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 like Arctic foxes (*Vulpes lagopus*) cross into the marine environment (sea ice) during winter to access marine resources. Arctic foxes kill seal pups and scavenge seal carrion (often remains 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 remained untested. We evaluated tundra food web dynamics at the terrestrial–marine interface from an ecosystem-level perspective by assessing: (i) how winter environmental conditions affect rodent abundance and marine subsidy availability, (ii) the responses of the Arctic fox population to this seasonal food variability, and (iii) the subsequent effects of Arctic foxes on Canada goose (*Branta canadensis interior*) reproduction. Arctic foxes responded numerically to rodent abundance, which was positively related to snow persistence. Arctic fox abundance was positively related to polar bear body condition metrics, which were used as a proxy for marine subsidy availability. Canada goose reproductive success, in turn, was negatively related to Arctic fox abundance. Long-term trends in goose reproduction and snow persistence also indicate an ongoing phenological mismatch between nesting initiation and spring onset. Our results reveal near-term apparent competition between rodents and geese through a shared predator, Arctic foxes, contrasting with prior studies evaluating rodent–goose–predator relationships. Moreover, we establish a link between tundra and sea ice food webs by demonstrating how seal availability can affect goose reproduction indirectly by increasing Arctic fox predation on goose nests via a population response of foxes to marine resources. These marine resources are often provisioned by polar bears, and with both Arctic foxes and polar bears undergoing long-term regional declines evidently driven by climate-related changes in prey abundance and availability, 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 in recipient ecosystems (Polis et al., 1997). In general, the effects of allochthonous subsidies on recipient food webs are higher when they subsidize systems with low levels of comparable resources (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 respond numerically to resource subsidies only 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.

Despite simple food web structures, complex indirect trophic interactions can arise in tundra ecosystems through fluctuating prey populations and resource availability. Tundra rodents (namely lemmings [*Lemmus* spp. and *Dicrostonyx* spp.]) are renowned for their 3–5 yr cycles in abundance (Stenseth, 1999), and their irruptive population dynamics can have strong effects on 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 both intrinsic (density dependence) and extrinsic factors (food supply, environmental conditions, predator abundance) (Oli, 2019). In particular, snow conditions can affect lemming abundance in some systems (Kausrud et al., 2008; Bilodeau et al., 2013a), as winter reproduction plays 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 (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) (Bêty et al., 2001, 2002; Juhasz et al., 2020). For tundra-nesting birds, predation rates by foxes tend to increase during years of low lemming abundance (McKinnon et al., 2013; Dulude-de Broin et al., 2023). Although 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).

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 tundra predator diets are often influenced by marine resources (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 (Stirling & Archibald, 1977). Arctic foxes are also capable of killing seal pups within their lairs (Lydersen & Gjertz, 1986), with one study estimating Arctic foxes killed ~26% of ringed seal pups in the area (Smith, 1976). The use of marine resources helps stabilize Arctic fox population dynamics (Nater et al., 2021), particularly when other foods 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 predator access to reindeer (*Rangifer tarandus*) carrion by increasing reindeer mortality (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 assessed how environmental conditions affect the abundance of primary terrestrial prey (rodents) and the availability of marine subsidies (seal biomass) 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 spring, 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 harsh 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., 2025), and we hypothesized that snow persistence on the tundra drives goose nesting phenology; we thus predicted geese initiate nesting later during years snow persists longer. We also predicted rodent abundance and marine subsidy availability positively affected fox den occupancy. Our study area lacks annual data on seal abundance, so we used polar bear energetics as a proxy for marine subsidy availability to Arctic foxes, given that both species feed on the same resource and Arctic foxes frequently scavenge seal carrion left from polar bear kills (Stirling & Archibald, 1977; Roth, 2002). Finally, we predicted goose nest success would be lower during years when fox abundance was high, demonstrating an indirect effect of rodents and/or marine subsidies on goose reproduction 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 (Fig. 2; Roth, 2003; Johnson-Bice et al., 2023). Arctic foxes are the main fox species and predator of goose nests in the area (responsible for >80% of nest failures in some years; Walter, 1996; Reiter & Andersen, 2011). Recent research has demonstrated Canada geese proactively choose nesting sites in areas less-used by foxes and nesting success is lower in areas most used by foxes (Johnson-Bice et al., 2025). We have located 88 natal fox dens within Wapusk, but this study focuses on the closest 22 dens to the goose nesting study area, which we monitor annually by foot in the goose nesting period. Although red fox occurrence has increased in recent years (Moizan et al., 2023), the 22 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.

During winter, Arctic fox diets are heavily influenced by rodents (*Dicrostonyx* , *Microtus*) in this region but they also consume large amounts of marine resources (namely ringed seal biomass), particularly when rodent abundance is low (Roth, 2002; Dudenhoeffer et al., 2021). In this region, marine resources may constitute up to 67% of Arctic fox diets (Roth, 2003), and preliminary results from an ongoing study indicate Arctic foxes are the most common scavenger of seal carcasses (*personal communication*, H.E.L. Gamblin, University of Manitoba). Although caribou carrion can be an important winter food for Arctic foxes in some areas, caribou is a secondary food source in this system, as the local caribou herd migrates tens to hundreds of kilometers inland from the study area during winter (Dudenhoeffer et al., 2021; Lochansky et al., 2024). Arctic fox summer and fall diets are heavily influenced by geese, but goose resources appear to have minimal effect on Arctic fox reproduction (McDonald et al., 2017).

This study uses individual Canada goose nest data from 2014–2024. The most common goose species in our study area is the Canada goose, but a lesser snow goose (*Chen caerulescens caerulescens*) colony historically occurred ~12 km west (Cooke et al., 1995). For simplicity, we limit our analysis to only Canada goose nests, which comprised >95% of nests detected.

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 ~87% of captures).

We used polar bear energetics data from the Western Hudson Bay population as a proxy for seal availability (pups and carrion; annual seal abundance data is unavailable). Energetic models of polar bears indicate sea ice availability strongly influences polar bear body condition by controlling access to ice-dependent seals and the length of time bears remain on land, largely fasting, during the ice-free season (Stirling et al., 1999; Johnson et al., 2020; Pagano et al., 2020). Because Arctic foxes and polar bears both feed on seals on the sea ice, we assumed that polar bear energetics, which are influenced by both the abundance and accessibility of prey, adequately represent seal availability to Arctic foxes (i.e., conditions that are good for polar bear hunting success also benefit foxes). This rationale is supported by diet studies showing Arctic foxes frequently consume seal biomass in the region (Roth, 2002, 2003; Dudenhoeffer et al., 2021), and that regional Arctic fox abundance in the 1980s and '90s was positively related to polar bear body condition (Roth, 2003). We used energetic estimates of solitary adult female polar bears, as this demographic class has a reduced ability to compete with larger bears for food and annual changes in body condition are thus more likely to reflect environmental conditions (i.e., annual seal availability) (Johnson et al., 2020). Energetics data from bears captured during 2014–2023 were used in this study, as only one solitary adult female bear was captured in fall 2024 (avg. 11.6, range: 5–20 in all other years). Additional details are in Appendix S1.

We evaluated how environmental conditions affected winter food availability to foxes by assessing the effects of snow cover and sea ice duration on rodent abundance and polar bear energetics, respectively. Our study area lacks detailed snow depth/hardness measurements, so we used satellite imagery to derive estimates of snow cover temporal extent (ordinal date when snow cover disappeared on a per-pixel basis, averaged across the study area) to characterize winter snow conditions for rodents. Implicit in the relationship between polar bear energetics and sea ice duration is that longer sea ice seasons result in greater polar bear consumption of seals by prolonging the hunting season, allowing bears to store more energy. We used satellite imagery to estimate sea ice break-up date from our study area (ordinal date when sea ice cover in Hudson Bay was <50% for 3 consecutive days). See Appendix S1 for additional details on both metrics.

