven more by rodents than geese where both prey are available (McDonald et al., 2017; Samelius & Alisauskas, 2017; Chevallier et al., 2020).

Data sources

We first assessed the effects of winter food abundance and availability (rodent abundance and marine subsidy availability) on Arctic foxes and the environmental conditions affecting these foods. We estimated rodent abundance (no./ha) using mark-recapture methods from animals live-trapped in June (full details in McDonald et al., 2017), pooling together both meadow vole (*Microtus pennsylvanicus*) and collared lemming (*Dicrostonyx richardsoni*) captures to estimate total rodent abundance (although, collared lemmings comprise 86% of captures).

We used polar bear energetics data from the Western Hudson Bay population as a proxy for seal availability (pups and carrion; seal abundance data is unavailable). Previous work from our area revealed a positive relationship between polar bear body condition and Arctic fox abundance in the 1980s and '90s (Roth, 2003), suggesting polar bear body condition can be a useful proxy of marine subsidy availability to foxes (i.e., conditions that are good for polar bear hunting success also benefit foxes, the main scavengers of bear kills). Additional details on our methods and rationale for estimating polar bear energetics are in Appendix S1.

We evaluated how winter conditions affected food availability to foxes by assessing the effects of snow cover and sea ice duration on rodent abundance and polar bear energetics, respectively. We used satellite imagery to derive estimates of snow cover (ordinal date when snow cover disappeared on a per-pixel basis, averaged across the study area) and sea ice break-up date from our study area (ordinal date when sea ice coverage in Hudson Bay was <50% for 3 consecutive days; see Appendix S1 for details on both metrics).

Finally, we used the proportion of dens occupied by foxes during the goose nesting period as our index of fox abundance/activity. During 2014–2023 (excluding 2020), we visited 21 dens on foot in June (20 dens during 2014–2016) to assess fox activity. Signs of digging/cleared burrows, fresh prey remains, and/or fresh scats, coupled with images captured by remote cameras placed on each den, were used to categorize dens as "occupied" or "unoccupied".

We conducted goose nest surveys using line-transect methods each year between June 8 and 18, 2014–2023 (excluding 2020; see Johnson-Bice et al., 2024 for full details of survey methods). Briefly, 3–5 observers located goose nests using binoculars while walking along 15 2-km long transects. Once a nest was detected, we approached the nest until the goose flushed and then counted clutch size and used egg flotation methods to estimate the date incubation was initiated, assuming a 28-day incubation period (Reiter & Andersen, 2008). Nests were revisited in late July or early August to assess nest fate; nests were categorized as successful if we observed large pieces of membrane, which correspond to at least one hatched egg (Reiter & Andersen, 2011).

To account for the effects of environmental conditions on nest success, we used daily temperature and total precipitation during the incubation period of each clutch (Juhasz et al., 2020). Daily temperature and precipitation data were obtained from Environment Canada's Churchill weather station.

All surveys and capture and handling procedures were approved by the University of Manitoba Animal Care Committee or Environment and Climate Change Canada's Western and Northern Animal Care Committee. Research was conducted under permits issued by Parks Canada, the Government of Manitoba, and Environment and Climate Change Canada.

Statistical analyses

We assembled five separate regression models to evaluate the effects of environmental conditions and trophic interactions on this coastal tundra food web (model formulas listed in Appendix S1). Our assembled regression models test the hypothesized causal (i.e., directed) relationships between each of the variables identified in our conceptual model (Fig. 1). Although food web dynamics are commonly assessed using structural equation models (SEMs), we were unable to use an SEM here due to the mixture of several different data sets. We note that individual model results would be the same as if we were to fit all models in a piecewise SEM.

We first assessed (*1*) the effects of sea ice conditions on the energetics of solitary, adult female polar bears using generalized additive mixed effects models (GAMMs) using the *mgcv* R package (Wood, 2011). Both storage energy (MJ) and energy density (MJ/kg) are useful metrics for characterizing energetics; storage energy typifies energy available for maintenance, reproduction, and growth, while energy density represents energy needed for maintenance (Johnson et al., 2020). We fit separate GAMMs to both energy density (*1a*) and storage energy (*1b*) metrics, with annual sea ice break-up date (ordinal date) as a parametric predictor variable. We also included the estimated age of each bear as a smooth term within each model to account for the possibility that energetics may have non-linear age-related traits (particularly for relatively young and old adults). We included a random intercept term for 'Year', but did not include a random intercept for 'Bear ID' due to the low number of recaptures in this subset of data (<10%). We then assessed (*2*) the effects of snow persistence (ordinal date) on rodent abundance using a generalized linear model with a Tweedie distribution within the *glmmTMB* package (Brooks et al., 2017), which can accommodate both zero and positive continuous values.

Next, we evaluated (*3*) the effects of winter food resources on Arctic foxes using a generalized linear model with a beta distribution using the *betareg* R package (Cribari-Neto & Zeileis, 2010), which is well-suited for modelling continuous proportional data. The proportion of fox dens that were occupied during the goose nesting period each year was the dependent variable (num. occupied/total num. surveyed), with rodent density and average annual polar bear energy metrics as predictor variables (we again assessed energy density [*3a*] and storage energy [*3b*] in separate models since both metrics capture slightly different energetic characteristics).

Previous work from our area demonstrated the date Canada geese initiate incubation can predict individual nest success, with nests incubated earlier having higher rates of success (Johnson-Bice et al., 2024). Snow coverage/duration is often assumed to control the timing of goose incubation, but this relationship has not been evaluated in our system. We therefore assessed (*4*) the effects of snow persistence on the date geese began incubation using a linear mixed effects model (LMM) implemented in the *lme4* R package (Bates et al., 2015). Incubation initiation date (ordinal date) of each clutch was the dependent variable, with snow persistence (ordinal date) as the predictor variable. We included a random intercept term for 'Year', but not for 'Nest ID' due to the low number of repeated nest sites in our data set (~13%).

Finally, we evaluated (*5*) the relationship between fox den occupancy and goose nest success using a generalized linear mixed-effects model (GLMM) with a binomial distribution using the *glmmTMB* package (Brooks et al., 2017). Nest success was the dependent variable (1=successful, 0=unsuccessful), with the annual proportion of fox dens occupied as a predictor variable. We also hypothesized that average daily temperature and total precipitation during incubation may influence goose nest success, and predicted that both average temperature and cumulative precipitation would be positively correlated with goose nest success as found in other studies (e.g., Juhasz et al., 2020). Incubation initiation date was also included to account for its effect on nest success (Johnson-Bice et al., 2024). We included a random intercept term for 'Transect ID', which accounts for both the annual and spatial clustering of the nest data, the latter of which we hypothesized may partially influence nest success.

