Functional roles of Arctic foxes in tundra ecosystems: ecosystem engineering, nutrient transport, and consumptive and non-consumptive effects on prey

by

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Abstract

Predators are widely recognized for their irreplaceable roles in influencing the abundance and traits of lower trophic levels. Yet, predators also shape community interactions and ecological processes via localized pathways, irrespective of their influence on prey density or behavior. I synthesized empirical and theoretical research and identified pathways by which predators have indirect ecological effects confined to discrete patches. This synthesis revealed how predators indirectly affect other species via patches – ranging from mediating scavenger interactions to influencing parasite/disease transmission risk – and ultimately provides a more holistic view of predation in ecosystems. I then demonstrated how satellite imagery could resolve whether Arctic foxes create biogeochemical hotspots via their denning behavior. Using satellite imagery, I showed that Arctic fox dens have greater plant productivity and green-up faster than reference sites, supporting the hypothesis that Arctic foxes cause the unique vegetation on their dens by concentrating nutrients derived from prey remains there. I then assessed how predators influence the reproductive ecology of Canada geese. Birds presumably select nest sites in areas they perceive are safer, but few links between spatial patterns of risk and nest habitat selection or nesting success exist. By comparing habitat selection models fit to goose nest locations and fox movement locations, I showed predator activity strongly affects the spatial distribution and reproductive success of geese. However, these effects were mediated by the date nest incubation started, revealing how nesting phenology and predator activity interact to shape bird reproduction. Finally, I assessed how fox predation affects goose reproductive success from an ecosystem-level perspective. I showed winter environmental conditions influence the abundance and availability of main winter foods for Arctic foxes, which in turn showed a numerical response to these foods and ultimately had a negative effect on goose reproductive success. These results demonstrate apparent competition between rodents and geese, and establish a link between the marine and terrestrial environments via Arctic fox use of marine subsidies. Given the importance of climate in mediating these trophic relationships, I contextualize the results of this thesis within ongoing climate change and highlight the vulnerability of coastal tundra ecosystems in a warming Arctic.

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Chapter 1: Introduction

Classic perspectives on the functional roles of top predators in ecosystems

Predators have numerous functional roles within ecosystems that result from direct and indirect interactions with other organisms (Prugh et al., 2009; Ritchie et al., 2012; Lacher Jr et al., 2019). Broadly speaking, the effects of predators on other species can be divided into two categories, consumptive and non-consumptive effects, depending on whether direct killing (i.e., consumption) of an animal occurs (Schmitz et al., 1997; Peers et al., 2018; Say-Sallaz et al., 2019). Predators have long been recognized for their ability to exert top-down control of lower trophic levels via direct killing (Paine, 1966; Estes & Palmisano, 1974; Paine, 1980), which falls under the umbrella of consumptive effects of predation. Non-consumptive effects of predation occur when predators alter the traits of lower trophic levels – usually behavior, but can also include changes to physiology – via non-lethal mechanisms (Lima & Dill, 1990; Lima, 1998; Preisser et al., 2005; Moll et al., 2017; Kohl et al., 2018; Wirsing et al., 2021). Although ecologists have traditionally focused on the effects that predators have on prey species in particular, we now widely recognize predators can also have strong top-down effects on other, generally subordinate, predator species through intraguild killing and predation-risk effects (Palomares & Caro, 1999; Elmhagen & Rushton, 2007; Levi & Wilmers, 2012; Prugh & Sivy, 2020; Ruprecht et al., 2021; Prugh et al., 2023). Top-down regulation of the abundance and traits of lower trophic levels is thus widely accepted to be the dominant role top predators play in ecosystems (Ripple et al., 2014).

The top-down effects of predators on lower trophic levels can also indirectly affect other species not directly associated with those interactions. Broadly speaking, these indirect effects of predators on other species have been previously categorized as either density-mediated or trait-mediated indirect effects. Density-mediated indirect effects occur as a function of changes in the density of the prey (or subordinate predator) species (Paine, 1980; Carpenter et al., 1985; Polis et al., 2000). A classic textbook example of density-mediated indirect effects comes from marine kelp ecosystems, whereby sea otter (*Enhydra lutris*) limitation of urchin density has indirect effects on kelp communities by reducing herbivory pressure from urchins (Estes & Palmisano, 1974; Wilmers et al., 2012; Rasher et al., 2020; Raymond et al., 2021). Density-mediated indirect effects like these are perhaps more commonly referred to as “trophic cascades”; however, the term trophic cascades refers specifically to indirect effects that reverberate down food chains (Ripple et al., 2016) and are thus just one category of density-

mediated indirect effects. Trait-mediated indirect effects are those that occur as a function of changes in the traits, often behavior, of the prey or subordinate predator species (Schmitz et al., 1997; Werner & Peacor, 2003; Schmitz et al., 2004; Peacor et al., 2020). A classic example of trait-mediated indirect effects comes from Yellowstone National Park, where the reintroduction of wolves (*Canis lupus*) in the mid-1990s led to changes in the spatial distribution of elk (*Cervus canadensis*), with reverberating effects on riparian plant communities (Ripple et al., 2001; Ripple & Beschta, 2003; 2012). However, I note that many of these findings have subsequently been disputed (e.g., Barber-Meyer, 2015; Ford & Goheen, 2015; Allen et al., 2017), and recent studies suggest the strength of these trait-mediated indirect effects have been exaggerated (Brice et al., 2022; Hobbs et al., 2024). Nonetheless, I use this example because it remains well-known and well-cited by researchers today despite the controversy. Generally, density-mediated indirect effects occur through consumptive mechanisms (i.e., from predators altering the density of lower trophic levels through direct killing/consumption); although, in theory, density-mediated indirect effects could occur if non-consumptive effects of predation reduce prey density through changes in prey fitness and/or survival, which, in turn, has subsequent indirect effects on another species. For instance, mesopredator avoidance of large carnivores may result in greater overall mortality risk by amplifying human-caused mortality in human-modified landscapes (Prugh et al., 2023), which in turn likely indirectly affects the mesopredators' prey by reducing predation pressure. Greater focus and research on these topics are revealing the complex and evermore diverse ways that predators affect communities through direct and indirect pathways, underscoring the need to better characterize the essential roles that predators play within ecosystems.

Effects of resource pulses and subsidies on predator population dynamics

Although predator population sizes are generally limited by the availability and biomass of prey species (Fuller & Sievert, 2001), several factors may influence predator populations that de-couple their dynamics from the dynamics of their prey. One of the most common factors is the addition of resource subsidies into ecosystems (Loreau & Holt, 2004; Marczak et al., 2007), which are donor-controlled food resources deposited into an ecosystem that can enhance consumer populations above the limitations imposed by natural prey abundance (Polis & Hurd, 1996; Polis et al., 1997). We can categorize the various types of resource subsidies based on their frequency, duration of availability, and origin – i.e., whether the subsidies arose within ecosystems (*in situ*), or whether the subsidies were transported across ecosystem boundaries (*spatial* or *allochthonous* subsidies). In general, resources that occur for short periods of time

but are highly abundant and readily available to consumers are considered *pulsed resources* (Ostfeld & Keesing, 2000; Holt, 2008; Yang et al., 2008). Well-known examples of resource pulses include mast-producing trees (Schmidt & Ostfeld, 2003; Clotfelter et al., 2007), periodical events of insect emergence (Yang, 2004), mass fish spawning events (Helfield & Naiman, 2001, 2006; Willson & Womble, 2006), and mass animal mortality events (Carpenter, 1988; Subalusky et al., 2017; Fey et al., 2019). Predator populations may respond directly to resource pulses (e.g., consuming carrion from mass mortality events), or indirectly via a numerical response to the *secondary pulse* from the response(s) of their prey (i.e., when a prey species demonstrates a numerical response to the original resource pulse, such as rodents responding numerically to acorn masting events; Schmidt & Ostfeld, 2008). However, many resource subsidies are available to predators more regularly than pulsed resources, such as resources from anthropogenic sources (Rodewald et al., 2011; Oro et al., 2013) or animal carrion (DeVault et al., 2003; Wilmers et al., 2003; Barton et al., 2013; Pereira et al., 2014; Prugh & Sivy, 2020). Predators that live in coastal areas can also have higher-than-average densities through regular access to spatial subsidies. Coyote (*Canis latrans*) populations in coastal California can be up to 10x denser than inland areas due to their access to allochthonous marine subsidies (Rose & Polis, 1998), while the highest jaguar (*Panthera onca*) density reported comes from the Brazilian Pantanal where the big cats feed almost exclusively on aquatic subsidies (Eriksson et al., 2022).

Whether predators respond numerically to these resource pulses and subsidies largely depends on the timing of the resources and the predators' life history strategies. Predators (focusing mainly on mammalian carnivores here) that reproduce while fasting, including many bear species (*Ursus* spp.), exhibit a capital breeding strategy that can often depend heavily on pulsed resources for successful reproduction. For instance, brown bear (*Ursus arctos*) fitness is highly influenced by the availability of abundant berry patches in inland systems (Proctor et al., 2023) and spawning salmon in coastal systems (Hilderbrand et al., 1999; Hilderbrand et al., 2000), both of which are pulsed resources that occur in the months leading up to hibernation. Declines in the abundance and regularity of spawning salmon events are thought to be a major cause of brown bear population declines in some regions (Levi et al., 2020). Carnivores with an income breeding strategy generally only respond numerically to resource subsidies and pulses if the resources are available immediately prior to reproduction. For instance, wolverine (*Gulo gulo*) reproduction was strongly influenced by carrion availability during winter months preceding the breeding season (Rauset et al., 2015). Wolves (*Canis lupus*) show strong dietary and behavioral responses to pulses of ungulate neonates in forested ecosystems during spring (Gable et al., 2018; Johnson-Bice et al., 2023), but their population densities are instead largely

driven by winter food abundance (Fuller et al., 2003; McRoberts & Mech, 2014). The timing of resource availability may be particularly important for systems with migratory prey. Eurasian lynx (*Lynx lynx*) that had access to migratory reindeer (*Rangifer tarandus*) only during summer showed lower reproduction and lower kitten recruitment compared to lynx with year-round access to reindeer (Walton et al., 2017). Subsidies that are available year-round thus provide ample opportunities for predators to access the supplementary foods, and often elicit a numerical response like the examples provided earlier regarding coyotes and jaguars (Rose & Polis, 1998; Eriksson et al., 2022). Indeed, a review of predator responses to anthropogenic resource subsidies, which are generally available year-round, revealed nearly every study on this topic documented greater predator abundance in areas with access to anthropogenic subsidies (Newsome et al., 2015). Collectively, accounting for the timing, availability, and life history of the predator are important considerations for predicting the effects of seasonal or unpredictable resource pulses on predator population dynamics.

Indirect trophic interactions in subsidy- and pulse-driven systems

Within multiple-prey systems, the influence of predators on alternative prey populations is often linked to changes in their behavioral and numerical responses to primary prey populations. When primary prey are abundant, predators may reduce predation pressure on alternative prey, a positive indirect interaction commonly referred to as apparent mutualism (Abrams and Matsuda 1996). However, negative indirect interactions between prey species can also arise when predators exhibit a numerical response to one prey species and then increase predation pressure on a second, alternative prey species – a phenomenon commonly referred to as apparent competition (Holt 1977, Holt and Bonsall 2017). For example, apparent competition is thought to be the main proximate mechanism behind the recent declines of caribou in Canadian boreal forests. Increases in moose (*Alces alces*) and deer (*Odocoileus* spp.) abundance, largely driven by climate- and anthropogenic-associated environmental changes (Street et al., 2015; Dawe & Boutin, 2016; Laurent et al., 2021; Fuller et al., 2023), have led to greater wolf densities and, in turn, greater predation pressure on caribou (Latham et al., 2011; Latham et al., 2013; Frenette et al., 2020; Serrouya et al., 2021). These negative interactions may be asymmetrical or non-reciprocal in natural systems where only one prey species is negatively affected by the presence of the other (Chaneton & Bonsall, 2000). Moreover, the directionality and strength of indirect trophic interactions may change when evaluated across different time scales within the same food web, owing largely to prey switching behavior by predators (Bêty et al., 2002). Prey switching behavior is a common strategy used by

generalist predators that have a strong preference for one prey species (Murdoch, 1969), indicating that complex indirect trophic interactions may arise in food webs that are strongly influenced by generalist predators.

Predator responses to resource subsidies can have cascading indirect effects on other species due to predator prey switching behavior and/or a numerical response to the subsidies (Polis et al., 1997). Whether the subsidies have a negative or positive indirect effect on other species often similarly depends on the timing and duration of the subsidy (Sato et al., 2016; Sato et al., 2021). Pulsed resources that are only available for short time periods tend to have a short-term positive indirect effect on other species due to predator diet switching behavior. For instance, pulses of seaweed onto islands provided ample food to detrivores that was then consumed by anoles (*Anolis sagrei*); the dietary switch by anoles towards consuming the detrivores, in turn, reduced predation pressure on herbivorous insects (Spiller et al., 2010). However, over time, the anoles demonstrated a numerical response to the seaweed-associated detrivores and subsequently exerted stronger top-down effects on the herbivorous insects (Piovia-Scott et al., 2019), thereby demonstrating a long-term net negative effect of pulsed seaweed subsidies on terrestrial herbivores. Researchers studying the effects of emergent aquatic insects – which is a short-term resource pulse for consumers – on terrestrial food webs noted similar patterns: aquatic insects have short-term positive effects on alternative terrestrial prey due to diet switching behavior by the predator (Sabo & Power, 2002), but in the long run the aquatic subsidies enhance predator populations and can lead to subsequent top-down negative effects on alternative prey (Henschel et al., 2001; Murakami & Nakano, 2002). Most of this research to-date has demonstrated subsidy-driven, indirect trophic interactions in systems where the subsidies are available to the consumers within their natal habitat. Few examples exist that demonstrate subsidy-driven indirect effects via the consumers crossing ecosystem boundaries with movement.

Trophic interactions in tundra ecosystems

Arctic tundra ecosystems have relatively simple food web structures compared to temperate ecosystems (Krebs et al., 2003; Gauthier et al., 2011, but see Wirta et al., 2015), which makes them ideal systems to test theoretical patterns of direct and indirect trophic interactions with fewer linkages to account for. In general, bottom-up constraints appear to be most important in structuring food web relationships during winter (Stoessel et al., 2018), while top-down forces appear more important in structuring tundra food webs during summer (Krebs

et al., 2003; Legagneux et al., 2012). The comparatively strong predator-prey relationships in tundra ecosystems are thought to be due in part to climate-change induced increases in primary productivity (Gauthier et al., 2011; Legagneux et al., 2014); as ecosystem productivity increases, predator density also generally increases, which in turn can reduce herbivore abundance (Oksanen & Oksanen, 2000; Oksanen et al., 2020). Allochthonous resources are also thought to play a major role in tundra food web dynamics. The Arctic region in general has a very high perimeter to area ratio (i.e., extensive coastline), which provides ample opportunities for cross-ecosystem resource flows. Terrestrial predator use of marine subsidies is thought to contribute to the top-down control of tundra food webs (Gauthier et al., 2011; Legagneux et al., 2012), but this had not yet been supported empirically. Thus, studies focused on disentangling the influence of both climate change and allochthonous resource inputs on trophic interactions may help elucidate the dynamics of contemporary tundra food webs.