The proportion of dens occupied by foxes during the goose nesting period was used as our index of fox abundance/activity. During 2014–2024 (excluding 2020), we visited 20–22 dens on foot in June to assess fox activity (2014–2016: 20 dens; 2017–2023: 21 dens; 2024: 22 dens). Signs of digging/cleared burrows, fresh prey remains (goose eggshells, goose carcasses, lemming carcasses) and/or fresh scats observed at den sites, coupled with images captured by trail cameras 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, 2014–2024 (excluding 2020; see Johnson-Bice et al., 2025 for full details of survey methods). Briefly, 3–5 observers located goose nests using binoculars while walking along fifteen 2-km long transects. Once a nest was detected, we approached the nest until the goose flushed 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 assess 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 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 relationships between each of the variables identified in our conceptual model (Fig. 1). Error distributions of each model were determined based on the values and distribution of the response variable. 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, with the main drawbacks of our approach being that we are unable to perform a directed separation test nor quantify the strength of indirect interactions between consecutive significant paths.

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, whereas energy density is the amount of energy stored relative to the mass of tissue requiring it for somatic maintenance (Johnson et al., 2020). We fit separate models to both energy density (*1a*) and storage energy (*1b*) metrics, with annual sea ice break-up date (ordinal date) as a parametric predictor variable. Storage energy and energy density values were normally distributed, so we used GAMMs with a Gaussian distribution. We hypothesized that the bear's age may also affect bear body condition in a non-linear manner, such that both young and old adults may in relatively worse body condition due to a reduced ability to compete for and acquire food. We therefore 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. 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). The Tweedie distribution can accommodate both zero and positive continuous values (both present in our data set). Implementation of the Tweedie distribution in *glmmTMB* automatically estimates the power parameter using maximum likelihood.

Next, we evaluated (*3*) the effects of winter food resources on Arctic foxes using a generalized linear model with a beta distribution using the *glmmTMB* package (Brooks et al., 2017), which is well-suited to model 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 incubation initiation can predict Canada goose nest success, with nests incubated earlier having higher rates of success (Johnson-Bice et al., 2025). Snow cover/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 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 'Transect ID', which accounts for both the annual and spatial clustering of the nest data. We did not include a random intercept term for 'Nest ID' due to the relatively low number of repeated nest sites in our data set (~18%).

Finally, we evaluated (*5*) the relationship between fox den occupancy and goose nest success using a binomial generalized linear mixed-effects model with a complementary log-log ("cloglog") link 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. Clutches are found at different stages of incubation and thus vulnerable to predation for different lengths of time (i.e., exposure duration), which can bias clutch survival estimates (Shaffer, 2004). We accounted for the exposure duration of each clutch by including the log of exposure duration as an offset term in the model; exposure duration for successful nests was calculated as the number of days between the survey date and expected hatch date, while exposure duration of failed nests was the midpoint between these two dates (Johnson-Bice et al., 2025). 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., 2025). We included a random intercept term for 'Transect ID'.

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 (2014–2024) and that there was no residual temporal autocorrelation in our models. Time series plots of all response variables and plots/results from formal autocorrelation tests can be found 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. 3a). 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. S3). Total rodent abundance in June was greater during years when snow persisted longer on the tundra in spring (Table 1, Fig. 3b).

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. 3c) 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 (-11.86 vs. -11.18), suggesting the energetic metrics performed equally well in explaining fox den occupancy. Rodent abundance positively affected fox den occupancy (Fig. 3d), 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=536 clutches). We found longer snow persistence on the tundra delayed the date that geese initiated nest incubation (Table 1, Fig. 4a). 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. 4b). As reported previously with this data set (Johnson-Bice et al. 2025), 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. 4c-d).

Discussion

By compiling data sources related to environmental conditions, the abundance and availability of winter food resources to a top predator, and the response of the predator population to these 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 Arctic foxes, which in turn negatively affect the reproductive success of Canada geese. Greater Arctic fox den occupancy during years polar bears are in better body condition indicates Arctic foxes show a numerical response to greater marine resource availability, suggesting marine resources can indirectly alter the reproductive success of a tundra 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 affecting when geese initiate nesting. Our study provides an ecosystem-level perspective on the dynamics of a tundra food web at the terrestrial–marine interface.

Lemming abundance in the Churchill, Manitoba region has declined significantly over the past century, and our results suggest climate-driven changes in snow conditions are likely a factor in this decline. Although not all lemming populations are affected by winter snow conditions (Gauthier et al., 2024), our finding that lemming abundance is greater following winters that snow persists longer on the tundra supports studies that demonstrate lemming survival and abundance are related to greater snow depth and snow quality (soft basal layer) in some areas (Kausrud et al., 2008; Bilodeau et al., 2013a; Fauteux et al., 2015; Poirier et al., 2023). Longer snow persistence may benefit lemmings by prolonging the length of time snow provides some protection from predators (Bilodeau et al., 2013b), and it may also be an indicator of greater snow depth accumulation. Regardless of the exact mechanism, snow persistence has been declining in our study area since at least 2000 (Appendix S1: Fig. S4), suggesting changing snow persistence is likely partially responsible for the long-term decline in lemmings; 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).

Sea ice availability influences polar bear energetics, a metric we used as an indicator of marine subsidy availability to Arctic foxes, suggesting sea ice conditions also affect marine resource availability to foxes. Lacking annual estimates of seal abundance in our area, 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 since they feed on the same ice-dependent prey. The relationships between Arctic foxes, polar bears, and seals on the sea ice are well-known, with reports of foxes scavenging seals killed by polar bears as early as 1928 and of foxes killing seal pups in 1879 (Soper, 1928). Our assumption is also supported by Arctic fox diet studies from our area that show fox consumption of seals (Roth, 2002, 2003; Dudenhoeffer et al., 2021). Nonetheless, the ability of Arctic foxes and polar bears to access seals clearly depends on sea ice availability. Hudson Bay sea ice duration has declined by ~10 days/decade over the past 40 yrs (Boonstra et al., 2020), and these degrading sea ice conditions are associated with declines in ringed seal body condition, reproductive output, and population size (Ferguson et al., 2017). Western Hudson Bay polar bears have also exhibited long-term reductions in body condition and energetics (Derocher & Stirling, 1995; Stirling et al., 1999; Johnson et al., 2020), causing demographic changes and a similar population decline (Lunn et al., 2016; Archer et al., 2025). Reduced ringed seal and polar bear abundance suggest the availability of seal biomass to Arctic foxes has also declined through time. Altogether, this study presents key evidence that changing winter climate has reduced 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, environmental conditions also affected Canada goose reproduction, with nest success rates positively related to greater precipitation and warmer temperatures during incubation (Table 1, Fig. 4c-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). Foxes also tend to move slower and be less successful in attacking goose nests in wetter tundra environments (Lecomte et al., 2008), suggesting greater precipitation hinders fox mobility and their ability to depredate nests. Regarding temperature, warmer temperatures are thought to reduce embryo mortality and metabolic costs for incubating females (Dickey et al., 2008). Warmer temperatures may also have a bottom-up effect on geese by increasing food availability, as plant productivity tends to be greater during warmer springs (Kelsey et al., 2021). Snow likely disappears earlier during warm springs as well, allowing geese to initiate nesting earlier (Fig. 4a; Madsen et al., 2007; Lameris et al., 2019), which, in turn, leads to greater nest success (Table 1). Female Canada geese also primarily rely on fat reserves for energy while incubating (Raveling, 1979; Murphy & Boag, 1989), so nesting earlier likely means they deplete less of these energy stores. Environmental conditions during incubation thus appear to influence goose nest success by mediating both top-down and bottom-up processes.