We assessed the fit of all models using residual diagnostic tools and verified the lack of collinearity in each model (VIF values all <3). We verified there were no significant temporal trends of any variables tested in our models during our study period (2014–2023), despite the presence of long-term trends for several of these variables (discussed later and in Appendix S1). All analyses were conducted using R version 4.4.1 (R Core Team, 2024).

Results

Influence of winter environment on Arctic fox foods, and subsequent effects on foxes

Winter environmental conditions affected the abundance and availability of the primary winter food sources for Arctic foxes. Using data from 92 solitary adult female polar bears captured on land during fall 2014–2023 (102 total captures), we found a positive relationship between polar bear energy density (MJ/kg) and the ordinal date of 50% sea ice break-up (Table 1, Fig. 2a). However, we found only weak evidence for a relationship between polar bear storage energy (MJ) and sea ice break-up date (Table 1), suggesting sea ice conditions may affect these energetic metrics in polar bears slightly differently. Age of the bear had no substantial effect on storage energy metrics in either model (Table 1), although younger and older bears tended to have lower energy stores (Appendix S1: Fig. S1). Total rodent abundance in June was greater during years when snow persisted longer on the tundra in spring (Table 1, Fig. 2b).

Arctic fox den occupancy during the goose nesting period was affected by both rodent abundance and marine subsidy availability. We found a positive relationship between fox den occupancy in June and both polar bear energy density (Fig. 2c) and storage energy (Table 1), which we used as proxies for marine subsidy availability. AIC_c values for the models with energy density and energy storage were within 2 (-21.96 vs. -21.18), suggesting the energetic metrics performed equally well in explaining fox den occupancy. Rodent abundance positively affected fox den occupancy (Fig. 2d), with similar results between both models tested (Table 1).

Effects of environmental conditions and fox activity on Canada goose reproduction

As expected, both environmental conditions and fox activity appeared to influence Canada goose reproduction (n=436 clutches). We found longer snow persistence on the tundra delayed the date that geese initiated nest incubation (Table 1, Fig. 3a). Fox activity affected Canada goose nest success, as demonstrated by a negative effect of fox den occupancy rate on the probability of individual nest success (Table 1, Fig. 3b). As reported previously with this data set (Johnson-Bice et al. 2024), nests incubated later had lower rates of nest success (Table 1). We also found both total precipitation and average daily temperature during the incubation period positively affected individual goose nest success (Table 1, Fig. 3c-d).

Discussion

By compiling data sources related to winter environmental conditions, the abundance and availability of food resources to a top predator, and the response of the predator population to these winter foods, we provide a comprehensive examination of how goose reproduction is affected by direct and indirect pathways in a coastal tundra food web. We found evidence that environmental conditions influence the abundance and availability of winter foods for a major nest predator, Arctic foxes, which in turn negatively affect the nest success of Canada geese. Of particular interest is our ability to now indirectly link marine resources – largely carrion provisioned by a marine apex predator, polar bears – to the reproductive success of a terrestrial prey species via the subsidization of a mobile predator crossing ecosystem boundaries. We also showed environmental conditions play a key role in influencing the susceptibility of goose nests to predation by controlling when geese can initiate nesting. Our study provides an ecosystem-level perspective on the dynamics of a tundra food web at the terrestrial–marine interface.

Our finding that both marine subsidy availability and rodent abundance appear driven by deeper winter environmental conditions highlights the susceptibility of these food sources to a warming Arctic. We used polar bear energetics as a proxy for marine subsidy availability based on the assumption that environmental conditions that promote polar bear hunting success also benefit Arctic foxes, which was supported by the relationships between fox den occupancy and polar bear energy density and storage energy (Table 1, Fig. 2c). The ability of foxes (and polar bears) to access seals depends on sea ice conditions, which are rapidly changing in Hudson Bay, where sea ice duration has declined by ~10 days/decade over the past 40 yrs (Boonstra et al., 2020; Verstege et al., 2023). Reduced sea ice duration is known to influence polar bear body condition and survival in the Western Hudson Bay population via reduced availability of seals and longer fasting periods (e.g., Stirling et al., 1999; Regehr et al., 2007; Lunn et al., 2016). Similarly, our results suggest that, in this system, rodent abundance is currently influenced by winter snow conditions (in contrast to many other systems; Gauthier et al., 2024). Current rodent abundance peaks at ~2/ha, substantially lower than peak abundance in the 1990s (~12/ha; Roth, 2003) and as far back as the 1930s and ‘60s (~40/ha or more; Shelford, 1943; Scott, 1993). Ostensibly, then, declining rodent abundance could be partially attributed to snow persistence conditions, which have been declining since at least 2000 (Appendix S1: Fig. S2). Altogether, this study presents key evidence that changing winter climate reduces the abundance and availability of the main winter foods for Arctic foxes (rodents and seals), and further supports the hypothesis that the ongoing, long-term decline of this Arctic fox population is largely being caused by climate-driven changes in their winter food supply (Verstege et al., 2023).

Consistent with our hypotheses, Canada goose reproduction also appears affected by environmental conditions, most of which are similarly changing as the region warms. Both greater precipitation and warmer temperatures during incubation had a positive effect on nest success (Table 1, Fig. 3c-d). Greater precipitation is thought to reduce the time females spend off nest to drink water, thereby reducing their susceptibility to predation (Lecomte et al., 2009;

Juhasz et al., 2020); however, water sources are ubiquitous in our wetland-dominated study area and geese already show strong selection for nest sites near water (Johnson-Bice et al., 2024), so we suspect precipitation may provide other nesting benefits. One plausible explanation is that greater precipitation may hinder fox mobility through the wetlands, thus reducing their ability to depredate nests. Regarding temperature, warmer temperatures are thought to reduce embryo mortality and/or enhance food resource availability for geese (Dickey et al., 2008), which may both be occurring here. Also, warmer spring temperatures likely reduce snow persistence on the tundra, and snow disappearance appears to drive the timing of incubation (Fig. 3a; Madsen et al., 2007; Lameris et al., 2019), which, in turn, affects goose reproductive success (Table 1). Yet, like many Arctic systems, Canada geese in our system are apparently not adjusting their nesting phenology enough to compensate for earlier springs (Appendix S1: Fig. S2), which may negatively affect gosling growth rates and ultimately survival and recruitment (Brook et al., 2015). Lameris et al. (2019) found early-breeding barnacle geese (*Branta leucopsis*) had the highest rates of nest success in the high Arctic, while geese breeding at intermediate dates had the highest rates of success in the low Arctic, suggesting low-Arctic geese may be more capable of adjusting to a warming climate. However, we have no evidence that Canada geese in our low-Arctic system show greater rates of nest success at intermediate dates (Appendix S1: Fig. S4), indicating an ongoing phenological mismatch between goose nesting and the onset of spring. This mismatch may help explain why Canada goose abundance has remained stable for decades (Luukkonen & Leafloor, 2021) despite likely greater plant productivity from warmer springs (Appendix S1: Fig. S3), lower Arctic fox abundance, and a recent collapse in the nearby colony of lesser snow geese (*unpublished data*), the main competitor of Canada geese.