Arctic foxes (*Vulpes lagopus*) are arguably the most important terrestrial predator in the Arctic, and much of the food web-related research from tundra ecosystems has centered around Arctic foxes and their main prey species. As top predators, Arctic foxes have a pronounced effect on tundra food web dynamics. In some areas, Arctic foxes contribute to the top-down regulation of rodent populations (Angerbjörn et al., 1999) and they can strongly influence the reproductive success of migratory birds during summer (e.g., Bêty et al., 2002; Iles et al., 2013; McKinnon et al., 2013; Dulude-de Broin et al., 2023). Arctic fox populations are notoriously linked to the irruptive population dynamics of their often-preferred prey, microtine rodents (lemmings and voles) where present (e.g., Elton, 1942; Macpherson, 1969; Gilg et al., 2006; Ehrich et al., 2017; Ims et al., 2017; Juhasz et al., 2020). Microtine rodents have historically been thought to exhibit 3–5 year cycles in abundance (Elton, 1924; Krebs & Myers, 1974; Ims & Fuglei, 2005; Krebs, 2011), though a recent large-scale synthesis evaluating lemming population dynamics from numerous study sites indicated that lemming cycles are likely more sporadic than previously assumed (Gauthier et al., 2024). Nonetheless, tundra rodent irruptions are generally considered to be an *in situ* resource pulse with reverberating effects on predator population dynamics (Therrien et al., 2014; Robillard et al., 2016; Chevallier et al., 2020) – including Arctic foxes, whose population sizes generally track lemming populations (Angerbjörn et al., 1999; Gilg et al., 2003; Elmhagen et al., 2011). However, Arctic foxes also display highly flexible foraging strategies, and are thus sometimes described as ‘opportunistic specialists’ that can switch to alternative prey when rodents are scarce (Elmhagen et al., 2000). Indeed, in many instances Arctic fox diets are highly diverse and reflect a more generalist foraging strategy (Hersteinsson & Macdonald, 1996; Goltsman et al., 2011; Carbonell Ellgutter et al., 2020;

Dudenhoeffer et al., 2021; Ungar et al., 2021). As a consequence of their ability to use other prey resources, Arctic foxes may significantly influence the reproductive success of alternative prey species in relation to rodent cycle phases (e.g., Bêty et al., 2001; Bêty et al., 2002; Gauthier et al., 2004; McKinnon et al., 2013; Nolet et al., 2013; McKinnon et al., 2014; Juhasz et al., 2020; Dulude-de Broin et al., 2023).

Allochthonous subsidies and pulsed resources other than irruptive rodents can also strongly influence Arctic fox diet and population dynamics. Migratory birds in tundra ecosystems represent a major flow of cross-environment resources during summer (Giroux et al., 2012; Moisan et al., 2023), as these birds – particularly geese – are often subsidized in temperate ecosystems during winter (Jano et al., 1998; Koons et al., 2019). However, despite geese and other migratory waterfowl being an important component of Arctic fox diets in summer (Bantle & Alisauskas, 1998; Eide et al., 2005; McDonald et al., 2017), goose abundance has little influence on Arctic fox recruitment because they are not present during the breeding season in late winter (Samelius et al., 2011; Eide et al., 2012; McDonald et al., 2017; Samelius & Alisauskas, 2017; Carbonell Ellgutter et al., 2020). In contrast, resource subsidies that are available to foxes in late winter often influence Arctic fox abundance. For instance, Arctic foxes show a numerical response to pulses of reindeer carcasses during winter in Svalbard (Fuglei et al., 2003; Hansen et al., 2013; Nater et al., 2021) and Russia (Ehrich et al., 2017; Terekhina et al., 2021). Arctic foxes will also readily venture onto the sea ice (Tarroux et al., 2012; Lai et al., 2015, 2017; Warret Rodrigues & Roth, 2023) to prey on seal pups and scavenge seal carcasses killed by polar bears (*Ursus maritimus*) (Smith, 1976; Stirling & Archibald, 1977; Roth, 2002).

Study system

My research was largely focused on the effects that Arctic foxes have on ecosystems through their denning activity and as a predator of goose nests. The main study area for this research was Wapusk National Park, which is a low-Arctic coastal tundra ecosystem along the western coast of Hudson Bay in northeastern Manitoba. Despite the lemming population appearing to have declined over several recent decades, Arctic fox reproduction still appears to be influenced by rodent availability (McDonald et al., 2017). Previous research from our study system has also shown that Arctic foxes in this area consume relatively high quantities of marine resources during winter (Roth, 2002; Dudenhoeffer et al., 2021), and their use of these marine subsidies appear to buffer the fox population against expected population declines

during years of low rodent abundance (Roth, 2003). However, less certain is how these resource subsidies indirectly affect other Arctic fox prey by enhancing local fox population sizes.

Research from our study system has also shown that Arctic foxes play an important role in tundra ecosystems through their denning activity. Arctic fox dens in the low Arctic tend to be prominent features on the tundra, with the average fox den in our area being ~560 m^2 in area (Gharajehdaghipour & Roth, 2018). These dens are characterized with substantially greater plant biomass than the surrounding landscape (Gharajehdaghipour et al., 2016; Fig. 1.1). Arctic fox dens also typically have greater soil and plant nutrient content than nearby areas (Smith et al., 1992; Gharajehdaghipour et al., 2016), and also unique plant assemblages (Bruun et al., 2005; Fafard et al., 2020). These dens thus function as important biogeochemical hotspots that, in our area at least, appear to attract wildlife from across the tundra (Zhao et al., 2022). Fox activity during the denning season is thought to be the main driver of these unique traits. Arctic foxes often re-use the same dens for decades or more (Macpherson, 1969), and it is thought that the accumulation of nutrients in the form of fox excrement and prey remains enhances plants on and around the dens (Bruun et al., 2005; Gharajehdaghipour et al., 2016). Consequently, Arctic foxes have been classified as *ecosystem engineers* in low-Arctic ecosystems – organisms that positively affect other species through physical modifications of their environment (Jones et al., 1994, 1997). However, owing to the longevity of the dens, it has remained difficult to provide support for the hypothesis that the foxes are the cause of these traits; the alternative hypothesis for the den traits is that Arctic foxes may choose pre-existing highly productive patches for their den sites, rather than being the engineers of the high productivity.

Research objectives and thesis organization

The main objective of this thesis is to provide a more thorough picture of the diverse functional roles that top predators play within ecosystems, with a focus on Arctic foxes in the low-Arctic tundra. I first begin the thesis with a synthesis of the multifaceted ways predators influence ecosystem dynamics via mechanisms that do not depend on predator-mediated changes in prey density or traits (i.e., mechanisms that do not fall into density- or trait-mediated indirect effects categories; Chapter 2). One of the major identified mechanisms from that synthesis is the concentration of nutrients derived from prey remains into a localized area (patch), which, as mentioned above, is the mechanism thought to cause the unique traits of Arctic fox dens. I then explore the use of satellite imagery and habitat selection models to help

provide evidence for this hypothesis that Arctic fox denning activity transforms low-productivity sites into localized high-productivity sites, thereby supporting their classification as ecosystem engineers (Chapter 3).

The second half of my thesis focuses more on the classical roles that predators play within ecosystems as top-down influencers on the abundance and behavior of lower trophic levels. I first evaluate how Arctic and red fox (*Vulpes vulpes*) activity affects the nest site selection and reproductive success of Canada geese (*Branta canadensis interior*), and how patterns in nesting phenology may mediate these spatial patterns of predation risk (Chapter 4). I then assess how Arctic foxes affect Canada goose reproduction again, but this time from a food web perspective. Specifically, I investigate how winter weather conditions influence the abundance and availability of winter foods for Arctic foxes – namely, rodents on the tundra and seals on the sea ice – affect Arctic foxes, and how their population response, in turn, affects goose reproduction (Chapter 5). This chapter tests the hypothesis that pulsed resources (rodents) and spatial subsidies (seal pups and carrion) during winter indirectly affect the reproduction of an alternative prey species (goose) during summer via the numerical response of a shared predator. Finally, I present a general discussion (Chapter 6) regarding the major findings of my research and some future directions of where the science and Arctic ecosystems may be headed going forward.

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Figure 1.1. Image of an Arctic fox den situated on an elevated beach ridge in Wapusk National Park, Manitoba, Canada. Credit: S. Johnson-Bice.

Chapter 2: Patchy indirect effects of predation: predators contribute to landscape heterogeneity and ecosystem function via localized pathways

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Abstract

Predators are widely recognized for their irreplaceable roles in influencing the abundance and traits of lower trophic levels. Predators also have irreplaceable roles in shaping community interactions and ecological processes via highly localized pathways (i.e., effects with well-defined and measurable spatio-temporal boundaries), irrespective of their influence on prey density or behavior. We synthesized empirical and theoretical research describing how predators—particularly medium- and large-sized carnivores—have indirect ecological effects confined to discrete landscape patches, processes we have termed *patchy indirect effects of predation*. Predators generate patchy indirect effects via three main localized pathways: generating and distributing prey carcasses, creating ecological hotspots by concentrating nutrients derived from prey, and killing ecosystem engineers that create patches. In each pathway, the indirect effects are limited to discrete areas with measurable spatial and temporal boundaries (i.e., patches). Our synthesis reveals the diverse and complex ways that predators indirectly affect other species via patches, ranging from mediating scavenger interactions to influencing parasite/disease transmission risk, and from altering ecosystem biogeochemistry to facilitating local biodiversity. We provide basic guidelines on how these effects can be quantified at the patch and landscape scales, and discuss how predator-mediated patches ultimately contribute to landscape heterogeneity and ecosystem functioning. Whereas density- and trait-mediated indirect effects of predation generally occur through population-scale changes, patchy indirect effects of predation occur through individual- and patch-level pathways. Our synthesis provides a more holistic view of the functional role of predation in ecosystems by addressing how predators create patchy landscapes via localized pathways, in addition to influencing the abundance and behavior of lower trophic levels.

Key words: density-mediated indirect effects, ecosystem engineering, nutrient cycling, predator-prey interactions, trait-mediated indirect effects, trophic cascade

Introduction

Predators are important contributors to ecosystem structure and function through **consumptive** (see Glossary) and **non-consumptive** effects (Ripple et al., 2014). Consumptive effects occur when predators have a lethal effect on lower trophic levels. If predation rates are high enough to affect the abundance (density) of lower trophic levels, this top-down limitation may then have cascading, *indirect effects* on other species (i.e., **density-mediated indirect effects**; Paine, 1980; Carpenter et al., 1985; Polis et al., 2000; Terborgh & Estes, 2010); for example, predators can alter plant communities through top-down control of herbivores (Estes & Palmisano, 1974), or influence predation rates on other prey by limiting subordinate predator density (Elmhagen et al., 2010; Levi & Wilmers, 2012). Non-consumptive effects occur through non-lethal changes in prey traits, broadly categorized as **predation-risk effects** (Creel & Christianson, 2008; Peacor et al., 2020). Predation risk elicits changes in flexible prey traits such as foraging preferences or space use (Lima & Dill, 1990; Lima, 1998) that, in turn, indirectly affect other species (i.e., **trait-mediated indirect effects**; Abrams et al., 1996). Predators are typically assumed to alter ecosystem structure and function primarily through density- and trait-mediated indirect effects, which have both been well-documented and synthesized in the literature (e.g., Lima, 1998; Schmitz et al., 2000; Werner & Peacor, 2003; Schmitz et al., 2004; Preisser et al., 2005; Ripple et al., 2014; Say-Sallaz et al., 2019; Wirsing et al., 2021). However, there is growing recognition predators can have outsized ecological effects via additional mechanistic pathways (Bump et al., 2009a; Schmitz et al., 2010; Gable et al., 2020; Monk & Schmitz, 2022).

One such pathway is the redistribution of nutrients by predators through their movements. Many animals—herbivores and carnivores alike—act as **mobile links** that connect separate habitats/ecosystems through their movement (Lundberg & Moberg, 2003). These movements help maintain ecosystem function and resilience through processes like dispersal, migration, and nutrient transportation (Polis et al., 1997; McCann et al., 2005; Bauer & Hoye, 2014; Doughty et al., 2016; Schlägel et al., 2020). Recent work has demonstrated that mobile links are a key component of **meta-ecosystem** dynamics (Massol et al., 2011)—a conceptual framework concerned with studying the flow of energy and organic material among ecosystems (Loreau et al., 2003; Leroux & Loreau, 2008; Gounand et al., 2018). Ellis-Soto et al. (2021) showed that the meta-ecosystem framework provides a useful roadmap for studying animal-transported nutrient dynamics, as it allows researchers to examine how landscape attributes and animal movement traits interact to influence spatiotemporal patterns of nutrient deposition.

Although these concepts can be applied to the many species that act as nutrient vectors (Schmitz et al., 2018; McInturf et al., 2019; Subalusky & Post, 2019; Schmitz & Leroux, 2020), predators are particularly important vectors because they transport **resource subsidies** high in limiting nutrients (e.g., calcium, nitrogen, phosphorous) (Schmitz et al., 2010; Monk & Schmitz, 2022). When predators transport these limiting nutrients into concentrated locations, they can create biogeochemical hotspots on the landscape (Gharajehdaghipour et al., 2016; de Miranda et al., 2023). Notably, these predator-mediated nutrient patches occur separate from whether or not predators alter the density or traits of prey.

Here, we synthesize the diverse ways predators indirectly affect ecosystems in a localized manner by creating or altering patches on the landscape—processes we term **patchy indirect effects** (PIEs) of predation. We define PIEs as *indirect consumptive effects of predation that are restricted to landscape patches with measurable spatial and temporal boundaries*. Although the term *patch* may be defined differently depending on the scale or system of interest (Leibold et al., 2004), we define patch here as a discrete microsite that contrasts with the surrounding landscape matrix.