Despite the apparent benefits that warmer springs and earlier snowmelt tend to offer Arctic nesting geese, Canada geese in our system are apparently not adjusting their nesting phenology enough to compensate for earlier springs (Appendix S1: Fig. S4). Arctic geese nesting phenology has evolved such that goslings hatch during peak vegetation quality, presumably to maximize growth (Dickey et al., 2008), so a mismatch in goose nesting phenology and peak vegetation may ultimately reduce gosling growth and survival (Brook et al., 2015; Nolet et al., 2020). Lameris et al. (2019) found early-breeding barnacle geese (*Branta leucopsis*) had the highest rates of nest success in the high Arctic whereas 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. S6), indicating an ongoing phenological mismatch between goose nesting and the onset of spring. This mismatch may be exacerbated in our study area where long-term grubbing by migrating snow geese have degraded large portions of the tundra and reduced food availability to geese (e.g., Kerbes et al., 1990; Jefferies et al., 2006), which may be particularly detrimental during the pre-nesting period by restricting the replenishment of protein reserves following migration (Baldwin et al., 2022). Phenological mismatch may also help explain why Canada goose abundance has remained stable for decades (Luukkonen & Leafloor, 2021) despite warmer springs (Appendix S1: Fig. S5), lower Arctic fox abundance (Verstege et al., 2023), and a recent collapse in the nearby colony of lesser snow geese (Hudson Bay Project, 2024), the main competitor of Canada geese.

Our finding that increasing rodent abundance has an immediate, 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 found no 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 (Walter, 1996), 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 reduces bird nest success (e.g., Bêty et al., 2001; Bêty et al., 2002; McKinnon et al., 2013; Juhasz et al., 2020). However, most of these prior studies evaluated rodent–goose–predator interactions in systems with higher average rodent densities and breeding goose colonies numbering tens of thousands of pairs (e.g., Bylot Island). Arctic foxes may be able to meet their energetic demands by mostly consuming rodents in these systems during high-rodent years (Beardsell et al., 2022), thereby releasing predation pressure on geese. Nests from dispersed-breeding birds are also less spatially predictable than goose colonies (Dulude-de Broin et al., 2023), likely resulting in longer search times and thus acting as a stronger limiting factor in egg acquisition rates by Arctic foxes from dispersed-nesting geese compared to colonial geese. Marolla et al. (2019) reported a positive indirect effect of rodent abundance on lesser white-fronted goose (*Anser erythopus*) reproduction, another dispersed-breeding goose species, but rodent abundance in their study area was substantially greater than in our study (peak densities of ~111 rodents/ha [40 rodents per 60x60 m grid] *vs.* peak densities of 2.0/ha in this study). Peak rodent abundance in Wapusk may no longer be sufficient to sustain foxes without supplemental alternative prey, so foxes continue to consume geese and their eggs regardless of rodent abundance; indeed, no relationship between rodent abundance and the proportion of Arctic fox diet comprised of geese was previously documented (McDonald et al., 2017). In other words, rodent abundance may not be high enough in Wapusk to elicit prey-switching behavior by foxes during the goose nesting period, resulting in near-term apparent competition between rodents and geese due to greater encounter rates with foxes following the fox's numerical response to rodents. We suggest these patterns indicate that absolute goose and rodent abundance, as well as their spatial dispersion, shapes whether the indirect effects of rodents on geese are positive or negative, demonstrating context-dependency in the relationship between tundra geese and rodents.

We provide evidence that marine resources may alter tundra food webs via the population response of a mobile terrestrial predator, 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. 3c), 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 increases adult survival or retention, resulting in greater den occupancy rates. Our finding that Arctic fox den occupancy, in turn, was negatively related to goose nest success suggests 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 these relationships. 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; any indirect effects of seals on goose reproduction would thus be mediated by the fox's apparent numerical response to seals in winter. These inferences align well with a study from Fennoscandia that indicated reindeer carrion abundance in winter can indirectly alter goose reproduction in spring by subsidizing foxes (Marolla et al., 2019). Our study adds to the literature demonstrating the timing of spatial subsidies can play a role in influencing food web dynamics (Sato et al., 2016).

Although this study suggests Arctic marine and tundra food webs are linked 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 poised for further disruption. 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 are associated with an ongoing decline in ringed seal abundance (Ferguson et al., 2017), a main prey for Western Hudson Bay polar bears and Arctic foxes. The combination of fewer seals, coupled with fewer polar bears and longer fasting periods for bears (Archer et al., 2025), likely means fewer seal pups and 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 (Brook et al., 2015), 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 collaborative research efforts and monitoring of these food webs, as typified by the current study, to better understand how the effects of climate change are reshaping trophic interactions through direct and indirect pathways in a rapidly warming Arctic.

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Author contributions: S.M.J-B. and J.D.R. led the study conceptualization. S.M.J-B. led the data curation, data analysis, data visualization, and writing and editing of the manuscript. S.M.J-B., E.S.R., and J.D.R. helped collect the data. All authors contributed to the study design and revising of the manuscript.

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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**	**SE**	**Conf. interval**	**Statistic**	***p*-value**
1a. Polar bear energy density	Deviance explained = 20.9%				
Sea ice breakup (ordinal date)	$\hat{\beta}=0.207$	0.095	(0.021, 0.393)	$t=2.17$	0.032
f_{Age}	edf=2.172	-	-	F=1.85	0.218
f_{Year}	edf=3.002	-	-	F=0.80	0.087
1b. Polar bear storage energy	Deviance explained = 26.6%				
Sea ice breakup (ordinal date)	$\hat{\beta}=22.53$	12.94	(-2.83, 47.89)	$t=1.74$	0.085
f_{Age}	edf=2.416	-	-	F=1.63	0.214
f_{Year}	edf=4.326	-	-	F=1.72	0.012
2. Rodent abundance	*Pseudo* R^2 = 0.501				
Snow duration (ordinal date)	$\hat{\beta}=0.069$	0.026	(0.014, 0.121)	$z=2.67$	0.008
3a. Fox den occupancy rate	*Pseudo* R^2 = 0.858				
Rodent abundance	$\hat{\beta}=0.580$	0.109	(0.367, 0.794)	$z=5.33$	<0.0001
Polar bear energy density	$\hat{\beta}=0.073$	0.019	(0.036, 0.109)	$z=3.93$	<0.0001
3b. Fox den occupancy rate	*Pseudo* R^2 = 0.846				
Rodent abundance	$\hat{\beta}=0.525$	0.117	(0.296, 0.755)	$z=4.49$	<0.0001
Polar bear storage energy	$\hat{\beta}=0.0006$	0.0002	(0.0003, 0.0009)	$z=3.68$	0.0002
4. Incubation initiation date	Cond. R^2 = 0.678, Marg. R^2 = 0.459				
Snow duration (ordinal date)	$\hat{\beta}=0.554$	0.041	(0.040, 0.714)	$z=13.52$	<0.0001
$\sigma_{\text{Transect ID}}$	3.095	0.272	(2.56, 3.65)	-	-
5. Canada goose nest success	Cond. R^2 = 0.569, Marg. R^2 = 0.569				
Fox den occupancy rate	$\hat{\beta}=-1.963$	0.847	(-3.623, -0.303)	$z=-2.32$	0.020
Incubation initiation date	$\hat{\beta}=-0.217$	0.018	(-0.253, -0.182)	$z=-12.00$	<0.0001
Avg. temp. during incubation	$\hat{\beta}=0.184$	0.059	(0.068, 0.301)	$z=3.10$	0.002
Total precip. during incubation	$\hat{\beta}=0.014$	0.003	(0.008, 0.019)	$z=5.16$	<0.0001
$\sigma_{\text{TransectID}}$	<0.001	-	-	-	-

edf = Effective degrees of freedom; SE = Standard error.