Our finding that increasing rodent abundance has a short-term negative indirect effect on goose reproduction via the numerical response of a shared predator stands in contrast to other studies from the Arctic. Previous research from our study area did not find an effect of rodent abundance on Canada goose nest survival between 1993–2004 (Reiter & Andersen, 2011); however, the authors used population reconstruction methods to estimate rodent abundance rather than live-trapping, and Arctic foxes were being lethally removed by managers during the study, both of which may have affected their results. Most studies evaluating the indirect effects of rodents on tundra breeding birds found support for the “alternative prey hypothesis”, whereby prey switching behavior by predators during low lemming years causes lower nest success of birds (e.g., Bêty et al., 2001; Bêty et al., 2002; McKinnon et al., 2013; Juhasz et al., 2020). The positive indirect effects of lemmings on nesting birds appears driven by lower activity levels of Arctic foxes when lemmings are abundant, thereby releasing predation pressure on birds (Beardsell et al., 2022). Notably, however, most of these studies evaluated rodent–goose–predator interactions in systems with colonially breeding geese and generally higher lemming densities. Predators must spend more time searching for dispersed breeding birds relative to colonial breeding birds, suggesting search time may be a limiting factor in the acquisition rate of Canada goose eggs by Arctic foxes. But rodent abundance here may not be high enough during peak years to sustain foxes, so foxes must still consume relatively large quantities of geese and their eggs and thus maintain high activity levels regardless of rodent abundance; indeed, we previously documented no relationship between rodent abundance and the proportion of Arctic fox diet comprised of geese (McDonald et al., 2017). Collectively, these patterns suggest the negative indirect effect of rodents on Canada goose nest success is likely driven by greater encounter rates between foxes and goose nests due to foxes being more abundant in high-rodent years. Additionally, since snow persistence affects both rodent abundance and goose nesting phenology, fox predation success may be greater during high-rodent years due to geese being in worse body condition from snow-related delays in nesting (Johnson-Bice et al., 2024). Regardless of the exact mechanism, this study presents novel evidence for short-term apparent competition between rodents and geese via a shared predator in the low-Arctic tundra.

We provide evidence that the use of marine subsidies by a mobile terrestrial predator can indirectly affect other tundra prey via the predator's numerical response, a dynamic that is likely widespread throughout the Arctic due to the circumpolar distributions of Arctic foxes, polar bears, seals, and geese. Arctic fox den occupancy was higher following winters when adult female polar bears were in good body condition (Fig. 2c), suggesting foxes respond numerically to greater marine resource availability during winter (Roth, 2003). Arctic foxes in our area tend to disperse in winter during food scarcity (Warret Rodrigues & Roth, 2023), but increased access to marine subsidies evidently leads to greater fox reproduction and/or allows adults to persist longer on the tundra, resulting in greater den occupancy rates. Our finding that Arctic fox den occupancy, in turn, was negatively related to goose nest success demonstrates an indirect link between marine subsidies and tundra food web dynamics. Tundra food webs are strongly regulated by top-down forces during summer, and predator use of allochthonous subsidies was previously hypothesized to strengthen these top-down effects (Gauthier et al., 2011; Legagneux et al., 2012) but had never been supported prior to this study. The different timing in the availability of seals and geese likely drives this interaction and allowed us to parse out the causal pathways. Seal pups/carrion are available only in winter/early spring, which is when fox mating and reproduction occurs, while geese are available only during late spring and summer; the indirect effects of seals on goose reproduction in spring are thus mediated by the fox's numerical response to seals in winter. Our study adds to the literature demonstrating the effects of resource subsidies on food webs can be strongly influenced by their timing (Sato et al., 2016).

Although we revealed an intricate link between Arctic marine and tundra food webs via the subsidization of a terrestrial predator on the sea ice, the rapid climate-driven degradation of coastal Arctic ecosystems suggests the strength of these interaction pathways are declining and may be poised to disrupt entirely. When prey (seals) are abundant, polar bears preferentially strip the blubber off of seals they kill (Stirling & Archibald, 1977), leaving large amounts of carrion for scavengers like Arctic foxes. However, warming Arctic conditions may cause a decline in ringed seal (*Pusa hispida*) abundance, a main prey for Western Hudson Bay bears, through changes in seal pup survival and shifts in the community composition of seal prey (Reimer et al., 2019; Florko et al., 2021). The combination of fewer seals, coupled with fewer polar bears and longer fasting periods for bears, likely means less carrion for scavengers due to fewer seal carcasses generated and higher rates of carcass utilization by bears (Petherick et al., 2021). Shorter sea ice seasons also imply foxes have access to marine resources for shorter periods of time (Nater et al., 2021). Collectively, these patterns indicate an ongoing and future weakening of the marine subsidization of Arctic foxes that, along with declining lemming abundance and lower overall goose production likely due in part to a reproductive phenological mismatch (Canadian Wildlife Service Waterfowl Committee, 2023), will continue to have consequences for tundra ecosystems. Our work sheds light on the linkage between Arctic tundra and marine food webs, but also highlights the importance of continued long-term monitoring of these food webs to better understand how the effects of climate change are reshaping trophic interactions through direct and indirect pathways.

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Table 1. Summary results from the five regression models evaluating the direct and indirect drivers of Canada goose reproductive success in Wapusk National Park, Canada.

Model	***Model statistics***				
Variable	**Estimate ($\widehat{\beta}$, edf)**†	**SE**	**Conf. interval**	**Statistic (t, z, F)**‡	***p*-value**
1a. Polar bear energy density	Deviance explained = 20.9%				
Sea ice breakup (ordinal date)	0.207	0.095	(0.021, 0.393)	2.17	0.032
f_{Age}	2.172	-	-	1.85	0.218
f_{Year}	3.002	-	-	0.80	0.087
1b. Polar bear storage energy	Deviance explained = 26.6%				
Sea ice breakup (ordinal date)	22.53	12.94	(-2.83, 47.89)	1.74	0.085
f_{Age}	2.416	-	-	1.63	0.214
f_{Year}	4.326	-	-	1.72	0.012
2. Rodent abundance	*Pseudo* $R^2 = 0.568$				
Snow duration (ordinal date)	0.064	0.025	(0.015, 0.113)	2.58	0.010
3a. Fox den occupancy rate	*Pseudo* $R^2 = 0.858$				
Rodent abundance	0.580	0.109	(0.367, 0.793)	5.34	<0.0001
Polar bear energy density	0.073	0.019	(0.036, 0.109)	3.93	<0.0001
3b. Fox den occupancy rate	*Pseudo* $R^2 = 0.846$				
Rodent abundance	0.525	0.117	(0.297, 0.754)	4.50	<0.0001
Polar bear storage energy	0.0006	0.0002	(0.0003, 0.0009)	3.67	0.0002
4. Incubation initiation date	Cond. $R^2 = 0.655$, Marg. $R^2 = 0.572$				
Snow duration (ordinal date)	0.558	0.081	(0.040, 0.714)	6.85	<0.0001
σ_{Year}	1.898	0.553	(0.937, 2.983)	-	-
5. Canada goose nest success	Cond. $R^2 = 0.326$, Marg. $R^2 = 0.314$				
Fox den occupancy rate	-3.155	1.469	(-6.034, -0.276)	-2.15	0.032
Incubation initiation date	-0.154	0.032	(-0.217, -0.091)	-4.78	<0.0001
Avg. temp. during incubation	0.229	0.102	(0.029, 0.430)	2.24	0.025
Total precip. during incubation	0.018	0.005	(0.008, 0.027)	3.76	0.0002
$\sigma_{\text{TransectID}}$	0.250	0.553	(0.013, 4.660)	-	-