We begin our synthesis by providing an overview of the three main pathways by which predators have PIEs within ecosystems: 1) creating and distributing carcasses across the landscape, 2) creating biogeochemical hotspots by repeatedly transporting nutrients derived from prey to discrete areas, and 3) by killing **ecosystem engineers** that create patches. For each pathway, we synthesize numerous examples from empirical studies and provide a case study that collectively demonstrate how each pathway indirectly affects other species, irrespective of changes to the density or traits of lower trophic levels. We then provide some guidance on how to quantify the effects of each pathway at the patch and landscape scales, provide predictions about when and where PIEs are likely to be relatively more or less important, and finally discuss how our synthesis provides a more holistic view of the functional role of predation in ecosystems. Our synthesis focuses on predators of medium and large body size because the patches they create/interact with are larger, but the concepts can be extended to smaller species. Although our synthesis is embedded within theoretical concepts, we also summarize empirical research that highlights the variety and complexity of ways predators influence ecosystem dynamics via localized pathways.

Carcass pathway: prey carcasses are ephemeral ecological hotspots

Carrion is an essential yet often-overlooked ecosystem component that drives myriad inter-specific interactions between predators, scavengers, and local invertebrate, plant, and soil communities (DeVault et al., 2003; Wilson & Wolkovich, 2011; Barton et al., 2013a; 2019). And predators, particularly large carnivores, play a key role in generating carrion within ecosystems through predation. Predators positively affect a wide range of scavengers by provisioning carrion (Moleón et al., 2014; Pereira et al., 2014), a resource subsidy many species rely upon as an important (and sometimes essential) food resource (Prugh & Sivy, 2020). Carcasses may become sites of 'fatal attraction' (Sivy et al., 2017) where smaller scavengers are killed by larger animals while competing for the same carcass. Ephemeral landscapes of fear and disgust may establish around carcasses as well (Moleón & Sánchez-Zapata, 2021; Newsome et al., 2021): smaller animals may be at risk of predation and thus avoid carcasses to reduce fatal encounters with larger scavengers ("landscape of fear"; Cunningham et al., 2018), while other species may avoid carcasses to prevent parasitism and infection risk ("landscape of disgust"; Buck et al., 2018; Muñoz-Lozano et al., 2019). Opportunistic scavengers attracted to carcasses may even kill other prey near carcasses (Cortés-Avizanda et al., 2009a; Cortés-Avizanda et al., 2009b; Spencer et al., 2021).

Prey carcasses release a pulse of nutrients into the soil that affect local invertebrate, soil, and plant communities. Individual invertebrates are larger and invertebrate assemblages are different at carcasses compared to adjacent areas (Barton et al., 2013b). High arthropod abundance may in turn attract other species to carcasses (Moreno-Opo & Margalida, 2013; Morris & Bump, 2020). While flesh remains on carcasses, invertebrates, particularly fly larvae and beetles (Coleoptera), play a key role in converting flesh into nutrients (e.g., nitrogen, phosphorous) and regulating the rate these nutrients are delivered to belowground communities (Ilardi et al., 2021). Consequently, as carcasses putrefy, the biogeochemistry of soils under carcasses change (Keenan et al., 2018). This nutrient influx is readily taken up by fungi, microbes, and plants, resulting in unique species compositions at carcass sites (Bump et al., 2009b; Barton et al., 2016; Risch et al., 2020). Changes in phosphorous concentration and plant composition may persist for a long time and leave distinct patches decades after carcass decomposition (Danell et al., 2002; Bump et al., 2009b; Barton et al., 2016). Because most studies evaluating carcass effects on soils, plants, and invertebrates come from experimentally-placed carcasses rather than depredated animals (but see Bump et al., 2009a; Barry et al., 2019; Risch et al., 2020), expanding research on the similarities and differences between

carcasses created through predation vs. other mortality sources will be beneficial for understanding when and how prey carcasses uniquely alter ecosystems (Bump et al., 2009a; Ellis-Soto et al., 2021).

The ecological importance of individual prey carcasses does not necessarily depend on whether the traits or population density of the prey are substantially altered by the predator. Rather, individual predation events can produce important PIEs at each kill site. Carcasses are continuously deposited within ecosystems through numerous sources of mortality (e.g., disease, starvation, human hunting), but predators distinctively influence the timing, spatial distribution, and rates of carcass deposition (Wilmers et al., 2003b; Ellis-Soto et al., 2021). Indeed, predators help stabilize carrion abundance in ecosystems by reducing the temporal variation of carrion (Wilmers & Getz, 2004), which may even buffer the effects of climate change on scavengers (Wilmers & Getz, 2005). On Isle Royale, carcasses of moose (*Alces alces*) killed by wolves (*Canis lupus*) were deposited in some areas up to 12x more often than other areas (Bump et al., 2009a), creating heterogeneity in the distribution of carcass-mediated effects across the landscape.

The unique spatiotemporal distribution of prey carcasses implies that predators drive landscape heterogeneity from the top-down (Wilmers et al., 2003a; Bump et al., 2009a; Schmitz et al., 2010; Monk & Schmitz, 2022). However, environmental characteristics also have an influence on the spatiotemporal distribution of prey carcasses. Landscape features such as topography influence spatial patterns of predation risk (Gaynor et al., 2019), whereas phenological drivers like vegetation green-up can influence the spatiotemporal distribution of prey (Merkle et al., 2016). Ultimately, these environmental characteristics help shape when and where prey are killed (Kauffman et al., 2007), and, consequently, all of the PIEs associated with prey carcasses. From a meta-ecosystem perspective, prey carcasses can be viewed as predator-mediated nutrient inputs influenced by environmental conditions. These nutrient inputs, in turn, indirectly affect both above- and below-ground communities in unique spatiotemporal patterns.

Box 2.1: Case study: The ecological importance of puma-killed carcasses

Pumas (*Puma concolor*) are apex predators with the widest geographic range of any terrestrial mammal in the Western Hemisphere. They have an important ecological role by regulating prey density, affecting prey behavior through predation risk, and generating carrion (LaBarge et al., 2022). Pumas predominantly kill large ungulates but because pumas are

solitary predators it often takes a long time to fully consume prey, which means other scavengers may have time to locate and respond to puma-killed carcasses. Indeed, a greater diversity of scavengers are found at puma kills than from any other predator studied (Elbroch et al., 2017), which often results in complex interspecific interactions at kill sites.

Pumas face direct competition at carcasses from other dominant scavengers, i.e., wolves and bears (Box 2.1, Fig. 1B), which may result in fatal encounters or force pumas to abandon their kills. Kleptoparasitism by black bears (*Ursus americanus*) can occur often enough that pumas increase their kill rates to compensate for food losses (Elbroch et al., 2015a; Allen et al., 2021), thereby increasing carcass availability. Smaller scavengers tend to exhibit species-specific responses to kill sites. Some species, like coyotes (*C. latrans*), incur both costs and benefits by interacting with puma kills. In Oregon, USA, coyotes scavenged nearly every puma kill, resulting in high diet overlap between coyotes and pumas (Ruprecht et al., 2021). Coyotes showed a strong response in their space use towards kill sites, but they avoided pumas to presumably reduce fatal encounters; pumas killed ~ 23% of the coyote population annually (Ruprecht et al., 2021). Other species such as bobcats (*Lynx rufus*) and birds show more limited responses to puma-killed carcasses (Allen et al., 2015; Ruprecht et al., 2021), whereas red fox (*Vulpes vulpes*) responses vary depending on the season (O'Malley et al., 2018). In South America, puma-killed carcasses subsidize and help structure sex-specific dietary partitioning of Andean condors (*Vultur gryphus*) (Perrig et al., 2017; Barceló et al., 2022), scavengers that preferentially feed on carcasses in low vegetation and flat areas to reduce predation risk from other predators near kill sites (Perrig et al., 2022).

Puma-killed carcasses provide a unique, ephemeral habitat for beetles. Relative to control sites, puma-killed carcasses support a greater abundance, species richness, and diversity of beetles (Box 2.1, Fig. 1C) (Barry et al., 2019). Carcasses also release limiting nutrients into soils (Box 2.1, Fig. 1D), leading to greater nitrogen concentrations in soils and plants at puma kill sites relative to control areas (Peziol et al., 2023). Landscape-scale biogeochemical effects of puma-killed carcasses were quantified by multiplying individual kill rates by puma density, concluding that pumas contribute 44.1 kg of carrion per km^2 annually (Peziol et al. 2023). Puma-killed carcasses thus represent a comprehensive example of how predators can generate PIEs via the carcass pathway by influencing spatiotemporal interactions among scavengers and facilitating local plant, invertebrate, and soil communities.

Nutrient accumulation pathway: predators create biogeochemical hotspots by concentrating prey-derived nutrients into patches

As discussed earlier, animals are important nutrient vectors because they often deposit nutrients at different rates, locations, and directions (i.e., against natural gradients) than passive resource subsidy sources (McInturf et al., 2019; Subalusky & Post, 2019). When predators concentrate nutrients derived from prey remains (prey-derived nutrients) into certain areas, they can generate biogeochemical hotspots with patchy indirect effects (PIEs) on other species.

Predator home sites (i.e., where predators raise offspring) often become biogeochemical hotspots. Adults repeatedly bring prey remains to home sites to provision offspring, and as breeding seasons progress the accumulation of prey remains, coupled with excrement from the predators, increases nutrient content around home sites. For instance, nutrient concentrations are elevated within top soils under ground-nesting eagle owl (*Bubo bubo*) nests, enhancing grass seedling growth (Fedriani et al., 2015). Home sites perennially used by predators may have long-lasting PIEs. Red fox (*Vulpes vulpes*) dens in the subarctic are used for decades or longer, resulting in greater nutrient concentrations at den sites (Lang et al., 2021) and greater annual growth and reproductive output of nearby mast-seeding trees (Kucheravy et al., 2021; Lang et al., 2022). Some PIEs associated with predator home sites may be due to disturbance behavior (e.g., burrowing activities; Kurek et al., 2014; Gharajehdaghipour et al., 2016; Lang et al., 2021), but experiments could disentangle the relative influence prey-derived nutrients and bioturbation have on generating biogeochemical hotspots.

Predators that socialize or breed in aggregations can alter local environments by transporting huge quantities of prey-derived nutrients into localized areas, often coupling separate ecosystems in the process. Seals and other marine mammals aggregate in haul-outs on land and concentrate marine prey-derived nutrients via excretion and transported prey (Fariña et al., 2003), which can influence terrestrial herbivore space use and foraging dynamics by enriching vegetation near the haul-outs (McLoughlin et al., 2016). In Antarctic ecosystems, nutrients around seal haul-outs and penguin colonies drive the abundance and richness of terrestrial plants and invertebrates (Bokhorst et al., 2019). Many seabirds, through colonial nesting, transform terrestrial ecosystems by depositing marine nutrients in and around their colonies (Polis & Hurd, 1996; Clyde et al., 2021). Studies evaluating the disruption of seabird-mediated nutrients through seabird population declines via predation have revealed the extent to which seabird colonies affect island ecosystems (Croll et al., 2005; Fukami et al., 2006; Maron et al., 2006; Towns et al., 2009; Graham et al., 2018; Benkwitt et al., 2021). Prey-derived

nutrients from seabird colonies can, in turn, subsidize fish (Benkwitt et al., 2019), mangrove (Adame et al., 2015), and coral communities (Lorrain et al., 2017) in marine habitats in the colony's immediate vicinity through runoff.

Predators also create nutrient patches through localized, repeated activities like scent-marking. Arctic foxes (*Vulpes lagopus*) repeatedly scent-mark to demark territory boundaries, creating a string of conspicuous vegetative 'islands' on the tundra (Goltsman et al., 2005). River otters (*Lutra canadensis*) are semi-aquatic predators that transport nutrients from aquatic prey onto land through scent-marking behavior (i.e., latrines). Soil and plant nutrient content and plant growth are greater at latrines than control sites (Ben-David et al., 1998; Crait & Ben-David, 2007), but variation in the frequency otters use latrines creates heterogeneity in their relative importance (Ben-David et al., 2005). Predator latrines also concentrate parasites, which can indirectly affect other animals. For instance, parasite-vulnerable species avoid raccoon (*Procyon lotor*) latrines but disease-tolerant species are attracted to them (Weinstein et al., 2018).

Repeatedly-used predator resting and foraging sites may also generate PIEs. In coral reef systems, schooling fish concentrate nutrients derived from prey *off* the reef into patches *on* the reef, which enhances coral growth and promotes grazing by herbivorous fish (Shantz et al., 2015). Studies have also demonstrated plant productivity is greater under common seabird perches (Powell et al., 1991; Herbert & Fourqurean, 2008). Perhaps the best-known example of PIEs from predator foraging comes from salmonid systems: bears, in particular, are key predators that create biogeochemical hotspots along streams by transporting salmon-derived nutrients onto land (Helfield & Naiman, 2006; Levi et al., 2020). Bear-transported salmon, in turn, benefit riparian soils (Holtgrieve et al., 2009), invertebrates (Hocking & Reimchen, 2006), and plants, including enhancing the growth of old-growth conifers (Reimchen & Fox, 2013).

The distinguishing characteristic between patches generated from prey carcasses and patches generated from nutrient accumulation is that in the latter pathway predators deposit the nutrients at different sites from where prey are killed. Moreover, PIEs from the carcass pathway occur through individual predation events whereas effects via nutrient transport occur through frequent, repeated nutrient deposits that have compounding effects. Relative to carcasses, patches created from nutrient accumulations also tend to be larger and have spatiotemporal boundaries that may be more challenging to delineate. For instance, prey-derived nutrients may be detected hundreds of meters from predator colonies (Bokhorst et al., 2019; Benkwitt et al., 2021). Nonetheless, the effects from these ecological hotspots are still limited in space and time and occur largely independently of prey density or behavior.

Predator movement and resource selection traits are the primary drivers of the spatiotemporal distribution of patches generated via nutrient accumulation. Predators transport prey-derived nutrients from one site to another, the location of which is often influenced by environmental characteristics: coastal topography influences the site selection of marine mammal haul-outs and seabird colonies, tree availability influences roosting sites, and habitat characteristics influence predator home site selection. Thus, the nutrient accumulation pathway demonstrates how predator behavior and movements work in tandem to link donor and recipient nutrient sites, and ultimately influence where patches are created.

Box 2.2: Case study: Arctic fox dens are ecological hotspots on the tundra

Arctic foxes give birth during spring while the tundra is still covered in snow and ice, which restricts their ability to excavate new dens. They instead re-use the same dens for decades—even centuries—to raise pups (Macpherson, 1969). For instance, in Manitoba, Canada, Arctic foxes re-use the same dens year after year presumably because suitable den sites are restricted to elevated beach ridges that are easy to excavate and prevent the den from flooding during snowmelt (Johnson-Bice et al., 2023; Chapter 3). As foxes repeatedly occupy the dens, the decay of accumulated prey remains and fox excrement increases soil nutrient concentration and plant production (Smith et al., 1992; Gharajehdaghipour et al., 2016), resulting in nutritionally enriched and locally diverse plant communities on Arctic fox dens (Bruun et al., 2005; Fafard et al., 2020). Throughout much of the Arctic, Arctic fox dens are characterized with lush, atypical vegetation that stands in stark contrast to the surrounding landscape (Box 2.2, Fig. 1A), earning them the nickname ‘gardens of the tundra’. Arctic fox dens are large enough that the productivity and phenology of den vegetation can be studied from satellite imagery (Johnson-Bice et al., 2023; Chapter 3).