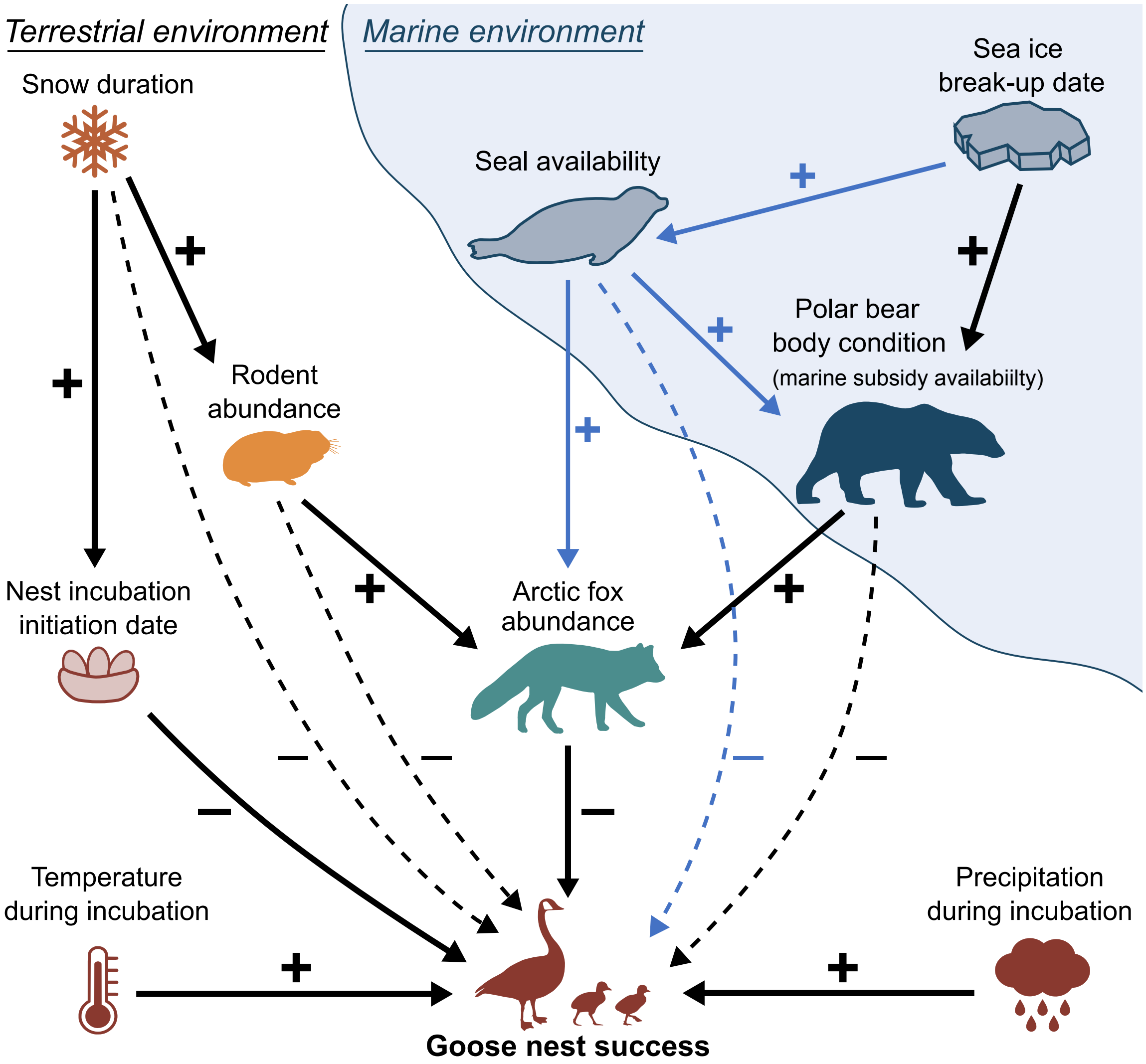

Figure 1. Conceptual model depicting our hypotheses on how winter environmental conditions, food abundance/availability, and predator activity interactively shape Canada goose nest success through direct and indirect pathways in a coastal tundra ecosystem. We hypothesized environmental conditions affect the availability 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 cover 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 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). Illustrations by Sean M. Johnson-Bice.

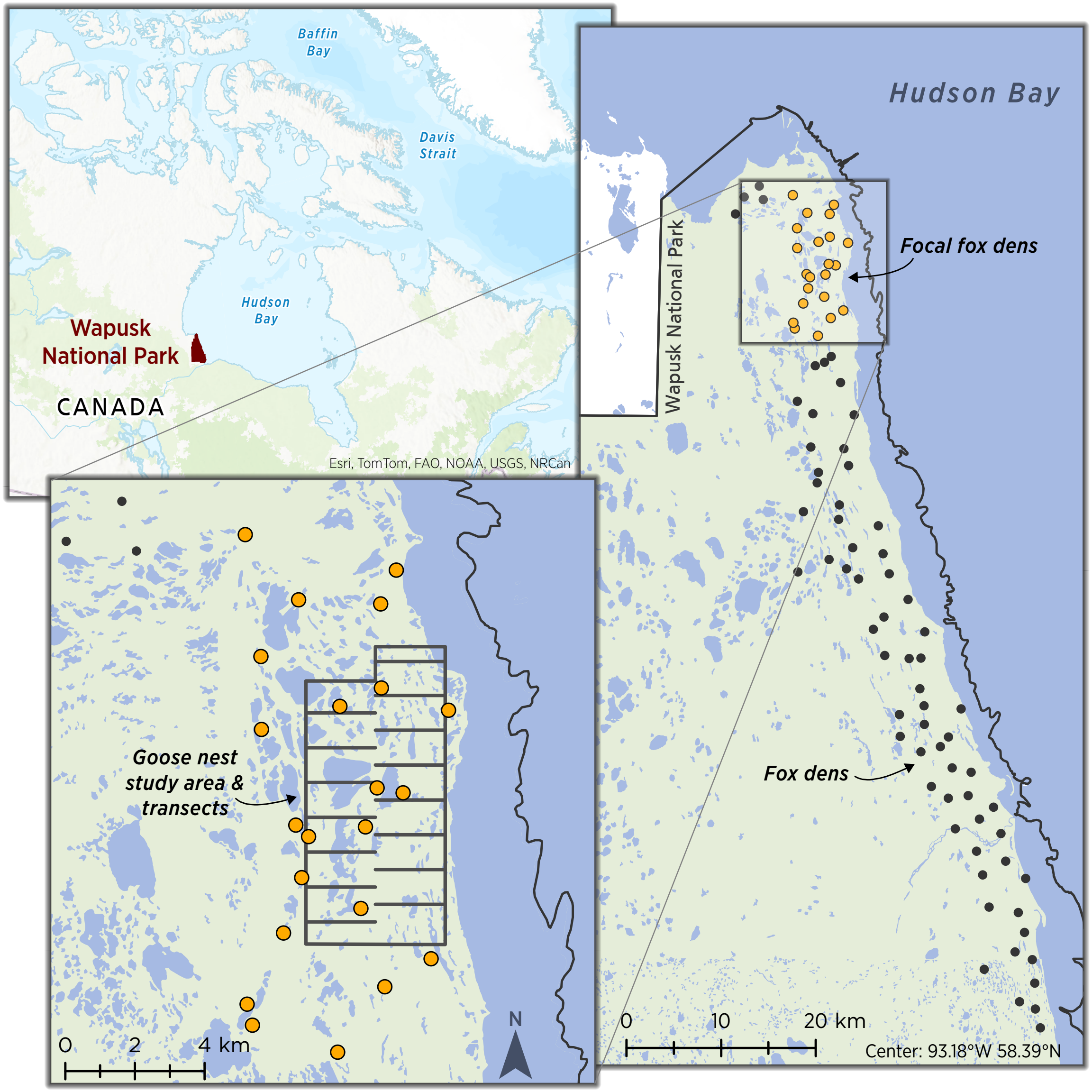

Figure 2. Map of our study area within Wapusk National Park, Manitoba, Canada, along the western coast of Hudson Bay. Right panel shows all 88 known fox dens on the tundra within Wapusk, with the subset of "focal dens" used for the present study in the inset map (orange circles). Lower left panel shows the goose nest study area (dark gray polygon outline) with one year of 2-km goose nest transects depicted (horizontal gray lines), and the 22 focal dens around the goose nest study area.