†Estimates are **edf** (effective degrees of freedom) for Models 1a, 1b, and $\widehat{\boldsymbol{\beta}}$ for all other terms.

‡Statistics are $\boldsymbol{t}$ for parametric terms of models 1, 2, **F** for smooth terms of models 1a, 1b, and $\boldsymbol{z}$ for models 3–5.

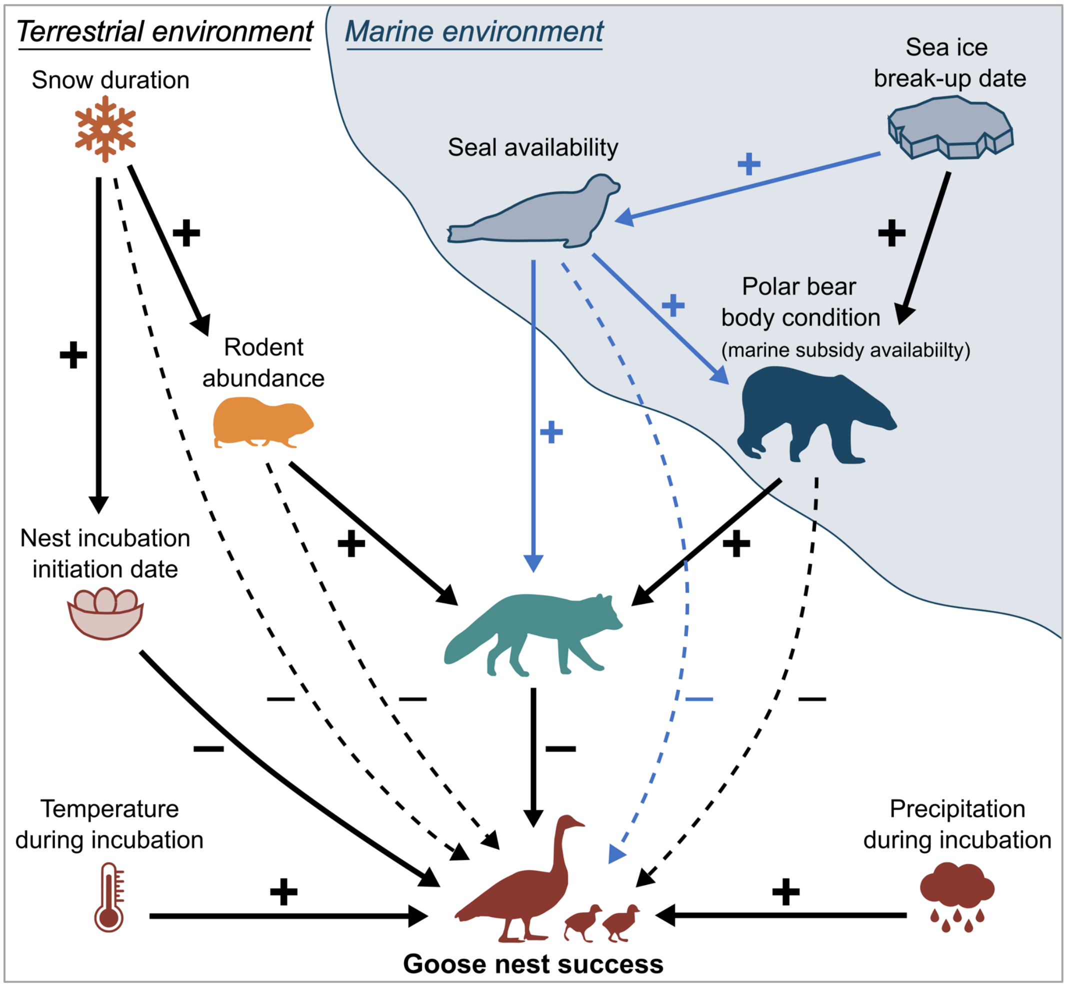

Figure 1. Conceptual model depicting our hypotheses on how winter environmental conditions, food abundance/availability, and predator activity interactively shape Canada goose nest success through direct and indirect pathways in a coastal tundra ecosystem. We hypothesized environmental conditions affect the availability/abundance of winter food resources for Arctic foxes, with greater snow and sea ice duration having positive effects on rodent abundance and seal carrion availability (marine subsidies), respectively. We also hypothesized that greater fox activity/abundance would negatively affect goose nest success, which would demonstrate indirect negative effects of marine resources and rodents on goose reproduction that are mediated through a shared predator (foxes). We hypothesized environmental conditions play a strong role in goose reproduction, with snow coverage affecting the timing of nest incubation, and temperature and precipitation during incubation affecting the availability of resources for breeding geese. Solid black lines represent hypothesized causal (i.e., directed) relationships and pathways evaluated in this study. The solid blue lines relating to seal availability represent latent direct relationships that we could not test due to an absence of seal abundance data. Dashed lines represent the hypothesized indirect effects of rodents, seals, and snow conditions on goose reproduction (blue = latent indirect effect).