Wildlife from across the tundra are attracted to Arctic fox dens for both food and shelter. Predators and scavengers are detected far more frequently on Arctic fox dens than similar tundra areas (Zhao et al., 2022), likely attracted by the prey remains found on dens. Indeed, numerous species have been observed consuming or removing prey remains from Arctic fox dens including ravens (*Corvus corax*), eagles (*Haliaeetus* spp.), sandhill cranes (*Antigone canadensis*), and polar bears (*Ursus maritimus*) (Box 2.2, Fig. 1C-E; Mallory, 1987; Zhao et al., 2022). Caribou (*Rangifer tarandus*) also visit Arctic fox dens twice as often as reference sites, likely to forage on the enhanced vegetation (Box 2.2, Fig. 1F; Zhao et al., 2022). Perhaps counterintuitively, Arctic fox dens even attract their main prey, lemmings. Tall vegetation on dens traps snow and provides suitable winter habitat for lemmings (Gharajehdaghipour & Roth,

2018). Observations of greater wildlife occurrence at fox dens relative to comparable areas suggest that these other animals adjust their space use toward den sites across the landscape. When wildlife visit Arctic fox dens they may also excrete nutrients at or near the dens (Box 2.2, Fig. 1B), creating a positive feedback that further enriches den sites. Through both direct (provisioning prey remains) and indirect (vegetation changes from nutrient deposition) pathways, Arctic fox dens have substantial PIEs on other tundra species that are spatially constrained by landscape characteristics.

Ecosystem engineer removal pathway: predators alter ecosystems by killing ecosystem engineers that create and maintain patches

Ecosystem engineers are organisms that influence the availability of resources to other species by physically modifying their environment (Jones et al., 1994). Ecosystem engineers can be found throughout most biomes on earth and they exhibit considerable variation in the magnitude of their ecological impact (Hastings et al., 2007). Although some engineering species have more diffuse ecological effects, engineers that build structures or create patches indirectly affect other species in a localized manner. For instance, termites build mounds and underground cavities that indirectly affect soil microbiota communities, nutrient cycling, and vegetative production at mound sites (Dangerfield et al., 1998; Jouquet et al., 2011). Some birds build large, perennially used nests (e.g., eagles) that can become biodiversity hotspots (Maciorowski et al., 2021). Despite the fact that most ecosystem engineering species occupy mid-trophic levels (see Coggan et al., 2018), surprisingly few studies have evaluated how predators indirectly affect other species by hunting ecosystem engineer prey.

We draw upon what few studies have been conducted on predator-ecosystem engineer interactions to suggest that predators have PIEs on ecosystems by killing ecosystem engineers that create and maintain patches. The effects follow a logical succession: 1) engineers create and maintain patches that indirectly affect organisms, 2) predators remove the engineer(s), resulting in no animals left to maintain patch functionality, and 3) over time the ecological effects of the engineered patch diminish and the environment reverts to its pre-engineered state. In these scenarios, predators have PIEs limited to the spatial boundaries of the engineered patch and the length of time it takes for the environment to recover at the patch site.

One empirical example of this pathway comes from mound-building ants (*Atta* sp.). *Atta* are leaf-cutter ants that build huge nest mounds (up to 250 m^2) that affect surrounding plant assemblages and soil characteristics (Corrêa et al., 2010; Meyer et al., 2013). Armadillos

(*Dasypus novemcinctus*) and army ants (*Nomamyrmex esenbeckii*) are both predators of *Atta* colonies capable of destroying young and mature colonies (Rao, 2000; Powell & Clark, 2004). Although more often recognized for their top-down control of *Atta* population density (Terborgh et al., 2001), predators that destroy these colonies also alter the manner in which the colony mounds affect other species by initiating the mounds' return to their pre-engineered state. Strong evidence that predators generate PIEs by killing ecosystem engineers comes from a case study on wolf predation of dispersing beavers (*Castor canadensis*), whereby wolves directly affect beaver pond dynamics and indirectly affect the wide variety of species that thrive in beaver-altered environments (Gable et al., 2020, detailed in Box 2.3).

Few studies have directly evaluated the indirect effects of predator-ecosystem engineer interactions (but see Sanders & Van Veen, 2011; Dunoyer et al., 2020), making it difficult to estimate how frequently predators alter ecosystems by killing engineers. However, we suggest it likely occurs anywhere predators kill patch-creating ecosystem engineers. The lack of examples is likely not a reflection of the frequency that this pathway occurs in nature but rather the amount of research on predator-ecosystem engineer dynamics.

The ecological implications of predator-ecosystem engineer dynamics are best understood from the engineer's perspective. Because patches created by engineers often persist beyond the death of the engineer, engineered patches go through periods of occupation, abandonment, and recolonization that are influenced by population dynamics of the engineers and the rate(s) of decay/recovery of the patches (Wright et al., 2004). Thus, the processes underlying engineered patch dynamics—mortality, immigration, persistence—are similar in many ways to metapopulation or source-sink dynamics (Fryxell, 2001). At a landscape perspective, these demographic and ecological processes lead to a mosaic of patches at various stages of occupation/abandonment that increase heterogeneity (Remillard et al., 1987). This process parallels the classic patch dynamics concept from landscape ecology whereby disturbance events drive heterogeneity (Bormann & Likens, 1979; Pickett & White, 1985). Although evaluations of ecosystem engineer-patch dynamics rarely incorporate predation into their models, predators will be inherently linked to the dynamics of engineered patches and all effects associated with the patches when predation is a substantial source of mortality for the engineer populations.

Box 2.3: Case study: Wolves alter ecosystems by killing pond-creating beavers

Beavers are renowned ecosystem engineers that create and maintain ponds by constructing dams. Beaver ponds alter the hydrologic, geomorphic, and vegetative characteristics around the dammed site (Naiman et al., 1988), providing numerous ecological benefits to plant, fish, amphibian, reptile, and mammal species (Rosell et al., 2005; Brazier et al., 2021).

In the Greater Voyageurs Ecosystem (GVE) in Minnesota, USA, wolves have an outsized effect by altering the creation and recolonization of ponds by killing dispersing beavers (Gable et al., 2020). Juvenile beavers typically disperse during spring and establish a new colony by either constructing a new pond, or recolonizing an abandoned pond by repairing an old dam (Box 2.3, Fig. 1A). When wolves kill a beaver in the process of creating or recolonizing a pond, the pond fails to persist into the fall (Gable et al., 2020). Occupancy rates of 'wolf-altered' ponds are substantially lower compared to reference ponds in the same year the predation event occurs (0% vs. 84%), and there is some evidence that indicates these effects may last for several years (Gable et al., 2020). Thus, wolves, by killing dispersing beavers, directly alter the ecological trajectory and fate of individual ponds, indirectly affecting other species that benefit from beaver-altered environments. To date, there is no evidence that wolf predation limits beaver abundance in this system (Gable & Windels, 2018; Johnson-Bice et al., 2021). Instead, wolves appear to be a top-down force that influences the spatial distribution and temporal occupancy of beaver ponds, rather than the number of ponds (Gable et al., 2020).

Put differently, the broader-scale effects of wolf predation on beavers are not mediated through changes in beaver density, but rather through changes in individual ponds distributed across the landscape. Like other engineered patch types, beaver ponds go through periods of occupation and abandonment, resulting in a mosaic of ponds at different ecological states that increases landscape heterogeneity and promotes ecosystem resilience (Remillard et al., 1987; Johnson-Bice et al., 2022). As a force influencing the spatiotemporal distribution of ponds, wolves are thus connected to this landscape mosaic. Using data on wolf density and kill rates, beaver dispersal, and the number of ponds maintained per beaver colony, Gable et al. (2020) estimated wolves alter the fate of 88 ponds annually (95% CI: 36-162). Considering ~120 ponds are created annually in the study area (authors, unpublished data), wolf predation appears to be an important influence of broader beaver pond dynamics (though individual variation in kill rates of beavers means there is likely intraspecific variation in how wolves affect pond dynamics; Bump et al., 2022). Because wolves and beavers co-occur across a large portion of the

Northern Hemisphere, this mechanism is likely widespread (Gable et al., 2018). And although wolves are the dominant predator of beavers, there is little reason to suspect this mechanism is unique to wolves as a variety of other large predators such as pumas, bears, coyotes, and lynx also kill beavers (Kertson et al., 2011; Lowrey et al., 2016; Gable et al., 2018).

Predicting where and when patchy indirect effects are important

We can make some general predictions about the relative importance of patchy indirect effects (PIEs) in ecosystems based on patch size and density/frequency, predator community dynamics, and ecosystem productivity. Here, we define importance generally to represent the relative magnitude of the PIEs, or the capacity for the resultant patch to affect ecological processes of interest.

First, logically, larger patches or patches with long-lasting effects are going to be more ecologically important, relatively speaking, than smaller or shorter-lasting patches (Fig. 2.1). Consider the disparity in ecological effects from small vs. large predator-killed carcasses. Smaller carcasses have less carrion, which may be quickly consumed by scavengers and, in turn, have reduced effects on plants due to fewer nutrients leaching into soils. This size difference is likely, in part, why predator-killed roe deer (*Capreolus caprelous*) (20–30 kg mass) have no detectable effects on soil or plants (Teurlings et al., 2020) but predator-killed large ungulates do (Bump et al., 2009a; Risch et al., 2020; Peziol et al., 2023). Second, the relative ecological importance of PIEs in an ecosystem will often be related to their density and frequency on the landscape. Patches that occur more frequently are likely more important from a cumulative, landscape-scale perspective (Fig. 2.1). For example, the greater the density of predator-created biogeochemical hotspots, the greater the likelihood that these patches influence ecosystem dynamics. Similarly, despite the small size of salmon carcasses, they can have large effects on ecosystems because they occur in such large numbers (e.g., Helfield & Naiman, 2001, 2006; Holtgrieve et al., 2009). Third, ecosystems that support greater predator diversity likely support a greater diversity of PIEs (Fig. 2.1). In ecosystems with diverse predator guilds, interspecific competition for prey may cause dietary (Elbroch et al., 2015b) or spatial partitioning (Vanak et al., 2013), which likely affects the spatiotemporal patterns of PIEs (i.e., variation in carcass type and kill site locations). Finally, ecosystem productivity and **rates of ecosystem recovery and turnover** likely also influence the magnitude of PIEs (Fig. 2.1). Patchy indirect effects in ecosystems with slower recovery and turnover rates will have greater relative ecological importance compared to ecosystems with faster recovery and turnover rates.

In general, the effects of above-ground animals on nutrient cycling are expected to be more pronounced in environments with abiotic constraints on nutrient cycling (Malhi et al., 2022). For instance, seabird-transported nutrient subsidies have a weaker relative impact on local terrestrial communities in highly-productive, tropical islands compared to high-latitude islands (Steibl et al., 2021), whereas prey carcasses can affect plants on the Arctic tundra for a decade or more (Danell et al., 2002).

These general factors (patch size, frequency/density, diversity, and ecosystem productivity) may have context-dependent effects within any given system. For example, patches that occur at a low density in tundra ecosystems could have a greater capacity to influence other species than patches that occur frequently in tropical forest ecosystems due to the predicted longevity of effects in ecosystems with low recovery/turnover rates. Ultimately, what we may identify as relatively more/less important will depend on the question and system of interest—are we interested in understanding conditions that predict the importance of prey carcasses for scavenger dynamics, or conditions that predict the importance of prey carcasses for soil and plant species? These conditions may or may not be the same. We expect considerable variation in how the general factors mentioned earlier affect PIEs, often depending on the question, scale, and system of interest.

Finally, although PIEs are better studied and likely more common in terrestrial ecosystems, we contend this mechanism has often been overlooked in aquatic ecosystems. From a nutrient deposition standpoint, PIEs are likely more important for terrestrial ecosystems because nutrients can get distributed widely by water in aquatic ecosystems (Monk & Schmitz, 2022). Nonetheless, PIEs are probably more common than assumed in aquatic ecosystems, particularly when predators kill large marine mammals. For instance, *hundreds* of vertebrate scavengers may respond to, and benefit from, large whale carcasses killed by orcas (*Orcinus orca*) (Totterdell et al., 2022), before the carcasses fall to the sea floor where a unique scavenger community awaits (Roman et al., 2014). Orcas will also sometimes cache whale carcasses along the sea floor, providing carrion for benthic and even terrestrial scavengers when pieces of the carcass wash ashore (Barrett-Lennard et al., 2011). Though not yet extensively examined, we predict depredated marine mammals are distributed in different spatiotemporal patterns compared to other sources of mortality, similar to depredated carcasses in terrestrial ecosystems.

Quantifying patchy indirect effects of predation at local and landscape scales

Here, we provide some approaches for quantifying PIEs of predation at both local and landscape scales. There is considerable variation and flexibility in the methods available to researchers depending on the system, but our point in illustrating numerous examples here is to demonstrate the efficacy and feasibility of quantifying PIEs of predation at multiple scales.

Quantifying PIEs at the local (patch) scale is relatively straightforward since, by our definition, the indirect effects are generally constrained within patch boundaries. A paired reference-treatment approach is often the most effective method for delineating the patch boundary and quantifying effects at this scale (Ellis-Soto et al., 2021), particularly for patches created via the carcass and nutrient accumulation pathways. Reference sites can be paired adjacent to the patch, ideally matching characteristics between the sites to be better able to attribute any differences to the predator(s). For instance, invertebrate and plant characteristics can be directly compared at a carcass or nutrient accumulation patch with nearby reference sites (e.g., Ben-David et al., 1998; Bump et al., 2009b; Barton et al., 2016; Gharajehdaghipour et al., 2016; Barry et al., 2019). Alternatively, quantitative models based on the characteristics of carcass or nutrient patches could be used to generate reference locations matching the nutrient patch characteristics for comparison (Johnson-Bice et al., 2023, Chapter 3). Manipulative experiments or remotely sensed trail cameras can be used to evaluate food web-related effects that occur in and around patches (Cortés-Avizanda et al., 2009a; Ruprecht et al., 2021; Spencer et al., 2021; Zhao et al., 2022). Similarly, remote cameras can be used to estimate rates of nutrient accumulation by recording the rate, type, and quantity of prey remains brought to and concentrated at specific locations (de Miranda et al., 2023).