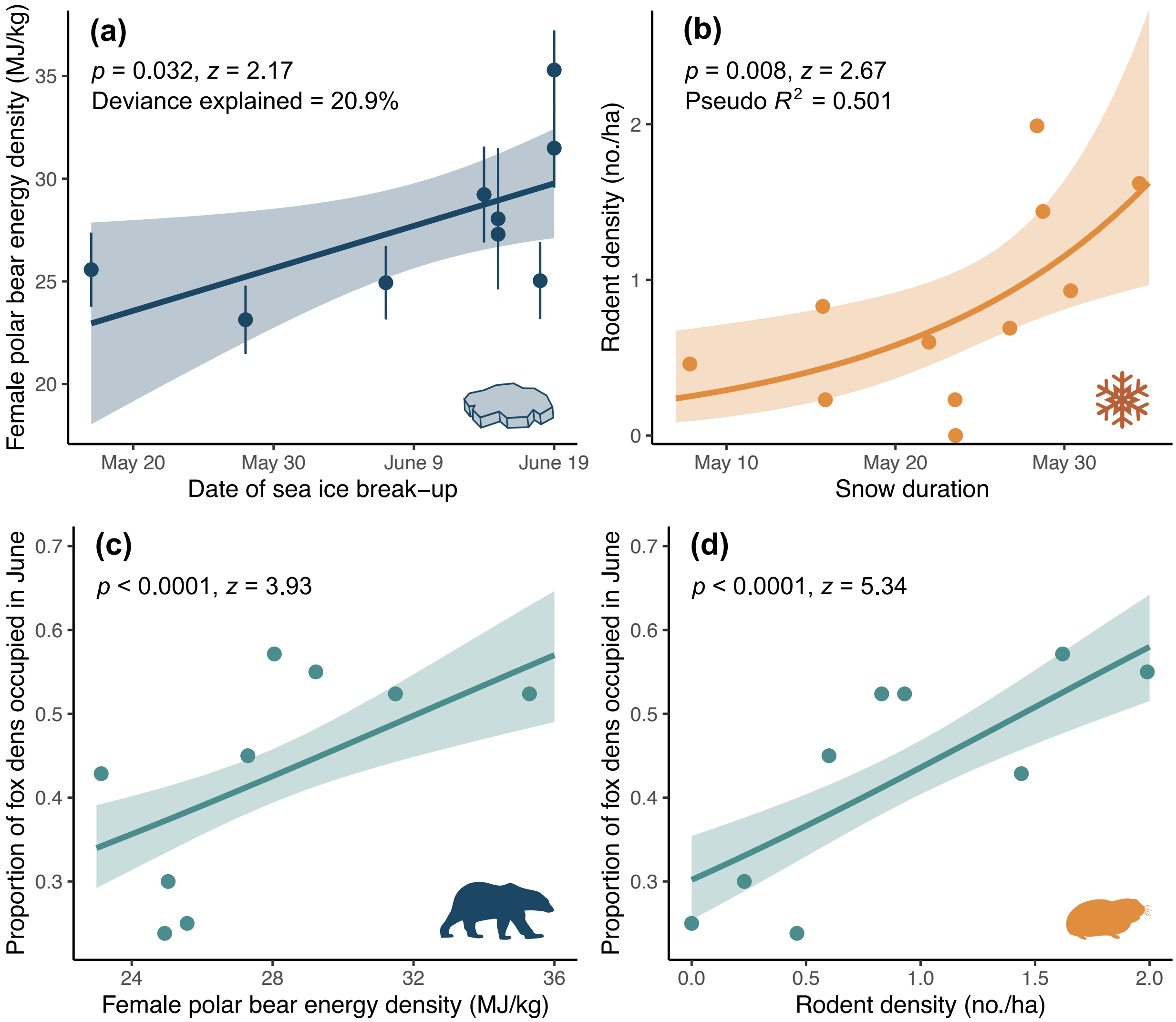

Figure 3. Results depicting how winter environmental conditions affect winter food availability for Arctic foxes, which, in turn, appear to respond numerically to greater food resources. Panel (a) shows the estimated effect of sea ice duration on female polar bear energy density (MJ/kg). Individual points 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 predicted relationships between 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. Illustrations by Sean M. Johnson-Bice.