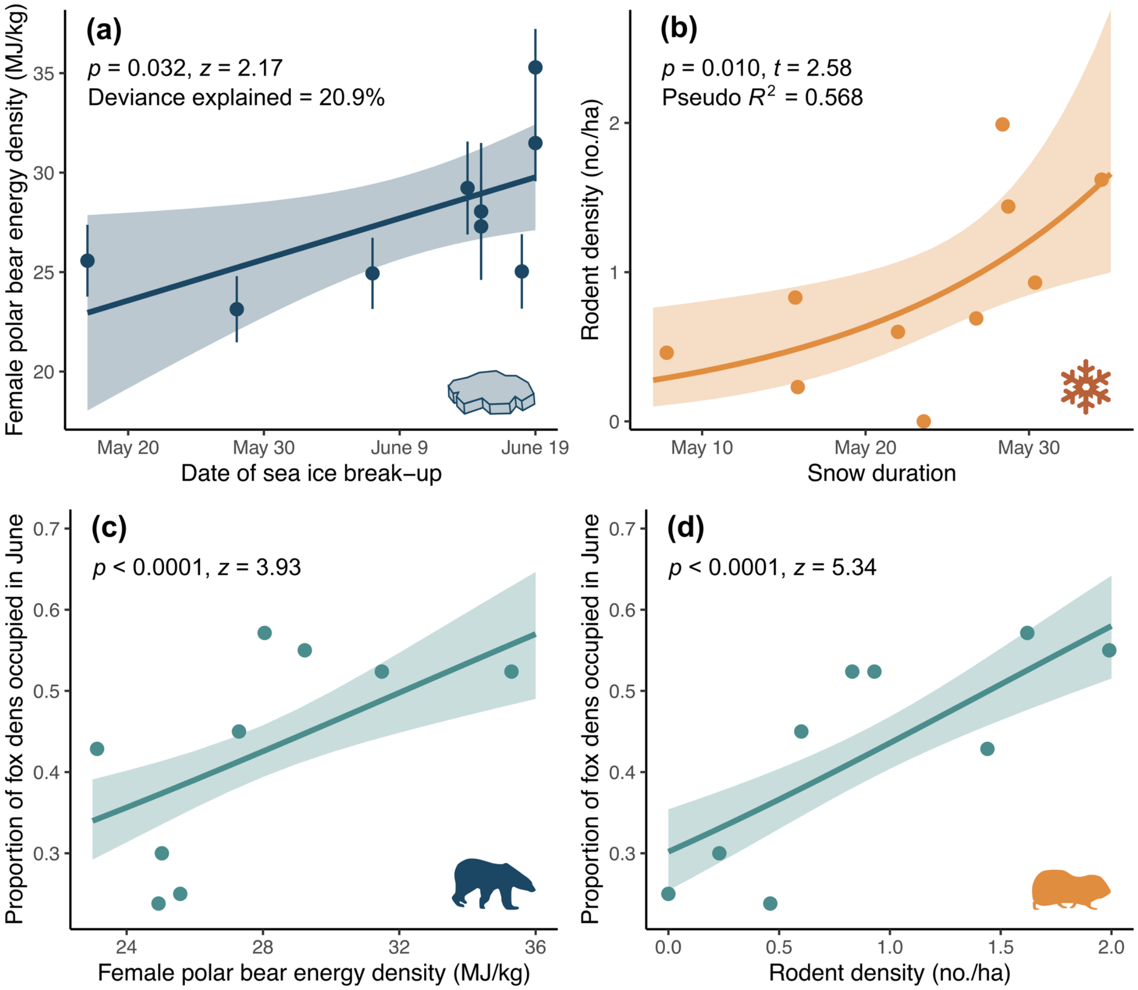

Figure 2. Results depicting how winter environmental conditions affect winter food abundance and availability for Arctic foxes, which, in turn, respond numerically to greater food resources. Panel (a) shows the estimated effect of sea ice duration on female polar bear energy density (MJ/kg). Individual points show the annual average values +/- std. error. Panel (b) depicts the estimated relationship between snow duration and rodent abundance on the tundra. Panels (c) and (d) show the marginal effects of female polar bear energy density and rodent density, respectively, on fox den occupancy rates. Points in panels (b–d) depict the raw data used in the models. Ribbons represent +/- 95% confidence intervals of each estimated relationship. Colors and icons correspond to linkages from Fig. 1.