Knowledge about the ecology of predator-prey interactions is needed to quantify the landscape-scale effects of patches created through carcass deposition. The number of carcasses generated for each prey species in a system can be estimated by multiplying predator kill rates (prey killed/predator/unit time) by predator density to yield per capita carcass density estimates (carcasses/km^2/unit time) (Barton et al., 2019; Morant et al., 2022). Prey density estimates may also be needed to estimate large-scale prey carcass abundance if predator kill rates vary based on prey abundance (Vucetich et al., 2002; Morant et al., 2022). The amount of carrion available to scavengers can be estimated by multiplying carcass density by the average proportion of carcasses left by predators (Allen et al., 2015; Prugh & Sivy, 2020; Peziol et al., 2023). Through time, carcass deposition patterns can provide spatially explicit estimates of areas that receive higher/lower nutrient inputs (see Bump et al., 2009a; Ellis-Soto

et al., 2021; Peziol et al., 2023 for methods and detailed examples), including insight on how environmental features influence spatiotemporal patterns of carcass deposition.

Information and methods needed to quantify the landscape-scale effects of patches created through the nutrient accumulation pathway depend on the patch type of interest. Surveys are likely one of the easiest ways to quantify home site density. For instance, census survey methods have been used to quantify Arctic fox den density (Johnson-Bice et al., 2023, Chapter 3), and thus the landscape-scale impact fox denning behavior has on other tundra species. If predator home sites (or colonies, haul-outs) vary in size, these size-dependent effects can be accounted for when quantifying their broader scale impact (Bokhorst et al., 2019). Individual-based data collection methods can also be used to estimate patch density at the landscape scale if predator density is known (e.g., num. latrines per individual * individuals/km^2). For instance, biologging devices can be used to identify scent-marking and foraging behaviors (Bidder et al., 2020; Clermont et al., 2021), which, when combined with location data, may be used to identify and quantify nutrient deposition hotspots. With knowledge of the rate of nutrient deposition at each nutrient hotspot (e.g., g/m^2/unit time of nitrogen), estimates of the landscape-scale magnitude of predator nutrient deposition can be quantified (Ellis-Soto et al., 2021).

Measuring patch-scale effects from the ecosystem engineer removal pathway—if they occur at all—is more challenging, since the natural periods of occupation, abandonment, and recolonization of patches by other engineers obscures the effects of direct predation. After a predator kills an engineer, it may be difficult to determine whether changes to the patch are a direct result of predation as opposed to alternative explanations. Consider possible scenarios that may occur after a predator kills a dispersing beaver: if a second beaver occupies the affected pond shortly after the first beaver dies, then the predation event had little ecological effect. Despite the simple chain of events (predator kills engineer, engineered patch changes), careful study designs are needed to demonstrate predators cause any changes to the engineered patch.

One general approach that may be useful is to repeatedly monitor patches affected by the predator (i.e., where predators kill engineers) and also reference patches that provide baseline information on the occupancy dynamics of engineer-created patches (Gable et al., 2020). The approach involves: 1) identifying predation events where predators killed engineers that occupied or were creating a patch, 2) documenting how each patch was or was not changed by other engineers after predation, 3) identifying reference patches to assess expected conditions at patches if engineers were not killed, and 4) comparing differences between

reference and predator-altered patches. Any meaningful differences could then be plausibly attributed to predators. Researchers could also experimentally simulate “predation events” on the engineer prey via non-lethal methods, such as removing or translocating engineers, and compare ecological patterns at the manipulated patches vs. reference patches. Depending on the species or systems of interest, there may be other approaches that are simpler or more appropriate for similar evaluations.

Gauging the landscape-scale effects of predator-engineer interactions is similarly difficult. As discussed earlier, occupancy dynamics of engineered patches are influenced by both patch characteristics and the demography of the engineer. Specifically, not all engineers are successful in creating patches and/or the engineer(s) may be responsible for +/- 1 patch per individual. These factors (engineer mortality, patch creation/recolonization rate, and the number of patches affected per engineer) affect landscape-scale patch dynamics (Wright et al., 2004), and must be accounted for. Individual-based designs that assess both the creation and recolonization of patches, and the proportion of engineer mortality due to predation, can reveal these landscape-scale effects. Alternatively, Gable et al. (2020) demonstrated the feasibility of quantifying landscape-scale effects using a predator-centric study design by combining data on predator density, kill rates of engineers, and data on the engineered patch dynamics. Generalizing the approach from Gable et al. (2020), we can estimate the number of patches (*P*) predators affect:

$$P = N_{pred} * KR_{pred} * P_{established} * P_{individual} * P_{occupancy} \quad \text{(Eq. 1)}$$

where N_{pred} is the number (or density) of predators, KR_{pred} is the kill rate of engineers, $P_{established}$ is the proportion of engineers that successfully establish patches, $P_{individual}$ is the number of patches established per engineer, and $P_{occupancy}$ is natural occupancy rate, all measured over a time period of interest. Together, these metrics account for the proportion (or number) of patches predators affect in relation to the occupancy dynamics of the engineered patch mosaic.

Perhaps the most straightforward method to assess large-scale predator-engineer dynamics is to use a paired approach that compares patch dynamics in similar landscapes with and without predators (or before and after predator introduction). However, this approach is likely most feasible for systems where the engineered patches are small and easy to monitor. The take-home message is that because engineered patch dynamics are affected by the ecology and movements of engineers themselves, resolving the role predators play is difficult and requires study designs that can decompose the relative influence of predators and engineers.

By quantifying PIEs at both the local and landscape scales, researchers can obtain not only a more thorough and multi-scale perspective of predators' impacts on ecosystems, but this process can also help identify larger spatiotemporal patterns of PIEs. For instance, several studies have demonstrated that patches of enhanced vegetation created through predator-mediated nutrient deposition can affect the foraging dynamics and space use of herbivores at larger spatial scales (Shantz et al., 2015; McLoughlin et al., 2016; Zhao et al., 2022). Landscape (or spatial) heterogeneity is widely recognized as a key driver of numerous ecological patterns and processes, including species biodiversity and richness (Tews et al., 2004; Stein et al., 2014), space use and dispersal patterns (Pyke et al., 1977; Gustafson & Gardner, 1996; Avgar et al., 2013; Davies et al., 2021), and the dynamics and persistence of populations (Hanski, 1999). Research efforts that quantify predator-mediated landscape heterogeneity will further elucidate the unique role predators play in these broader ecological processes that help govern ecosystem structure and function.

Interaction, co-occurrence, and distinction of patchy, density-mediated, and trait-mediated mechanisms

Patchy indirect effects (PIEs) are a distinct mechanism from density- or trait-mediated mechanisms because i) they do not require predators to substantially alter the population density or behavior of prey, and ii) they are limited to the spatial and temporal boundaries of the created patch (carcass pathway, nutrient accumulation pathway) or affected patch (engineer removal pathway). This does not mean the mechanisms cannot co-occur in predator-prey systems, as is often the case with density- and trait-mediated indirect effects (DMIEs and TMIEs) (Peacor & Werner, 2001; Werner & Peacor, 2003; Preisser et al., 2005; Pruett & Weissburg, 2021).

Consider predator-prey systems where predators influence the spatial distribution of their prey. In these systems, predation risk (a non-consumptive/trait-mediated mechanism) alters the spatial (and likely spatiotemporal) distribution of where prey congregate on the landscape. As a consequence of the altered prey distribution, when predators kill these prey the resulting carcass locations will have, in turn, been influenced by non-consumptive mechanisms that altered the prey's distribution in the first place. Thus, there is an interaction (or feedback) between patchy and trait-mediated mechanisms that occurs within these predator-prey systems. Moreover, when predators affect the abundance of their prey, there will be a similar feedback

between the predators' effects on prey density and the number of carcasses generated (lower density of prey, lower density of carcasses).

We can see evidence of the co-occurrence and interaction of these mechanisms in a system like Yellowstone National Park. Wolves in Yellowstone affected both the population density (Peterson et al., 2014; Metz et al., 2020) and, to a lesser degree, space use of elk (*Cervus canadensis*) (Kohl et al., 2018; Cusack et al., 2019), which has had a weak but measurable cascading effect on tree recruitment (DMIEs and TMIEs; Brice et al., 2022). But wolf-killed elk carcasses also have PIEs on local plant and soil communities separate from DMIEs and TMIEs (Risch et al., 2020); the number and location of these carcasses are nonetheless influenced by wolves' ability to alter the traits and regulate the abundance of elk. Similarly, expanding on our earlier example of how predators have PIEs by destroying leaf-cutter ant (*Atta* sp.) colonies, predators may also have co-occurring DMIEs by reducing *Atta* colony abundance, thereby preventing the transformation of tropical forest communities through their herbivory (Terborgh et al., 2001). Thus, although PIEs are a distinct mechanism by which predators alter ecosystems, they certainly can operate simultaneously and in tandem with density and trait-mediated mechanisms.

Distinguishing between PIEs, DMIEs, and TMIEs requires examining the indirect effects of the predator-prey interaction(s), identifying the mechanism(s) that led to the effects, and defining the scale (spatial and temporal) of interest. For instance, although indirect non-consumptive effects of predation may be confined to the boundaries of a patch, these effects are not PIEs. In the Andes, puma predation risk influences the diel migration patterns of vicuñas (*Vicugna vicugna*), resulting in patches of nutrients in the lower-risk areas (Monk et al., 2023). Although these nutrients are spatially confined, the mechanism shaping the spatial patterning of nutrient deposition—predation risk—would fall under the umbrella of TMIEs because it is non-consumptive (expanded in greater detail in Monk and Schmitz, 2022). In a system where predators limit the abundance of patch-creating ecosystem engineers (e.g., the *Atta* leafcutter system described above), distinguishing between PIES and DMIEs may depend upon viewing these effects at different spatial scales. Density-mediated mechanisms may influence the density of patches on the landscape, whereas patchy mechanisms drive the indirect effects on other species at the patch scale. If there are characteristics of individual patches created by engineers that make these patches more/less prone to being affected by predators, then we could reasonably conclude density-mediated mechanisms have a greater influence on the total

number of patches but patchy mechanisms influence the spatial distribution of patches through variation in the susceptibility of each patch being affected by the predator(s).

These examples demonstrate how, in many ways, disentangling the relative effects of patchy, density-mediated, and trait-mediated mechanisms is challenging in natural systems, and may require approaching the same question from different angles. We do not see this difficulty of distinguishing between the various predator-mediated mechanisms as a weakness, but rather as an accurate reflection that indirect effects resulting from predator-prey dynamics within natural systems are often complex, nuanced, and may not fall neatly within our pre-defined categories.

Concluding remarks

Through our synthesis and case studies, we demonstrated the diverse ways predators indirectly affect other species via highly localized pathways limited to the boundaries of a patch—whether the patch is a carcass, a homesite or latrine, or a patch created by ecosystem engineer prey. The carcass distribution and nutrient accumulation pathways have been previously discussed both empirically and theoretically (Schmitz et al., 2010; Leroux & Schmitz, 2015; Schmitz & Leroux, 2020; Ellis-Soto et al., 2021; Newsome et al., 2021; Monk & Schmitz, 2022), which helped lay the foundation for part of our synthesis. However, these previous studies have largely focused either on just one pathway (Newsome et al., 2021) or on the nutrient cycling/deposition aspects of the pathways (e.g., Schmitz et al., 2010; Monk & Schmitz, 2022), and thus do not account for the multitude of other interspecific interactions and indirect effects that occur at these patches (e.g., scavenger interactions, opportunistic predation, parasite risk/transmission).

Our synthesis builds upon this previous body of work by defining and linking together all of these different ways predators affect ecosystem dynamics via a unifying element, a discrete *patch*. We provided examples of PIEs that spanned a wide diversity of taxa and ecological disciplines—studies on mammalian, avian, invertebrate, and fish predators that incorporated elements from plant and soil ecology, behavioral ecology, spatial ecology, and food web dynamics. We offered explicit predictions of when and where these patches are likely to be important, and provided numerous different approaches researchers could take to quantify patchy indirect effects of predation (PIEs) at both the patch and landscape scales. Although most of the research on these topics (and thus the examples we provided) are biased towards large terrestrial mammals in the Northern Hemisphere, by providing specific terminology for

these processes (*patchy indirect effects of predation*) we hope that the concepts discussed here will be more broadly recognized and appreciated.

As predator populations decline globally (Estes et al., 2011; Ripple et al., 2014), there is a need for a broader, more holistic understanding of the functional roles of predators in order to manage and conserve their populations—actions that can have broader benefits for the ecosystems they inhabit (Natsukawa & Sergio, 2022). To date, the justification for conserving, managing, and reintroducing predators frequently hinges on their ability to influence ecosystems through changes to the abundance and traits of lower trophic levels at the *population* scale (i.e., density- and trait-mediated indirect effects; Sergio et al., 2008; Ritchie et al., 2012; Blossey & Hare, 2022). However, our synthesis demonstrates predators also have important ecological effects that function at the *individual* or *patch* scale regardless of whether the predator(s) substantially affect prey populations. We have clearly shown that predators, through PIEs, have *irreplaceable ecological roles within ecosystems that influence nutrient cycling, community interactions, local species biodiversity, and myriad other ecological processes that ultimately increase landscape heterogeneity and contribute to ecosystem functioning*. Predators' ability to create patchy landscapes through these localized pathways adds to the growing evidence that they affect ecosystem structure and function in ways that are not easily replicated by humans (Lennox et al., 2022). We therefore see the PIEs concept as a step towards a unified view of predation in ecosystems by providing a spatially-explicit, multi-scale perspective of how predators affect ecosystems through patch-scale pathways. Considerable theoretical and empirical research has demonstrated that ecological patterns and processes can vary or be linked across multiple spatial scales (Levin, 1992), and our synthesis demonstrates that predation is yet another ecological process that can be better understood through this multi-scale perspective.