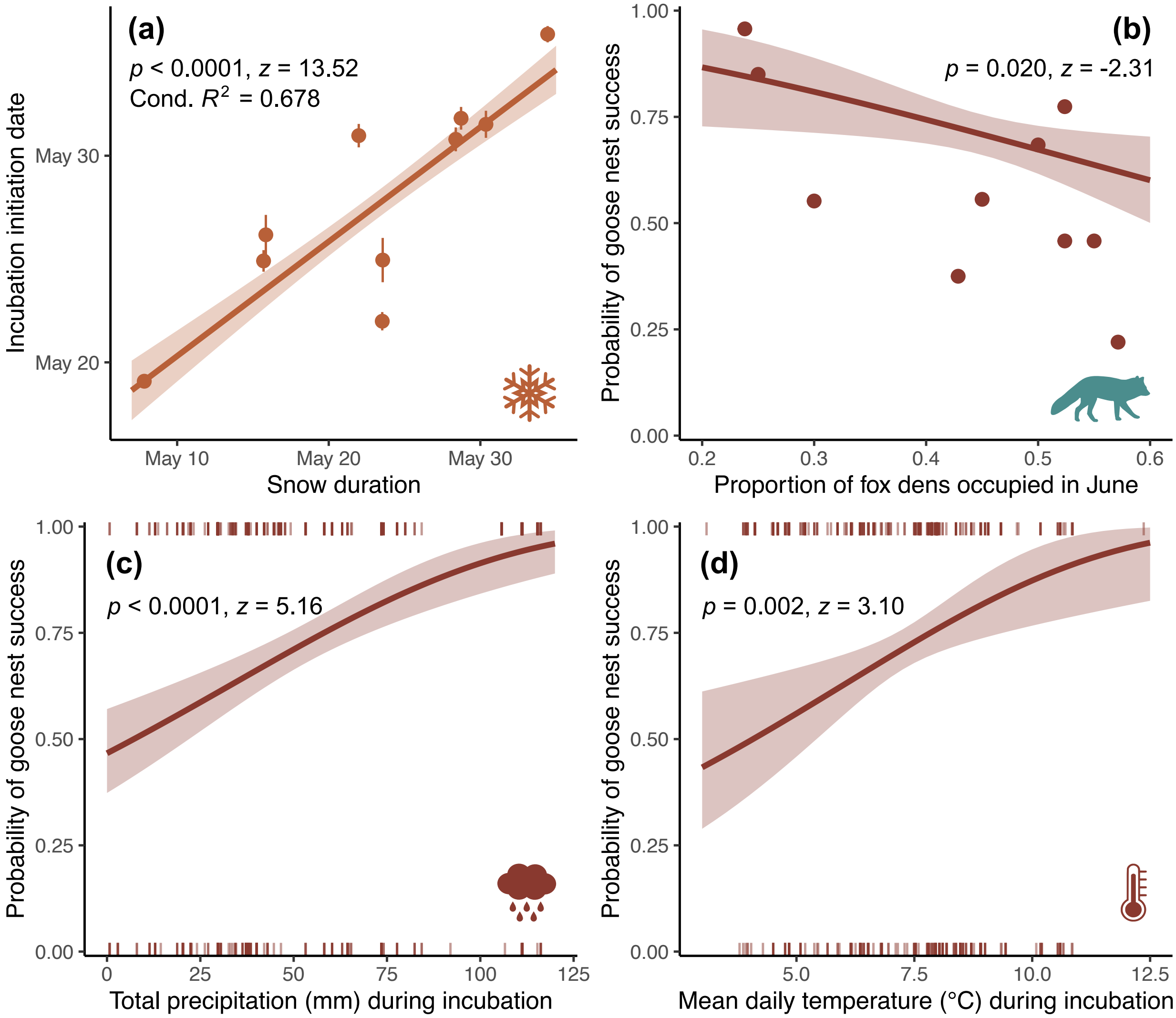

Figure 4. Results depicting how environmental conditions and fox activity affect Canada goose reproduction. Panel (a) shows the estimated effect of snow duration on incubation initiation date. Individual dots show the annual average values +/- std. error, highlighting the relatively low intra-annual 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 panel (b) are the average annual nest success values. Ribbons represent +/- 95% confidence intervals of each estimated relationship. Predictions in panels (b–d) were conditioned on the median average exposure duration (9 days). Colors and icons correspond to linkages from Fig. 1. Illustrations by Sean M. Johnson-Bice.

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), 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; 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 (m). 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 ($M = 0.00006039G^{1.762}L^{1.249}$, where G is axillary girth in cm and L is straight-line body length in cm). 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.

<u>*Model 1a*</u>:

$$EnergyDensity_{ij} \sim N(\mu_{ij}, \sigma^2)$$
$$\mu_{ij} = SeaIceBreakup_{ij} + f_1(Age_{ij}) + f_2(Year_i)$$
$$Year_i \sim N(0, \sigma^2)$$

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 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_1 using thin plate regression splines comprised of 9 basis functions; and $f_2(Year_i)$ is a random effect spline fit with a smoothing component f_2 with one basis function for each year i, and was assumed to have mean 0 and variance σ^2 (equivalent to a single-level random intercept term; (Pedersen et al., 2019). $EnergyDensity_{ij}$ is assumed to follow a Normal distribution with mean μ_{ij} and variance σ^2.

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:

$$
\begin{aligned}
RodentAbundance_i &\sim Tweedie(\mu_i, \phi, p) \\
\mathrm{E}(RodentAbundance_i) &= \mu_i \\
\mathrm{Var}(RodentAbundance_i) = \mathrm{Var}(\mu_i) &= \phi\mu_i^p \\
\log(\mu_i) &= SnowDuration_i
\end{aligned}
$$

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. $RodentAbundance_i$ is assumed to follow a Tweedie distribution with mean μ_i and variance $\phi\mu_i^p$, where ϕ is a dispersion parameter to be estimated by the model, and p is the mean-variance power parameter. When implemented in the *glmmTMB* R package (Brooks et al., 2017), p is restricted to $1 < p < 2$ and is estimated using maximum likelihood estimation.

Model 3a:

$$
\begin{aligned}
PropDenOccupied_i &\sim Beta(\mu_i, \phi) \\
\mathrm{E}(PropDenOccupied_i) &= \mu_i \\
\mathrm{Var}(PropDenOccupied_i) &= \frac{\mu_i(1-\mu_i)}{1+\phi} \\
\mathrm{logit}(\mu_i) &= RodentAbundance_i + EnergyDensity_i
\end{aligned}
$$

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. $PropDenOccupied_i$ is restricted to the (0,1) interval and assumed to follow a Beta distribution with a mean μ_i and variance $\frac{\mu_i(1-\mu_i)}{1+\phi}$, where ϕ is a measure of precision to be estimated by the model (inverse of dispersion) (Douma & Weedon, 2019).

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:

$$
\begin{aligned}
IncubationDate_{ij} &\sim N(\mu_{ij}, \sigma^2) \\
\mu_{ij} &= SnowDuration_{ij} + TransectID_i \\
TransectID_i &\sim N(0, \sigma^2)
\end{aligned}
$$

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

<u>*Model 5*</u>: $NestSuccess_{ij} \sim Bernoulli\left(\pi_{ij}, \pi_{ij}(1-\pi_{ij})\right)$

$$\mathrm{E}\left(NestSuccess_{ij}\right) = \pi_{ij}$$

$$\begin{aligned}\text{cloglog}\left(\pi_{ij}\right) &= PropDenOccupied_{ij} + Temp_{ij} + Precip_{ij} \\ &\quad + offset\left(\ln\left(Exposure_{ij}\right)\right) + TransectID_i\end{aligned}$$

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

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. The natural log of exposure duration is included as an offset term in the model ($Exposure_{ij}$). Exposure duration was calculated as the number of days between when clutch *j* was detected and when the clutch was estimated to hatch for successful clutches, whereas exposure duration was calculated as the midpoint between these two dates for failed clutches. $NestSuccess_{ij}$ follows a Bernoulli distribution with mean π_{ij} and variance $\pi_{ij}(1-\pi_{ij})$, and $TransectID_i$ is a random intercept term that is assumed to be normally distributed with mean 0 and variance σ^2.

Supplementary results

Time series results

Time series plots of all response variables from models evaluated in this study are shown in Figure S1, including rodent abundance (no./ha), adult female polar bear energy density (MJ/kg), fox den occupancy, average goose nest incubation date, and average annual goose nest success, spanning 2014–2024. Data gaps in 2020 are due to the COVID-19 epidemic.

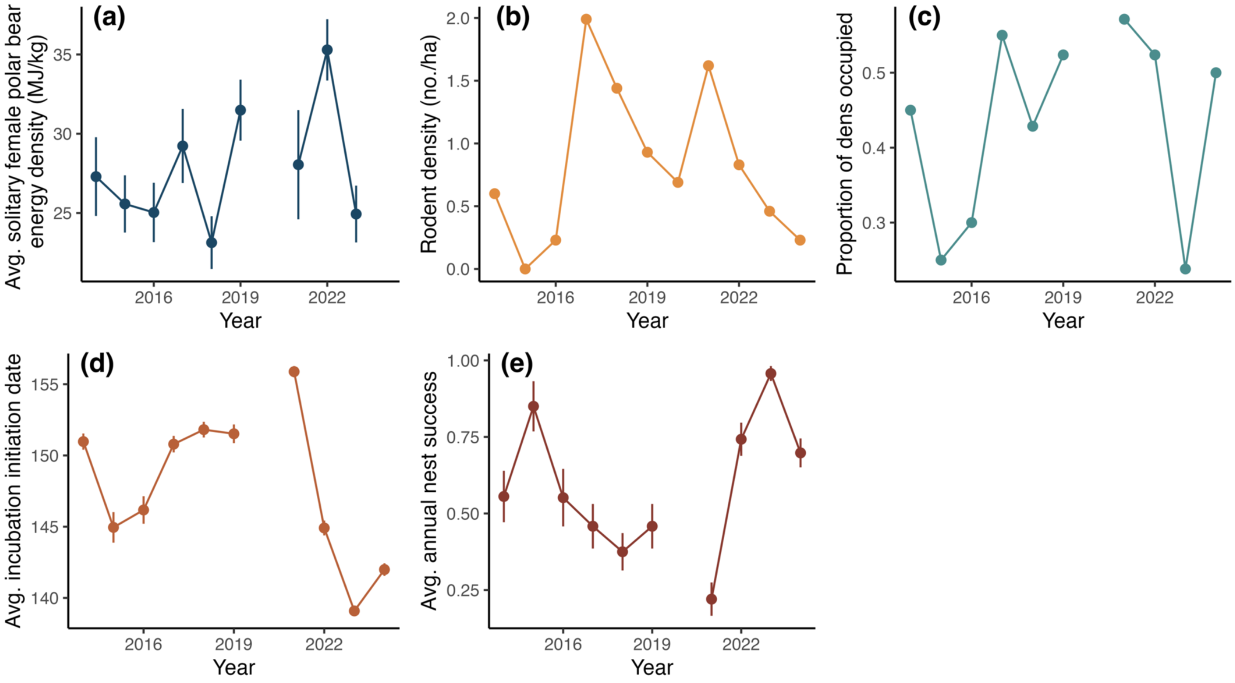

Figure S1. Time series plots of adult female polar bear energy density (MJ/kg; *a*), rodent abundance (no./ha; *b*), fox den occupancy (proportion occupied; *c*), average incubation initiation date (ordinal day; *d*), and average annual goose nest success (%; *e*) in the Wapusk National Park Region, spanning 2014–2024. Error bars are standard error (*b, d, e*).