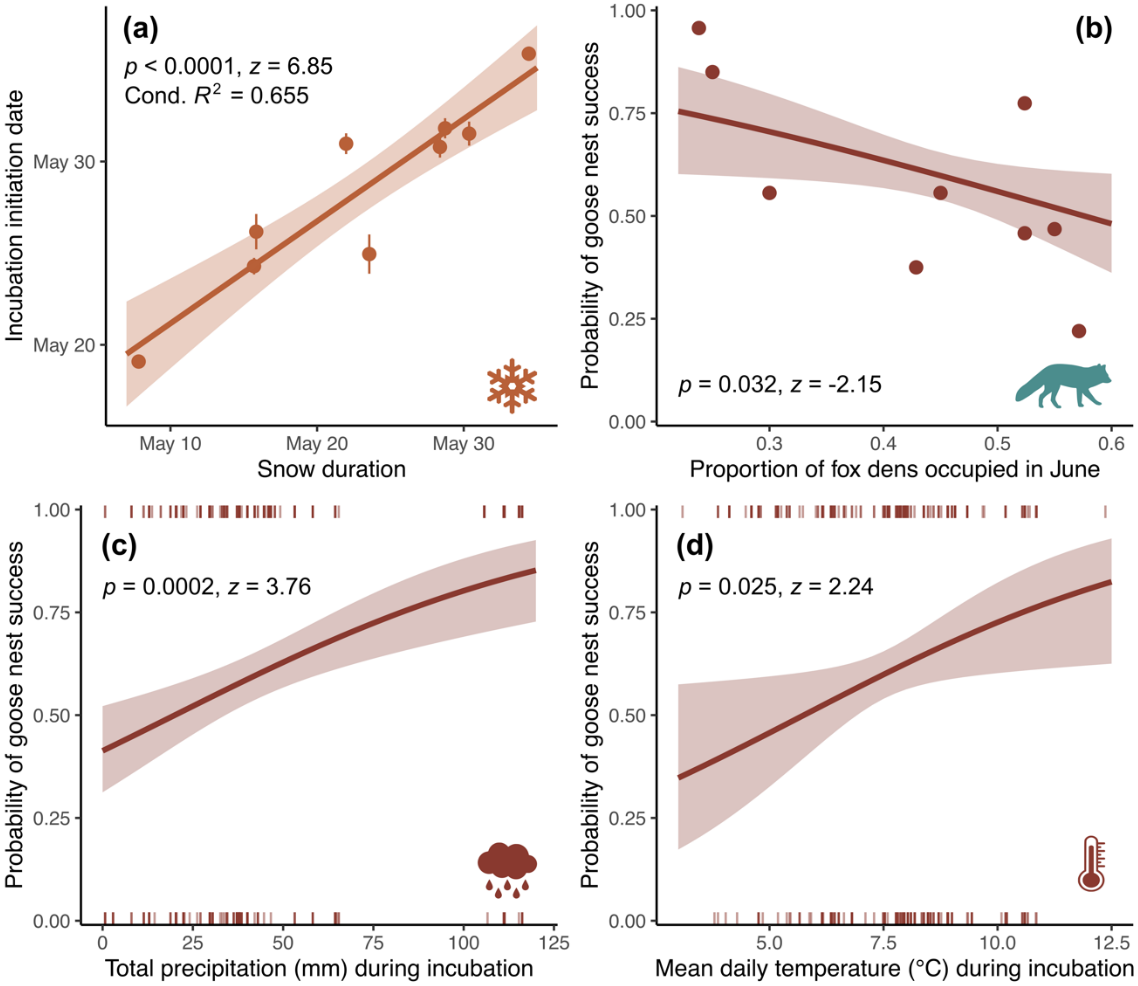

Figure 3. Results depicting how environmental conditions and fox activity affect Canada goose reproduction. Panel (a) shows the estimated effect of snow duration on incubation initiation date. Individual dots show the annual average values +/- std. error, highlighting the low intra-annual variation in timing of incubation throughout the goose population. Panels (b–d) depict the marginal effects of fox den occupancy, cumulative precipitation during incubation, and average daily temperature during incubation, respectively, on the probability of goose nest success. Dots in panels (b) are the average annual nest success values. Ribbons represent +/- 95% confidence intervals of each estimated relationship. Colors and icons correspond to linkages from Fig. 1.

Supplementary material for: "Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice"

Authors: Sean M. Johnson-Bice, Frank B. Baldwin, Evan S. Richardson, James D. Roth

Data sources

Polar bear energetics data

Polar bears were captured on land during September and October, 2014–2023, as part of long-term research and monitoring of the Western Hudson Bay polar bear population led by Environment and Climate Change Canada. Bears were captured opportunistically as they were encountered by research personnel, anesthetized, measured (straight-line body length and axial girth length), and individually marked with ear tags and tattoos and then released. Full details on capture and handling of bears can be found in Stirling et al. (1999) and Johnson et al. (2020).

Polar bear energetics are influenced by sea ice conditions, with solitary adult females being particularly vulnerable to low food availability due to their reduced ability to compete with large males for food (Johnson et al., 2020). We therefore hypothesized that solitary adult females would be the sex/age class that best reflected annual marine subsidy availability to foxes. Using equations from Molnár et al. (2009), we calculated storage energy (MJ) and energy density (MJ/kg) for solitary adult female bears captured during September and October 2014–2023 (excluding 2020):

$$Storage\ energy\ (MJ) = 26.14M - 390.53L^3$$

where M is the body mass (kg) of the bear and L is the length of the bear (cm). Polar bear body mass was estimated using the regression equation presented in Thiemann et al. (2011) based on the axillary girth and straight line measurements. We followed methods used by Stirling et al. (1999) to correct each bear's mass based on capture date to account for ongoing fasting by bears. Specifically, we corrected mass to a constant capture date of September 21 and adjusted estimated mass to account for 0.85 kg lost each day fasting (subtracting 0.85 kg each day for capture dates before Sept. 21, or adding 0.85 kg each day for capture dates after Sept. 21).

Energy density is calculated as the ratio between $Storage\ energy$ and lean body mass:

$$Energy\ density\ (MJ\ kg^{-1}) = Storage\ energy/(M - M_{STO})$$

where $Storage\ energy$ is solved from the previous equation, M is the corrected body mass (kg) of each bear, and M_{STO} is the storage mass of each bear calculated as $(M - 14.94L^3)$ (Molnár et al., 2009).

Sea ice and snow cover duration data

Snow cover data derived from MODIS satellite imagery was used to assess when snow disappeared from the study area each year on a 500 m pixel-by-pixel basis following methods developed by Crumley et al. (2020) using Google Earth Engine. We censored any pixels that indicated snow melted before May 1 or after July 1, which largely corresponded to intertidal areas and misclassification of the pixels (these dates represent approximately the earliest and latest dates of snow disappearance based on our personal observations). We then calculated the mean snow disappearance date across all pixels within the study area using the 'Zonal statistics as table' tool in ArcGIS Pro (version 2.8; Esri, Redlands, CA, USA). Sea ice break-up dates for Hudson Bay were derived from satellite imagery from the National Snow and Ice Data Center (Boulder, CO, USA). Break-up date was defined as the ordinal date when >50% of all sea ice pixels had disappeared for 3 consecutive days (Boonstra et al., 2020; Johnson et al., 2020; Verstege et al., 2023).

Statistical analyses: additional details on models used in this study

As mentioned in the main text, we compiled 5 separate regression models to test a series of hypotheses about food web dynamics in our system: 1) the effects of sea ice break-up date and bear age on solitary adult female polar bear energy density (1a) and energy storage (1b) (generalized additive mixed-effects models [GAMMs]); 2) the effects of snow duration (ordinal date) on rodent abundance (generalized linear model with a Tweedie distribution); 3) the effects of rodent abundance and marine subsidy availability (using polar bear energetics as a proxy) on fox den occupancy during the goose nesting period (generalized linear model with a beta distribution); 4) the effects of snow persistence on Canada goose nest incubation initiation date (linear mixed-effects model); and 5) the effects of fox den occupancy, cumulative precipitation during incubation, average daily temperature during incubation, and incubation initiation date on the probability of goose nest success (generalized linear mixed-effects model [GLMM] with a binomial distribution). Details on each model are listed below.

Model 1a: $EnergyDensity_{ij} = SeaIceBreakup_{ij} + f(Age_{ij}) + Year_i + \varepsilon_{ij}$

$Year_j \sim N(0, \sigma^2)$

where $EnergyDensity_{ij}$ is the estimated energy density (MJ/kg) of a solitary adult female polar bear j in year i; $SeaIceBreakup_{ij}$ is the ordinal date of sea ice break-up for the jth energy density estimate of bear j in year i (same value for all bears captured in the same year); Age_{ij} is the age of bear j in year i, which was fit with a smoothing component f using thin plate regression splines comprised of 9 basis functions; $Year_i$ is a random intercept term that is assumed to be normally distributed with mean 0 and variance σ^2; and ε_{ij} is residual variance unexplained by the model.

Model 1b: Model 1b takes the same form as Model 1a, except that we are solving for $StorageEnergy_{ij}$ (MJ) instead of $EnergyDensity_{ij}$ (MJ/kg).

Model 2: $RodentAbundance_i \sim Tweedie(\mu_i)$

$$E(RodentAbundance_i) = \mu_i$$

$$\log(\mu_i) = SnowDuration_i + \varepsilon_i$$

where $RodentAbundance_i$ is the estimated rodent abundance (num. captured per hectare) obtained from capture-mark-recapture methods in year i, $SnowDuration_i$ is the date that snow disappeared from the study area in year i, and ε_i is residual variance unexplained by the model.