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Glossary 2.1

Carrion: the decaying flesh of dead animals

Consumptive effects: lethal effects of predators on their prey due to predation mortality

Density-mediated indirect effects: indirect effects of predation on other species that are mediated through reducing the population density of prey (or subordinate predators)

Ecosystem engineer: organisms that alter the flow of resources for other species through physical modifications of their environment

Ecosystem recovery rate: the rate at which an ecosystem returns to its pre-disturbance state following disturbance

Ecosystem turnover rate: the rate at which nutrients or other variables of interest flow through ecosystems

Meta-ecosystem theory: a theoretical framework centered around understanding how ecosystems are connected by spatial flows of organisms, organic matter, and nutrients across ecosystem boundaries

Mobile links: actively moving organisms that connect habitats and ecosystems in space and time

Non-consumptive effects: nonlethal effects of predation due to changes in prey behavior or other flexible prey traits in response to predation risk

Patchy indirect effects: indirect consumptive effects of predation on other species that are restricted to landscape patches with measurable spatial and temporal boundaries

Predation-risk effects: effects of predation risk on prey or other species that arise due to changes in flexible prey traits

Resource subsidy: energy resources transported from a donor habitat by either natural gradients (such as gravity, ocean currents; *passive subsidy*) or vectors (such as animals, humans; *active subsidy*), which alters the dynamics of a consumer in the recipient habitat

Trait-mediated indirect effects: indirect effects of predators on other species that are mediated through altering the behavior or other flexible traits of prey (or subordinate predators)

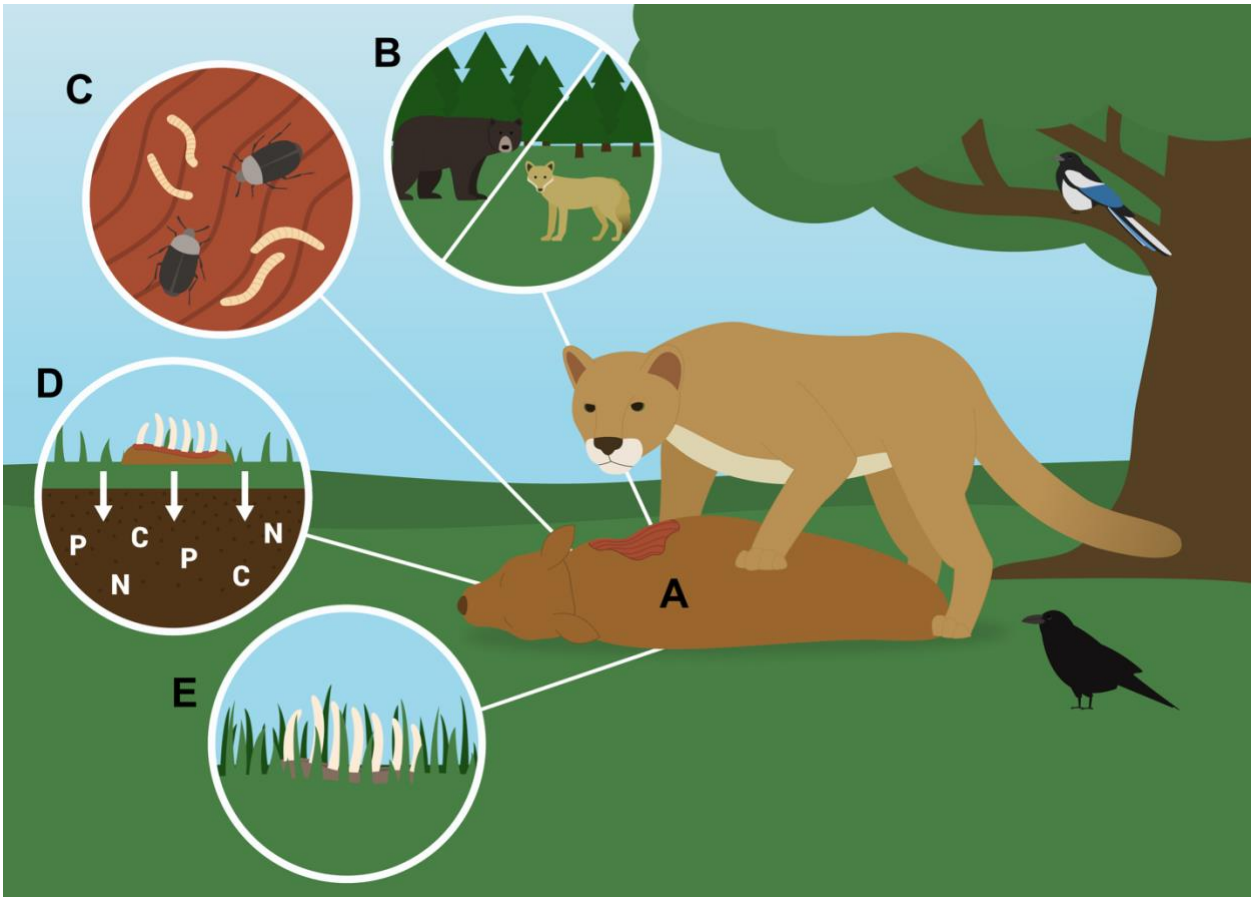

Figure 2.1. Patchy indirect effects that occur at puma-killed carcasses. Once a puma makes a kill (A), scavengers like corvids, bears, and coyotes may quickly respond to the carcass site (B). Since pumas often cache their prey, unique beetle communities develop on carcasses (C). As the carcasses decompose, nutrients like carbon, nitrogen, and phosphorous leach into the soil (D), which increases soil nutrient content and enhances plant growth in the immediate vicinity as the carcass decomposes entirely (E).

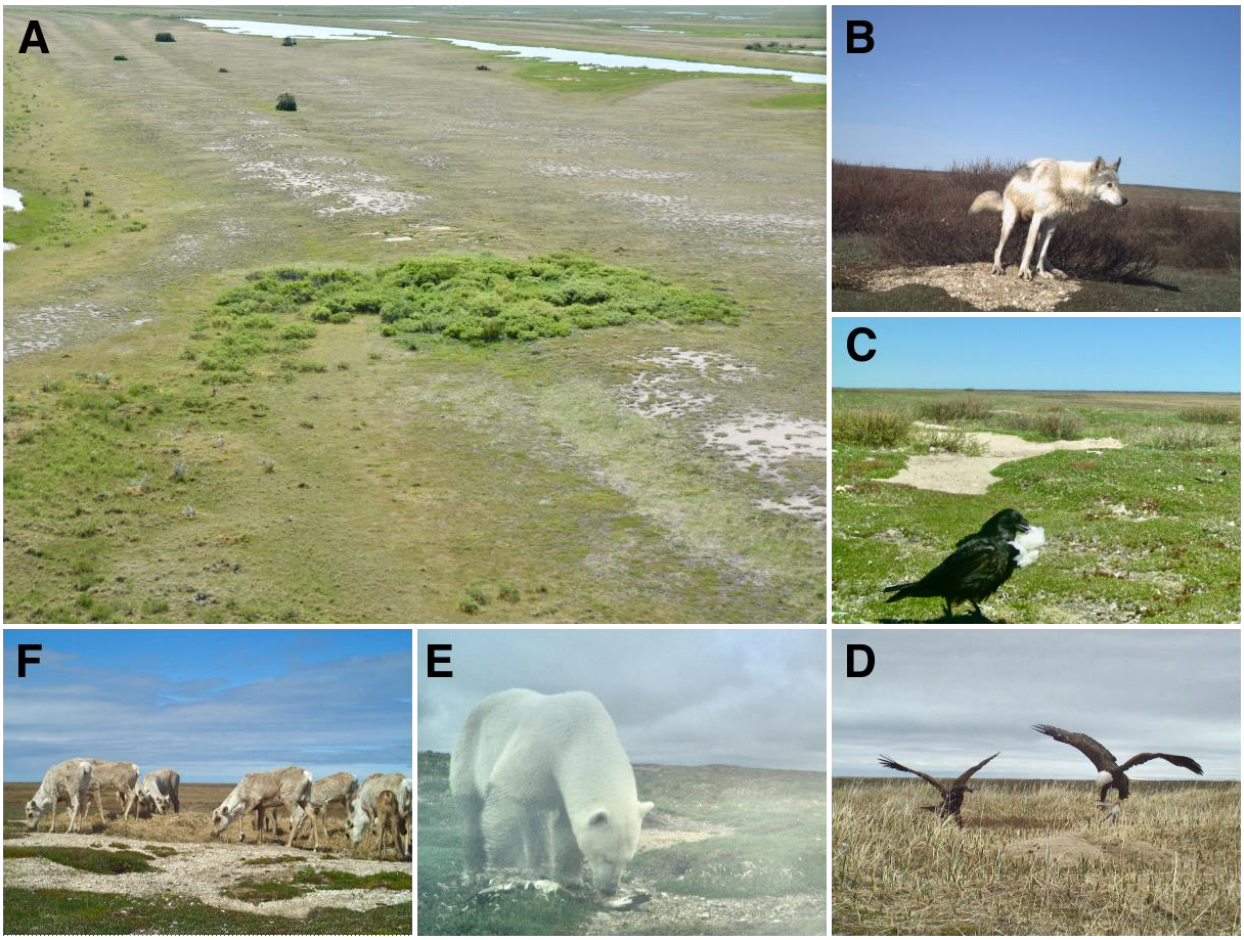

Figure 2.2. A collection of photos from Arctic fox dens near Churchill, Manitoba, Canada. Arctic fox dens are distinct biogeochemical patches with lush vegetation that stands out prominently on the tundra (A). Panels B-F are all photos taken with remote cameras placed on Arctic fox dens: a wolf defecating on a fox den (B), a raven stealing feathers from a goose carcass off a den (C), a juvenile and adult bald eagle sparring over prey remains from a den (D), a polar bear consuming prey remains on a den (E), and a small group of caribou foraging on a den in late spring (F).

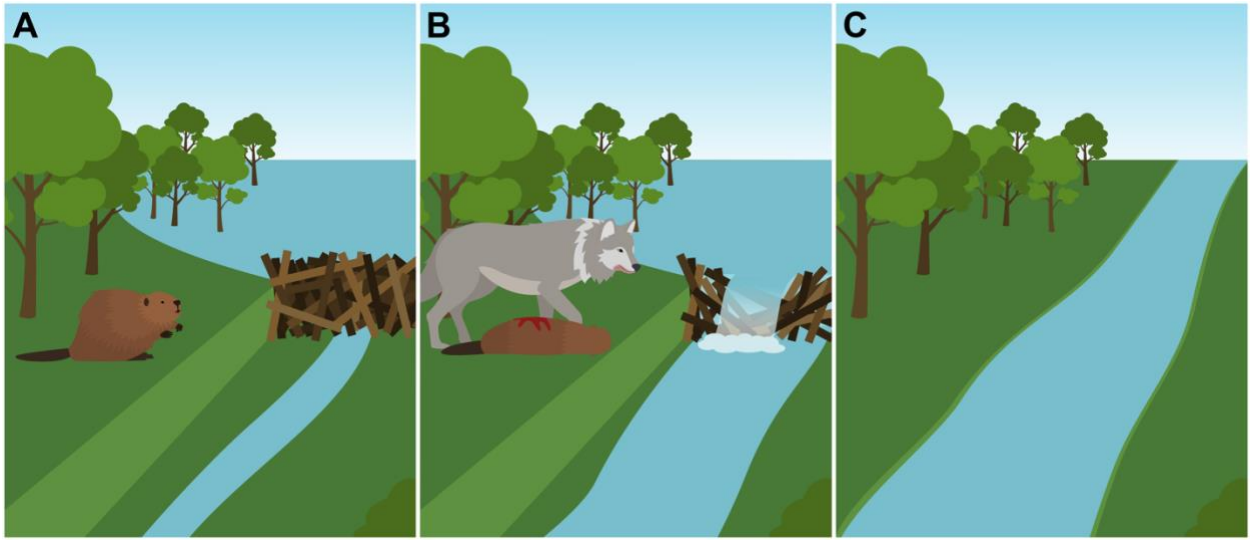

Figure 2.3. Dramatic representation of patchy indirect effects within riparian ecosystems that occur when predators kill dispersing beavers. Juvenile beavers disperse and create a new pond or recolonize an old pond (A). When a predator kills the dispersing beaver, the dam and pond begin to degrade over time (B). Eventually the dam may collapse, causing the riparian site to revert to its pre-engineered state (C).

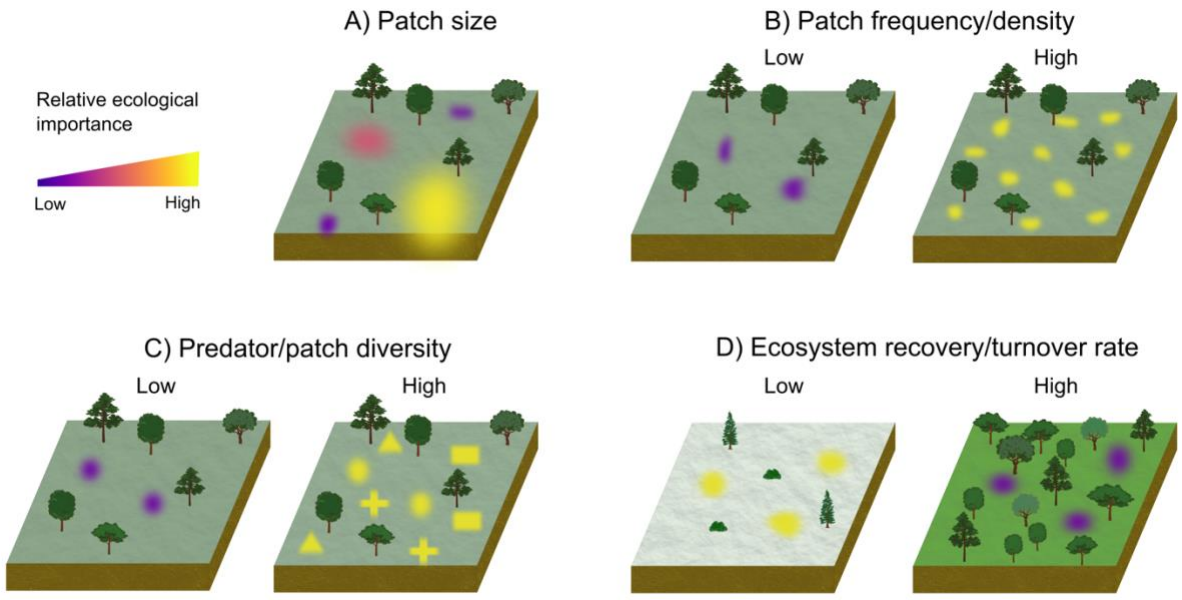

Figure 2.4. Conceptual diagram of ecological conditions that may influence the relative magnitude or ecological importance of patchy indirect effects (PIEs) of predation in ecosystems. Larger patches will generally have a larger ecological impact than smaller patches (A). Similarly, from a cumulative, ecosystem-level perspective, predator-altered patches that occur more frequently in time or space should be relatively more important than infrequent patches (B). Ecosystems that support a greater diversity of predators should likewise support a greater diversity of PIEs (e.g., unique spatial patterns of home sites and carcasses) (C). Finally, PIEs should be relatively more important in ecosystems that have a slow recovery or turnover rate (e.g., Arctic tundra) because the effects will generally persist longer in these ecosystems (D).