To ensure adequate model fit, we verified there was no residual temporal autocorrelation in each of our models. We used the *DHARMa* R package to simulate residuals from each fitted model (Hartig, 2022), plotted the residuals using the 'acf' base R function, and tested for significant residual autocorrelation using a Durbin-Watson test from the *lmtest* R package (Zeileis & Hothorn, 2002). Results from these tests demonstrated no residual autocorrelation in any model evaluated. Autocorrelation plots are shown in figure S2 for each model.

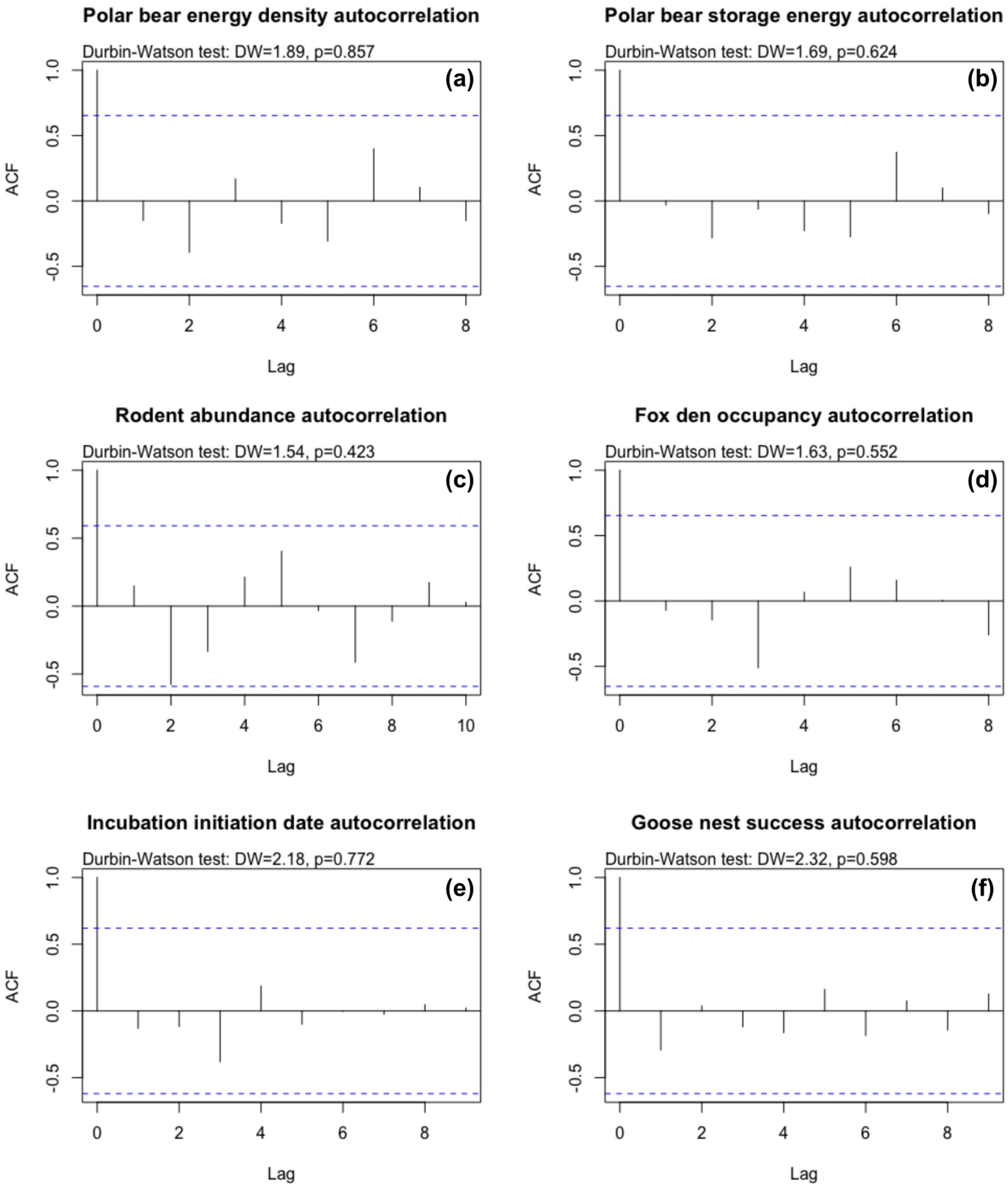

Figure S2. Temporal autocorrelation plots for each of the fitted models. We found no evidence of significant residual temporal autocorrelation in any model. (*a*) = polar bear energy density (model 1a); (*b*) = polar bear storage energy (model 1b); (*c*) = rodent abundance (model 2); (*d*) = fox den occupancy (model 3a; autocorrelation results from 3b are virtually the same); (*e*) = goose nest incubation initiation date (model 4); (*f*) = goose nest success (model 5).

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_1) 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. S3).

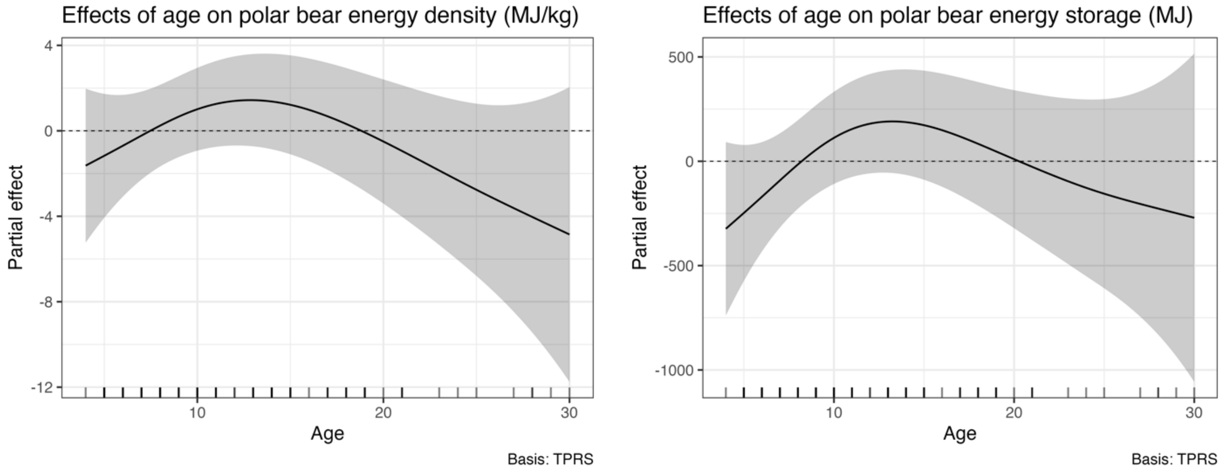

Figure S3. Results from the generalized additive mixed-effects models (GAMMs) evaluating the effects of polar bear age on the energy density (*left*) and storage energy (*right*) of solitary adult female polar bears from the Western Hudson Bay population. Graphs show the partial effects as predicted from the GAMMs, with the ribbons representing +/- 95% confidence intervals. Plots were made using the *gratia* R package (Simpson, 2024).