Model 3a: $PropDenOccupied_i \sim Beta(\pi_i)$

$$E(PropDenOccupied_i) = \pi_i$$

$$\text{logit}(\pi_i) = RodentAbundance_i + EnergyDensity_i + \varepsilon_i$$

where $PropDenOccupied_i$ is the proportion of fox dens occupied in year i, $RodentAbundance_i$ is the estimated number of rodents per hectare in year i, and $EnergyDensity_i$ is the average energy density (MJ/kg) of solitary adult female polar bears captured in year i.

Model 3b: Model 3b takes the same form as Model 3a, except that we are using the average storage energy (MJ) of solitary adult female polar bears captured in year *i* instead of average energy density (MJ/kg).

Model 4: $IncubationDate_{ij} = SnowDuration_{ij} + Year_i + \varepsilon_{ij}$

$$Year_i \sim N(0, \sigma^2)$$

where $IncubationDate_{ij}$ is the date incubation was initiated (ordinal day) for the *j*th nest in year *i*, and $Year_i$ is a random intercept term that is assumed to be normally distributed with mean 0 and variance σ^2.

Model 5: $NestSuccess_{ij} \sim Bernoulli(\pi_{ij})$

$$E(NestSuccess_{ij}) = \pi_{ij}$$

$$\text{logit}(\pi_{ij}) = PropDenOccupied_{ij} + Temp_{ij} + Precip_{ij} + TransectID_i + \varepsilon_{ij}$$

$$TransectID_i \sim N(0, \sigma^2)$$

where $NestSuccess_{ij}$ is the probability of nest success (1=success, 0=failed) of the *j*th clutch in Transect *i*, $PropDenOccupied_{ij}$ is the proportion of fox dens occupied in the year Transect *i* occurred, $Temp_{ij}$ is the average daily mean temperature during incubation of the *j*th clutch in Transect *i*, and $Precip_{ij}$ is the cumulative precipitation during the incubation of the *j*th clutch in Transect *i*. $TransectID_i$ is a random intercept term that is assumed to be normally distributed with mean 0 and variance σ^2.

Supplementary results

Effects of age on polar bear energetics

In our models evaluating the effects of sea ice break-up date on solitary adult female polar bear energetics, we included the age of each bear as a predictor variable in each model to account for the effects age may have on energy density and storage energy. We added a smoothing component (*f*) to the 'Age' variable, as we hypothesized that particularly younger and older bears may have poorer energetics due to likely worse hunting abilities. Our results did not detect a significant non-linear effect of Age on either energetic metric, although there was a tendency for younger and older bears to have lower energy density and storage energy (Fig. S1).

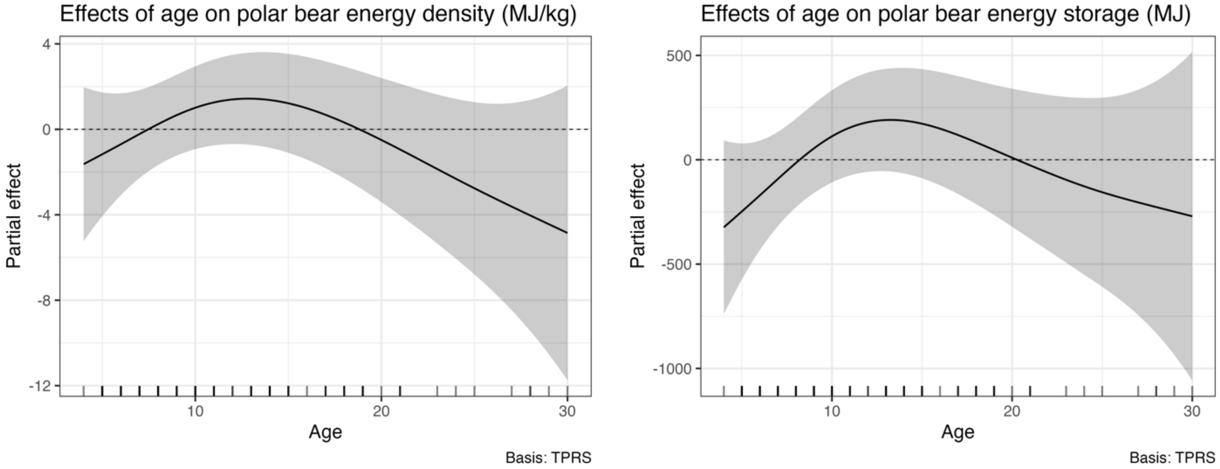

Figure S1. Results from the generalized additive mixed-effects models (GAMMs) evaluating the effects of polar bear age on the energy density (*left*) and storage energy (*right*) of solitary adult female polar bears from the Western Hudson Bay population. Graphs show the partial effects as predicted from the GAMMs, with the ribbons representing +/- 95% confidence intervals.

Climate and phenology trends related to Canada goose reproduction

We compared the linear trends in median goose nest incubation date for each year (Andersen et al. 2010) against the average snow persistence date spanning 2000–2023. Snow persistence date from 2000–2023 was obtained from MODIS satellite imagery using the methods described earlier in this supplementary material document.

Snow persistence in our study area has advanced ~0.60 days/yr from 2000–2023, while median goose nest incubation date has only advanced ~0.23 days/yr (Fig. S2). If we omit the 4 years of data that we do not have estimates for goose nesting phenology from the snow persistence trend (2011–2013, 2020), the rate of declining snow persistence still holds at -0.63 days/yr. These results suggest that Canada geese are not advancing their nesting phenology to keep up with climate-driven changes in snow persistence in the study area.