Chapter 3: A cosmic view of 'tundra gardens': satellite imagery provides a landscape-scale perspective of Arctic fox ecosystem engineering

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Abstract

Most animal ecology studies using remote sensing data have assessed how environmental characteristics shape animal abundance, distribution, or behavior. But the increasing availability of high-resolution data offers new opportunities to study how animals, in turn, shape ecosystems at diverse scales. We evaluate the efficacy of using Sentinel-2 satellite imagery to quantify the effects of Arctic fox (*Vulpes lagopus*) denning activity (nutrient accumulation, bioturbation) on vegetation. Using an imagery-derived metric (NDVI), we compared maximum plant productivity and plant phenology patterns on 84 Arctic fox dens vs. reference sites, i.e., points generated within preferred denning habitat areas (predicted from a habitat selection analysis). We show that high-resolution imagery can be used to measure the effects of Arctic fox denning activity on vegetation. Plant productivity and the rate of green up were both greater on fox dens compared to reference (preferred-habitat) sites. Productivity on reference sites was lower than average productivity on the tundra (i.e., random sites), indicating foxes primarily establish dens in low-productivity areas. Plant productivity on dens was also unrelated to recent occupancy patterns, indicating fox denning activity has long-term legacy effects on plants that last beyond the lifetime of foxes. Our findings support Arctic foxes being classified as ecosystem engineers in low-Arctic tundra ecosystems by converting low-productivity sites into relatively high-productivity sites through their denning activity. We demonstrate the efficacy of using remote sensing technologies to study how predators increase landscape heterogeneity and influence ecosystem dynamics through patch-scale mechanisms, and ultimately advance our understanding of animal functional roles.

Keywords: ecosystem function, landscape heterogeneity, NDVI, nutrient cycling, predator behavior, remote sensing, Sentinel-2, *Vulpes lagopus*

Introduction

Technological and methodological advancements in remote sensing in recent decades have provided novel insights into relationships between animals and their environment. For instance, researchers can use airborne and satellite-based light detecting and ranging (LiDAR) data to remotely quantify and describe the influence of ecosystem 3D structure on animals (Davies & Asner, 2014). Satellite imagery is similarly used to evaluate the influence of environmental factors like precipitation, temperature, and land cover type on animals (Pettorelli et al., 2014). In particular, satellite-derived metrics such as the normalized difference vegetation index (NDVI) —a metric frequently used to approximate vegetation and ecosystem productivity—have been used to assess animal-habitat relationships across space and time (Pettorelli et al., 2005; Pettorelli et al., 2011). Most studies using satellite-derived metrics to advance animal ecology have been conducted on large spatial scales, including revealing how herbivores track vegetation green-up throughout migration corridors (Sawyer & Kauffman, 2011; Bischof et al., 2012; van Moorter et al., 2013; Merkle et al., 2016; Aikens et al., 2017), how ecosystem productivity drives the structure of herbivore communities across the Arctic tundra (Speed et al., 2019), and modeling the distribution, abundance, and richness of animal species (e.g., Hurlbert & Haskell, 2003; Tognelli & Kelt, 2004; Bartoń & Zalewski, 2007; Evans et al., 2008; Nieto et al., 2015).

More recently launched satellites capable of capturing imagery at higher resolutions, such as the Sentinel series launched by the European Space Agency, offer the potential to decipher animal-habitat relationships at finer spatial scales (Pettorelli et al., 2014). Compared to 30-m resolution data from current Landsat satellites, 10-m resolution imagery captured by the Sentinel-2 satellite was a better predicter of bird richness patterns across the continental United States (Farwell et al., 2021). Integrating these high-resolution data sources can also improve the performance of species distribution models (Koma et al., 2022) and help identify microhabitat selection and suitability for small animals (Valerio et al., 2020; Alessandrini et al., 2022). Many remote sensing data sources are also freely available and easily accessible via platforms like Google Earth Engine. With advancements in the availability and accessibility of these data, we can expect researchers to use them to address a diversity of ever-evolving ecological questions (Turner et al., 2015; Schulte to Bühne & Pettorelli, 2018). In particular, finer-scale data sources may help unravel not only how environmental conditions affect animals, but how animals, in turn, influence ecosystem dynamics.

Predators are widely recognized for their ecological influence on prey abundance and behavior but they also alter ecosystems through localized, patch-scale pathways that contribute to landscape heterogeneity across space and time (Johnson-Bice et al., 2023, Chapter 2). These pathways include distributing carcasses across the landscape (Bump et al., 2009; Schmitz et al., 2010; Risch et al., 2020; Monk & Schmitz, 2022) and killing ecosystem engineers that create landscape patches (e.g., beaver [*Castor canadensis*] ponds; Gable et al., 2020), as well as concentrating nutrients derived from prey into discrete locations such as foraging (Holtgrieve et al., 2009), scent-marking (Ben-David et al., 1998; Crait & Ben-David, 2007), and social aggregation sites (Fariña et al., 2003; Bokhorst et al., 2019). Through each of these pathways, predators alter or create patches that influence landscape heterogeneity by indirectly affecting other species in a localized manner (Johnson-Bice et al., 2023, Chapter 2). For instance, predators that perennially re-use home sites may indirectly affect local plant and soil communities by concentrating prey-derived nutrients there. Soil nutrient levels and plant growth are greater at ground-nesting eagle owl (*Bubo bubo*) nests compared to reference sites (Fedriani et al., 2015), whereas the combination of bioturbation (from digging burrows) and nutrient deposition by badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) benefits plants around their dens (Kurek et al., 2014; Kucheravy et al., 2021; Lang et al., 2021). To date, few studies have looked at these patch-scale predator effects from a landscape-scale perspective (but see Bump et al., 2009; Gable et al., 2020).

Arctic foxes (*Vulpes lagopus*) are important terrestrial predators that occupy multiple functional roles in low-Arctic tundra ecosystems. Although often recognized for their role in regulating the abundance (Angerbjörn et al., 1999; Bêty et al., 2001; Iles et al., 2013) and altering the behavior (Bêty et al., 2002; Clermont et al., 2021) of their prey, their distinctive dens have also garnered considerable scientific and public interest. Throughout parts of their range, Arctic fox dens are characterized by unique vegetation compared to the surrounding area (Fig. 3.1) (Chesemore, 1969), earning them the nickname of the ‘gardens of the tundra’.

Arctic foxes are thought to be the main driver of these changes in plant composition in the tundra, but due to the incredible longevity of Arctic fox dens—one study estimated the average lifespan of a den to be 330 years (Macpherson, 1969) —it has been difficult to attribute the unique vegetation to the foxes. Nonetheless, the enhanced vegetation on fox dens aligns with other similar observations of predator home sites noted earlier (Kurek et al., 2014; Fedriani et al., 2015; Kucheravy et al., 2021; Lang et al., 2021), supporting the hypothesis that the predators are the cause of the enhanced vegetation. Most likely, the combination of disturbance

from digging burrows (bioturbation) and the accumulation of nutrients from prey remains and nutrients from predator excrement alters local vegetation. Arctic foxes, and other predators, have accordingly been classified as ecosystem engineers – organisms that benefit other species through physical modifications of their environment (Jones et al., 1994). In the case of Arctic foxes, their denning activity indeed positively affects both plant and wildlife species. Arctic fox dens have greater soil and plant nutrient content, greater plant biomass, and unique plant assemblages compared to nearby areas (Garrott et al., 1983; Smith et al., 1992; Bruun et al., 2005; Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Fafard et al., 2020). These plant and soil traits are thought to be influenced by the fact that the tundra is nutrient-limited, indicating that nutrients concentrated in a given location may induce large ecological effects (Gharajehdaghipour and others 2016). Tundra wildlife also adjust their space use towards dens, likely attracted there by the prospect of food subsidies – herbivores being attracted to the enhanced vegetation, and predators being attracted by the prey remains littered on the dens (Zhao et al., 2022). Despite this accumulation of evidence supporting Arctic foxes being classified as ecosystem engineers, these analyses were conducted on smaller spatial scales using comparisons with directly adjacent areas that were assumed to be representative of suitable denning habitat. Without explicitly accounting for den selection preferences across the full landscape, it has remained difficult to directly attribute fox activity to the plant characteristics found on their dens as opposed to alternative explanations.

Here, we apply a novel application of remote sensing data towards advancing our understanding of the ecological impacts of Arctic fox denning activity on the low-Arctic tundra. Specifically, we used freely available, high spatial and temporal resolution satellite imagery to quantify vegetative characteristics on Arctic fox dens, and ultimately unravel the role of Arctic foxes as ecosystem engineers through a landscape-scale analysis. We first developed a habitat selection model for fox dens to create *reference* sites, which are sites that effectively represent areas suitable for denning based on factors influencing current fox den locations (i.e., preferred-habitat sites). By quantifying factors contributing to fox den selection patterns, this approach allowed us to at least partially account for alternative explanations to the plant patterns on dens, namely that the den sites were already high-productivity patches. Then, using NDVI data derived from Sentinel-2 satellite imagery, we then compared 1) maximum plant productivity and 2) plant phenology patterns on (i) Arctic fox dens compared to (ii) reference sites on the tundra. We also compared plant productivity and phenology on fox dens and reference sites with (iii) fully *random* sites on the tundra (i.e., sites that represent all terrestrial habitats) to provide insight into how vegetation patterns on den and reference sites compare with average (random)

tundra sites. We predicted plant productivity would be greater and plant green up would start earlier and progress faster on fox dens compared to reference sites, supporting the hypothesis that Arctic foxes act as ecosystem engineers by altering local vegetation. Our study demonstrates the potential of using high-resolution remote sensing data to advance our understanding of the functional role(s) of predators in ecosystems.

Methods

Study Area

We conducted our study within a ~1200 km^2 tundra region of Wapusk National Park in northeastern Manitoba, Canada along the western coastline of Hudson Bay (Fig. 3.2A). Wapusk is part of the Hudson Bay Lowlands, one of the largest wetland ecosystems in the world. Monthly average temperature ranges from -26.0°C in January to 12.7°C in July (ECCC 2022). There is an average of 87 frost-free days (Jun. 19 to Sept. 15) annually in the area.

Arctic fox dens in Wapusk are predominantly located on ancient beach ridges formed from isostatic rebound after the melting of the Keewatin ice sheet (Ritchie, 1956; Roth, 2003; Sella et al., 2007). The ridges are relatively elevated and run roughly parallel to the Hudson Bay shoreline, with ponds, lakes, and wetland habitats between the ridges. Beach ridges are thought to be suitable denning habitats for foxes due to the low soil moisture levels and greater depth to permafrost layer, which allows for easier burrow digging (Chesemore, 1969; Smits et al., 1988; Dalerum et al., 2002). Our study area included all 84 known Arctic fox dens that were used for the NDVI analysis (density: ~7 dens/100 km^2), but in the habitat selection analysis we excluded two dens that were misclassified as ‘open water’ according to the 2015 Canada Land Cover data set. On these beach ridges, essentially the only patches of high-productivity vegetation are associated either with fox dens or spruce tree islands. Otherwise, these ridges are characterized with barren ground or prostrate shrub communities (Fafard et al., 2020). The vast majority of Wapusk dens were well-established prior to 1997 and most have been at least periodically occupied by foxes. The average surface area of Arctic fox dens in our study area is ~560 m^2 (Gharajehdaghipour and Roth 2018).

Arctic fox den habitat selection analysis

To evaluate how Arctic foxes select denning locations, we first delineated the area available for possible denning sites by creating a minimum convex polygon around all known fox

dens and then applying a 3-km buffer (clipped to the shoreline; Fig. 3.2a). This approach restricted the habitat selection analysis to only areas near known dens. Next, we generated 8200 random points (100 per den) within terrestrial habitats in the study area after removing all areas identified as 'open water' from the 2015 Canada Land Cover data set (Natural Resources Canada, 2019).

We performed the habitat selection analysis by comparing den and random sites (input as 1 and 0, respectively) using a binomial generalized additive model with a logit link function. We used four variables for the analysis: elevation, land cover type, and the latitude and longitude of each point. Latitude and longitude were included to control for spatial autocorrelation in the landscape data pre-emptively. Elevation data was obtained from the 30-m resolution FABDEM data set (Hawker et al., 2022). We reclassified the 2015 Land Cover data (Natural Resources Canada, 2019) into six categories: 'forest' (comprised of all forest cover types); 'shrub' (comprised of polar and non-polar shrub cover types); 'grass' (comprised of polar and non-polar grass cover types); 'lichen-moss'; 'wetland'; and 'barren'. We used 'wetland' as the reference level, as it is the most abundant habitat type in the study area. The habitat selection model is defined as:

$$logit(Y) = \ LandCover + f_1(elevation) + f_2(latitude, longitude)$$

where $LandCover$ is the point's land cover type (categorical variable), $f_1(elevation)$ is the point's elevation (in meters) fit with a smoothing component f_1 using a cubic regression spline, and $f_2(latitude, longitude)$ is the interaction between the point's latitude and longitude (in UTM units) fit with a smoothing component f_2 using a Gaussian process spline.

Habitat selection model validation

Creating 'reference' points for the NDVI analysis relied upon having a habitat selection model that could adequately predict known Arctic fox den locations, as this model would be used to generate new points in locations where foxes are likely to create dens but may not have done so yet. We therefore validated the habitat selection model performance using 5-fold cross-validation (detailed in Boyce et al., 2002; Roberts et al., 2017). Briefly, this process involved: 1) fitting 80% of the data to the habitat selection model, 2) creating a predictive habitat selection map (30-m resolution) of the study area from the model, 3) binning the map into 10 equal-sized quantiles, 4) identifying which quantile each den from the withheld (testing) data set was predicted to be in, and 5) performing a Spearman's rank correlation test (R version 4.2.0; R Core Team, 2022) on the withheld dens and their predicted quantile score. This process was

repeated four more times until each 20% of data was withheld as a testing fold. Because the dens in our area are well-dispersed (Fig. 3.2a) and landscape configuration does not differ substantially, we were comfortable using a random cross-validation approach. We also performed a Spearman's rank correlation on the predicted quantile data pooled across all five folds (Fig. 3.2b).

After model validation, which determined if the habitat selection model performed adequately in predicting Arctic fox denning locations, we fit the full data set to the habitat selection model. We then created a predictive habitat selection map from this model (Fig. 3.2c), reclassified the map into 10 equal-sized quantiles, and generated 84 random points within cells of the top quantile >250m from another reference site and from the nearest den (Fig. 3.2d). These 'reference' points effectively represent the 10% of terrestrial areas Arctic foxes are most likely to select for denning. All habitat selection models were fit using the 'gam' function from the *mgcv* package (Wood, 2011) in R.

Plant productivity and phenology analyses

Evaluating maximum plant productivity

We compared maximum plant productivity between 84 each of 1) 'den' locations, 2) 'reference' locations representing preferred but unused denning habitat (described earlier), and 3) 'random' locations, which represent the total terrestrial habitat availability in the study area (Fig. 3.2E). 'Random' points were randomly generated in ArcGIS Pro (version 2.8; Esri 2022) within terrestrial habitats in the study area >250m from every other point (den, reference, and random), a distance that would ensure sampled locations would not influence one another.