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 2000–2024. In addition to the incubation date data we collected from 2014–2024, population-level data on average nest success and incubation date are available from 2000–2010 from a separate long-term study using slightly different nest-searching methodology (Andersen et al. 2010). Snow persistence date from 2000–2024 was obtained from MODIS satellite imagery using the methods described earlier in this supplementary material document.

Snow persistence in our study area has advanced ~0.56 days/yr from 2000–2024, while median goose nest incubation date has only advanced ~0.28 days/yr (Fig. S4). 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 -0.59 days/yr ($F_{1,19}$=4.46, p=0.048). 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.

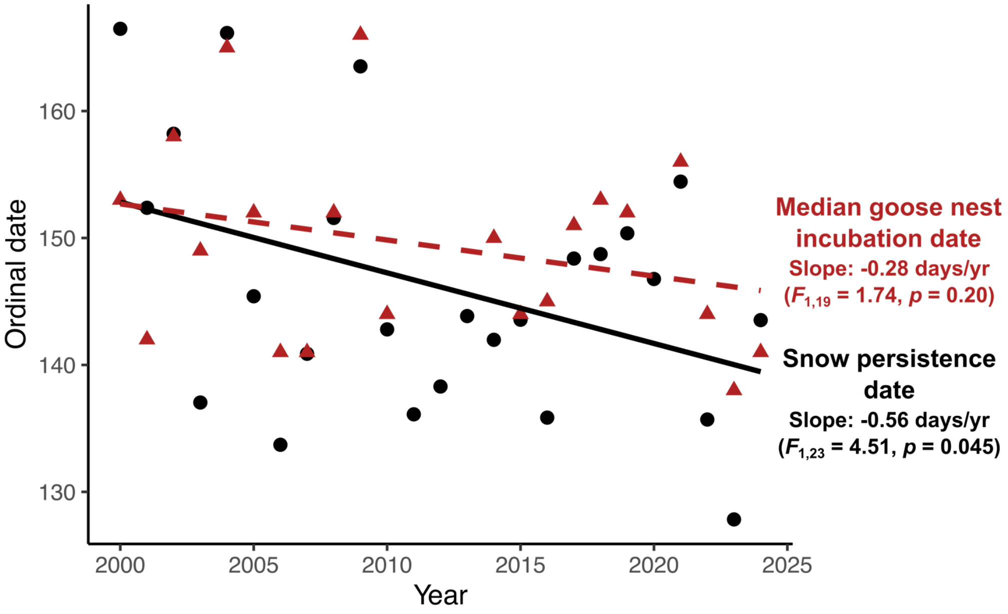

Figure S4. Linear trends of Canada goose median nest incubation initiation date (red triangles, red dashed line) and snow persistence date (black circles, solid line) from 2000 to 2024 in Wapusk National Park, Manitoba, Canada. The linear trends show the date that snow disappears from the study area is advancing roughly 2.0 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. S5).

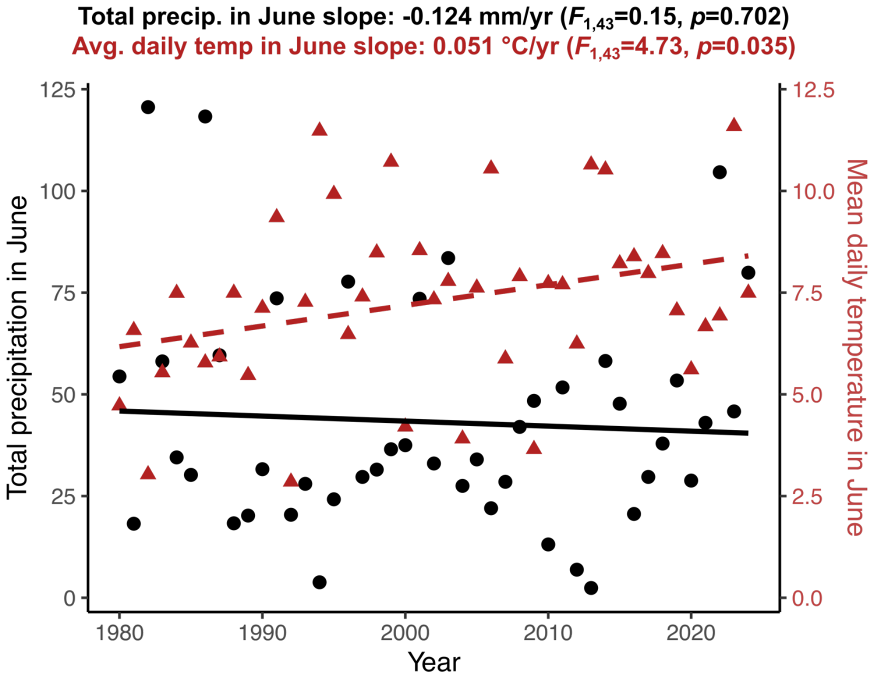

Fig. S5. Long-term trends in average temperature and total rainfall during June from the Churchill, MB weather station, 1980-2024. There has been a significant increase in average daily June temperature (~0.5°C per decade; 6.2°C in 1980 to 8.4°C in 2024), and no significant temporal trend in total precipitation.

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. S6). 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.

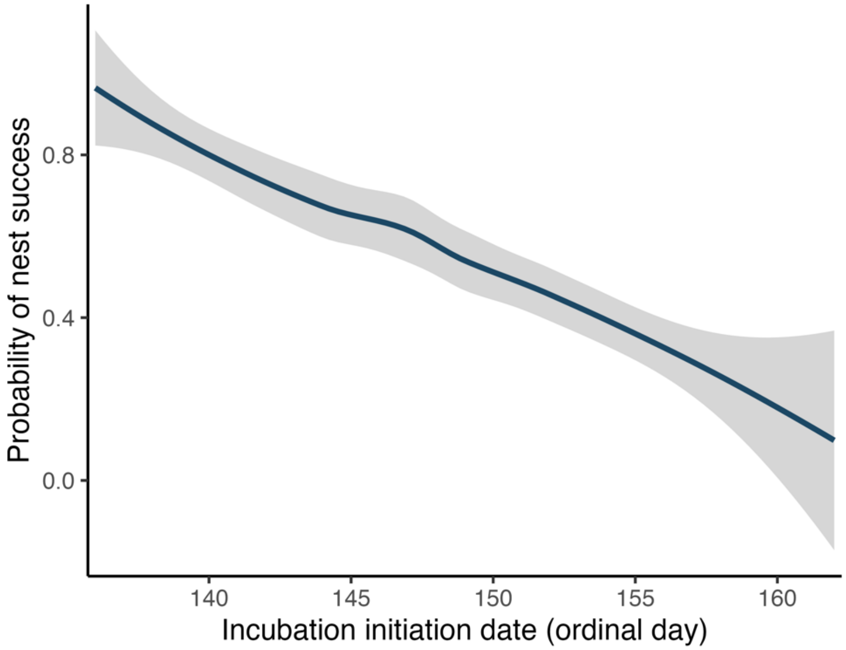

Figure S6. The relationship between incubation initiation date (ordinal day) and the probability of Canada goose nest success in Wapusk National Park, Manitoba, Canada, 2014–2024, fit with a Loess smoother. The data suggests no evidence of a non-linear relationship between nesting phenology and Canada goose nest success.

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