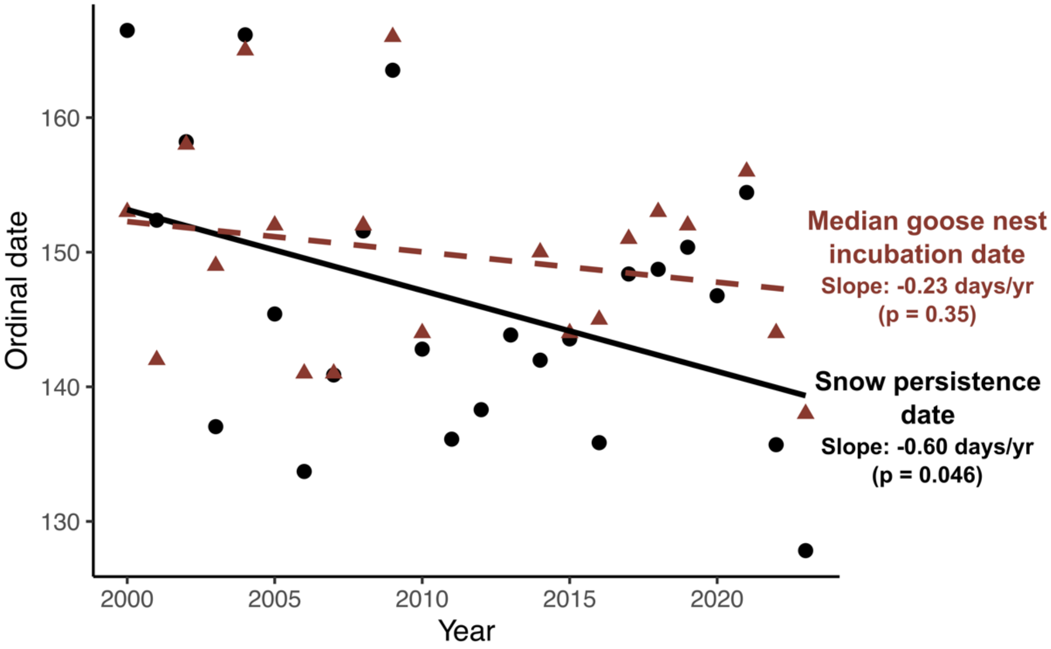

Figure S2. Linear trends of Canada goose median nest incubation initiation date (red triangles, red dashed line) and snow persistence date (black circles, solid line) from 2000 to 2023 in Wapusk National Park, Manitoba, Canada. The linear trends show the date that snow disappears from the study area is advancing roughly 2.6 times faster than median nest incubation date, suggesting an ongoing phenological mismatch between goose nesting and snow coverage.

To provide context for the significant effects of average daily temperature and cumulative precipitation during the incubation period on Canada goose nest success (*main text*), we assessed the long-term trends of each climate variable for the month of June using weather data from the Churchill, MB weather station from 1980–2023. Average daily temperatures have increased significantly, while precipitation has declined but the temporal trend was insignificant (Fig. S3).

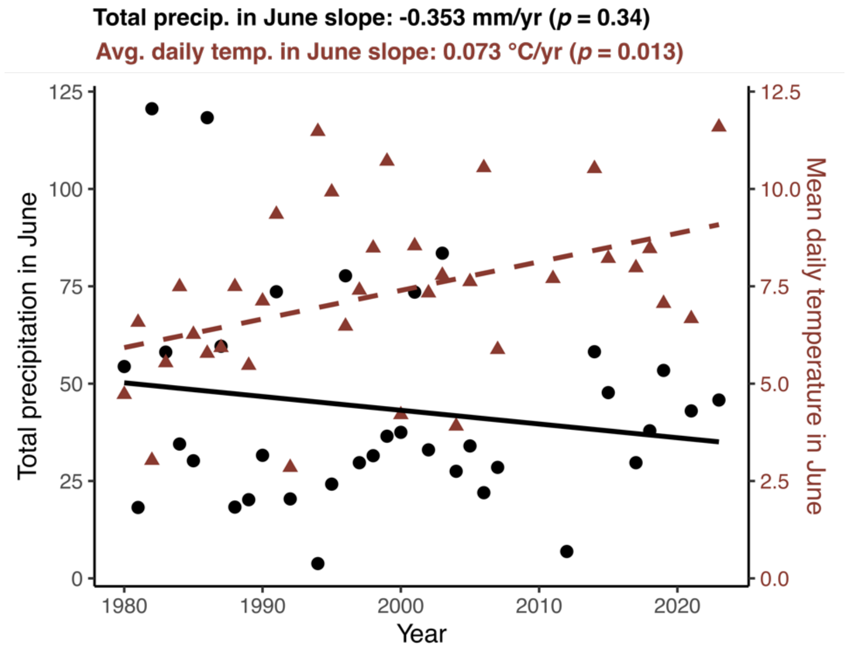

Fig. S3. Long-term trends in average temperature and total rainfall from the Churchill, MB weather station, 1980-2023. There has been a significant increase in June temperature (~5.9°C in 1980 to ~9.1°C), and a non-significant decrease in total precipitation.

Finally, previous research compared nesting success of barnacle geese (*Branta leucopsis*) in relation to nesting phenology between low- and high-Arctic populations (Lameris et al., 2019). The authors found that early-breeding barnacle geese had the highest rates of nest success in the high Arctic, while intermediate-breeding geese had higher rates of success in the low Arctic. Their conclusion from these results was that low-Arctic geese appear to be keeping up with changing phenology better than high-Arctic geese. However, we do not see that same trend in our population. We fit the relationship between incubation initiation date and probability of nest success to a Loess smoother to assess whether there was a non-linear relationship between these two variables, which may indicate geese that nest at intermediate dates have higher rates of success. We found no evidence that nest success increases at intermediate incubation dates (Fig. S4). Thus, we have more evidence for an ongoing phenological mismatch for a low-Arctic goose population, indicating some low-Arctic populations may be just as vulnerable to the effects of climate warming as high-Arctic populations.

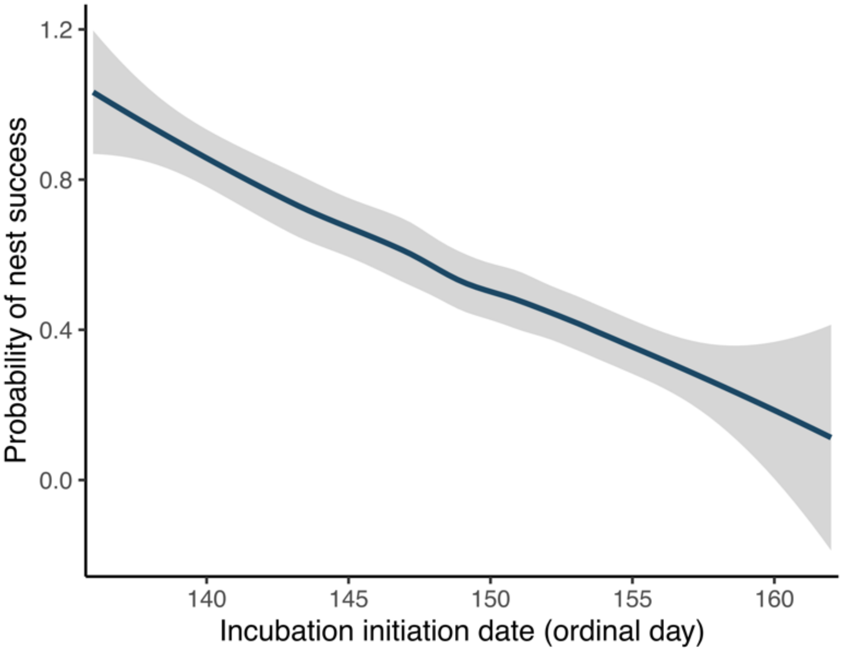

Figure S4. The relationship between incubation initiation date (ordinal day) and the probability of Canada goose nest success in Wapusk National Park, Manitoba, Canada, 2014–2023, fit with a Loess smoother. The data suggests no evidence of a non-linear relationship between nesting phenology and Canada goose nest success.

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