We assessed maximum plant productivity by creating a greenest pixel mosaic of 2A surface reflectance Sentinel-2 imagery (captured every 2-4 days in our study area) across the full growing season for 2019, 2020, and 2021 using Google Earth Engine (2019 is the earliest year 2A imagery is available for our study area). We defined the growing season as Jun. 16–Sept. 30, which was based on the average dates of last and first frost (Jun. 19 and Sept. 15) and suitable satellite image availability (cloud and snow coverage interference is high outside of this date range). Though essentially all greenest pixels would be from the middle/peak of the growing season, we chose to create the greenest pixel mosaic from across the full season to match the phenology analysis (see next section). This process involved first extracting all satellite images within the growing season, applying the 's2cloudless' (Zupanc, 2017) algorithm to mask clouds and shadows from each image, calculating NDVI values for each image pixel,

and then using the 'qualityMosaic' tool in Google Earth Engine to create a greenest pixel mosaic raster. This mosaic raster represents the maximum NDVI value on a pixel-by-pixel basis across the growing season. We exported the mosaic raster to ArcGIS Pro, excluded all cells with NDVI values <0.1 (as these cells corresponded to open water features or noise in the data), and calculated the mean NDVI value within a 20m buffer of each point using the 'Zonal Statistics as Table' tool. Notably, since the average den size in our study area is ~560 m^2, the 20-m radius (1257 m^2) includes area beyond many dens; NDVI estimates for dens should therefore be conservative. We compared 20m maximum NDVI values between dens, reference points, and random points (levels of our 'treatment' categorical factor) using a linear mixed effects model with 'point ID' and 'year' as random intercept terms (*lme4* package; Bates et al., 2015). Tukey's Honest Significant Difference pairwise comparisons were conducted using the 'pairs' function from the *emmeans* package (Lenth, 2022).

We were also interested in quantifying how prominent Arctic fox dens are on the landscape relative to the other locations used in the productivity analysis (reference and random groups). We therefore compared the difference in mean NDVI values within a 20m buffer vs. mean NDVI values within a 250m buffer for each point, each year (2019-2021). We averaged the mean maximum NDVI for each point across the 3 years and used Wilcoxon signed rank tests using base R functions to assess differences in average productivity between the two buffer distances for each group.

Finally, we assessed how recent fox reproductive success affected maximum plant productivity on dens. For each year spanning 2011–2021, we assessed the reproductive success of dens using on-the-ground and aerial surveys (details in McDonald et al., 2017). Briefly, we examined each den for signs of reproductive success, such as abundant prey remains on dens, fresh digging in burrows, and presence of fresh pup scats. To evaluate whether recent fox reproduction patterns influenced plant productivity, we used a Spearman's rank correlation test to evaluate the relationship between percent reproductive success (defined as the number of years each den produced pups divided by the number of years the den was surveyed) and maximum growing season NDVI averaged over the three years of imagery. We included only dens that had been surveyed at least 9 times for this analysis (n=78 dens).

Evaluating patterns of plant phenology

To understand whether plant phenology patterns on Arctic fox dens differed from other areas on the tundra, we examined whether dens start green-up earlier or stay green longer, and

when, during the growing season, any differences in plant productivity may arise. For this analysis, we used a similar 'greenest pixel mosaic' approach as described for the plant productivity analyses. We divided the growing season into seven equal time periods (Jun. 16-30, Jul. 1-15, Jul. 16-31, Aug. 1-15, Aug. 16-31, Sep. 1-15, Sep. 16-30) and generated greenest pixel NDVI mosaics for each time period spanning 2019-2021. Because of issues with cloud and shadow interference in the mosaics generated from the shorter time periods of this analysis, we manually inspected each mosaic raster and retained only the points where NDVI values could be satisfactorily calculated. Across all seven time periods spanning 2019–2021 we acquired 3,779 useable NDVI data points (71.4% total success rate in acquiring data to calculate NDVI, with a range across the seven time periods of 23.8% to 97.2%).

For each time period raster mosaic, we calculated mean NDVI within a 20m buffer of each point using the methods described earlier. We evaluated plant NDVI phenology using a hierarchical generalized additive model with a Gaussian distribution:

$$NDVI_{ijk} = f_{Group}(TimePeriod_{ijk}) + Group_{ijk} + PointID_i + Year_j$$

where $NDVI_{ijk}$ is the mean 20m NDVI value of the kth observation for point i in year j, and $PointID$ (categorical variable with unique values for point) and $Year$ are random intercept terms that were assumed to be normally distributed with a mean of 0. $f_{Group}(TimePeriod_{ijk})$ is the time period of the kth observation for point i in year j (coded as an integer from 1 to 7, representing the seven equal time periods) fit with a smoothing component f_{Group} using a thin plate regression spline comprised of seven basis functions. The spline varied by group level (den, reference, random) and had individual penalties (i.e., group-level factor smooth interactions with no shared penalty; Pedersen et al., 2019). The use of a smoother on time period was done to control for temporal autocorrelation in NDVI levels at the various time periods. The phenology model was fit using the 'gam' function in the *mgcv* package (Wood, 2011). We quantified pairwise differences among each of the factor smooth groups at each of the seven time periods using the 'difference_smooths' function from the *gratia* R package (Simpson 2022).

Results

Fox den habitat selection

Arctic foxes predominantly constructed dens in 'barren' or 'grass' land cover types and avoided 'wetland' areas (Fig. 3.2e). The smoothing components of elevation (effective degrees

of freedom [edf]=4.90, Chi-square=66.4, p<0.001) and the interaction between latitude/longitude parameters (edf=18.79, Chi-square=84.4, p<0.001) were both significant (edf values >1.0 indicate a non-linear and non-monotonic relationship), with fox dens occurring more frequently in elevated areas nearer to the coast than random sites.

Model validation results

Results from our five-fold cross-validation procedure indicated the den habitat selection model adequately characterized Arctic fox den locations. Spearman's rank correlation (r) results ranged from 0.43 (p=0.22) to 0.81 (p=0.005), with an average r of 0.67. Variation in r values may have been due in large part to the low sample size of dens used for each testing fold (n=16 or 17), whereby 1-2 dens categorized into low quantiles can greatly influence r values. When pooled across all five folds, the Spearman's rank correlation test on the binned quantiles was significant (r=0.86, p=0.002), with 71% (58/82) and 87% (71/82) of dens predicted to be within the top one and three quantiles, respectively (Fig. 3.2b). When fit to the full data set the habitat selection model explained 31.8% of deviance in Arctic fox den characteristics. We interpreted these results to indicate the habitat selection model had a moderate to good ability to explain current fox den characteristics and could be used to adequately characterize other areas foxes may select for when constructing new dens (i.e., could be used to generate 'reference' sites). The similarity in land cover types between den and reference sites within the top quantile supports this interpretation (Fig. 3.2e).

Maximum plant productivity

Maximum growing season plant productivity was significantly greater on Arctic fox dens compared to reference sites (p<0.001, T=4.89; Fig. 3.3a). The estimated marginal mean annual NDVI was 0.66 (95% confidence interval [CI]: 0.62–0.70) on dens compared to 0.59 (95% CI: 0.54–0.63) for reference sites (Fig. 3.3b). Plant productivity at random sites was significantly greater than productivity at reference sites (p<0.001, T=-3.94; Fig. 3.3a,b), suggesting that Arctic fox dens are typically constructed in relatively low-productivity areas. There was no difference in plant productivity between den and random sites (p=0.61, T=0.94).

Plant productivity was significantly greater on Arctic fox dens compared to the surrounding area, such that average maximum NDVI values within a 20m buffer around Arctic fox dens were greater than average NDVI values within a 250m buffer (T=8.07, p<0.001, df=83; Fig. 3.3c). As expected, plant productivity at reference and random sites did not differ from their surrounding areas (p=0.58 and 0.33, respectively; Fig. 3.3c).

Average fox den reproductive success (number of years pups were produced at each den divided by the number of years surveyed) over the last 11 years was 0.25 (SD=0.20). We found no relationship between recent fox reproduction and plant productivity on dens (Spearman's r=-0.076, p=0.51; Fig. 3.3d).

Plant phenology

We found Sentinel-2 imagery can be used to detect and visualize plant phenology patterns on Arctic fox dens (Fig. 3.4a). As expected, the temporal trends in plant productivity (NDVI) across the growing season were all statistically significant and non-linear for each group (den [edf=5.89, p<0.001], reference [edf=5.87, p<0.001], and random sites [edf=5.92, p<0.001]). Specifically, plant productivity increased from mid-June until a peak around mid-July, where it remained at peak productivity until the end of August (Fig. 3.4b). We found den NDVI values were significantly greater than reference NDVI values at time periods 2–6 (Jul. 1–Sept. 15), and greater NDVI values at random sites compared to reference sites at all time periods except the first (Fig. 3.4b,c). No difference in NDVI between den and reference sites at time periods 1 and 7 implies plants on dens do not start green-up earlier or stay green longer; however, judging by the slope of the increase in NDVI from time period 1 to 3, it appears that the rate of plant green-up is greater on dens (Fig. 3.4b).

Discussion

Using freely available software and high-resolution satellite imagery, our study provides a novel, landscape-scale perspective on the effects of Arctic fox denning activity on plant productivity and phenology. We demonstrated that plant productivity on Arctic fox dens is significantly greater than other areas in similar habitats, which are generally limited to relatively elevated but low-productivity areas. By using a habitat selection analysis to generate reference points, we were able to control for certain ecological factors that Arctic foxes select for when creating dens and thus help disentangle the relative effects of habitat vs. fox denning activity on plants. Our results provide further evidence that Arctic foxes are ecosystem engineers in low-Arctic tundra ecosystems.

Which came first: the foxes or the plants?

One of the lingering questions related to vegetation patterns on Arctic fox dens is whether their denning activity converts unproductive sites into productive sites through nutrient

deposition and bioturbation, or whether they select for preexisting high-productivity sites to build their dens. The easiest way to address this question is to monitor newly-created dens to see whether they (1) are created in pre-existing lush vegetation patches, or (2) are created in low-productivity areas that, through time, develop into lush vegetation patches. Although on the surface this seems straightforward, it is in fact far more challenging when the longevity of Arctic fox dens is factored in (estimated average lifespan of 330 years; Macpherson, 1969). In our study area, we know of only 2 dens that have been created since 1994 and both of these dens started in low-productivity areas with prostrate shrub vegetation typical of the elevated beach ridges (Fafard et al., 2020). Our approach to evaluate whether we can attribute plant characteristics on dens to fox activity was to use a quantitative method (habitat selection model) to develop paired reference sites that could be used to compare plant productivity. Despite the coarse variables included in our habitat selection model, our cross-validation results indicated it performed well in characterizing den site locations and could therefore be used to generate these matching 'reference' sites for comparison. The fact that the top quantile from the habitat selection model contained the habitat type the vast majority of dens are located on, elevated beach ridges, provides more support for its use in characterizing den characteristics. When comparing plant productivity between dens, reference sites, and random sites, we found that productivity on dens was much greater than reference sites, and that reference sites had lower productivity on average than random sites on the tundra (Fig. 3.3a,b). In other words, the results collectively indicate Arctic foxes select for low-productivity areas when digging dens (i.e., reference sites are less productive than average tundra sites), which likely turn into relatively high-productivity areas through their denning activity (i.e., dens have greater productivity than matching reference sites).

Moreover, our analysis also provided quantitative evidence that Arctic fox dens are in fact high-productivity patches that contrast strongly with the landscape, as we found plant productivity is significantly greater on Arctic fox dens compared to the immediately surrounding area (Fig. 3.3c). This result is not surprising given how visually prominent the dens are on the landscape (Fig. 3.1). Nonetheless, our objective with this portion of the analysis was to derive an index of 'prominence' that could quantify what our eyes perceive when viewing these dens. Given the fact that high-productivity patches on beach ridges in our area are essentially only associated with fox dens or tree islands (at which we have never documented denning activity), when we collate all available lines of evidence, the most parsimonious explanation for the vegetation found on fox dens in the area is that Arctic fox denning activity is the cause of these

vegetative patterns as suggested previously in research from our study area (Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Fafard et al., 2020).

Our approach from the present study thus provides greater evidence that Arctic foxes act as ecosystem engineers by converting sites of low productivity into sites of relatively high productivity. The fact that fox reproduction patterns spanning a decade were unrelated to maximum plant productivity on dens indicates the effects of fox denning behavior on plants are long-lasting—well beyond the lifetime of foxes. Indeed, the effects from nutrient deposition and bioturbation seem to compound through many generations of fox occupancy and reproduction. And once the changes to plant assemblages occur on dens, these legacy effects likely last for a long time. When comparing the spatial scale and temporal longevity of Arctic fox dens against other ecosystem engineers (reviewed by Hastings et al., 2007), Arctic fox dens are considerably larger (>500 m^2) and longer lasting (hundreds of years) than the vast majority of patches engineered by animals. Continued monitoring of plant productivity and assemblages may reveal greater information about how plant dynamics change through time on Arctic fox dens in relation to occupancy patterns (see *Future directions and concluding remarks* section for more discussion).

Harnessing high-resolution remote sensing data to assess animal-habitat relationships

Our first objective when planning this study was to conduct a “proof of concept” analysis evaluating whether satellite imagery could actually detect vegetation on Arctic fox dens. Prior to the launch of the Sentinel-2 satellite, freely available, high-temporal frequency imagery was available only on a coarser scale (e.g., 30-m resolution of the LANDSAT satellites). Arctic fox dens are represented by ~1 pixel at this resolution (900 m^2), making it challenging to distinguish dens. Sentinel-2 imagery clearly provides a fine enough spatiotemporal scale to detect and quantify plant productivity and phenology patterns on Arctic fox dens (Figs. 3.3, 3.4). Although plants on dens do not appear to start green-up earlier or stay green longer than other tundra areas, we found green-up rates were higher on dens than reference sites and were able to assess when, during the growing season, plant productivity begins to differ between these areas (~mid-July, near the peak growing season; Fig. 3.4b). Assessing plant phenology patterns on these dens at a similar spatiotemporal scale using field-based methods would have been prohibitively costly and time intensive, as the majority of the dens in our 1200-km^2 study area (~65-70%) are accessible only via helicopter during the growing season.

As remote sensing data further increases in availability and spatiotemporal resolution, it will continue to offer new perspectives and insights on animal functional roles within ecosystems at diverse spatial scales. Most animal ecology studies using remote sensing data have applied it towards understanding how environmental conditions affect animals. But as we demonstrated, remote sensing data can also be used to understand how animals shape ecosystems themselves. Our study is not alone in applying remote sensing methods towards evaluating animal impacts on ecosystems. For instance, satellite imagery has been used to identify how spatiotemporal fluctuations in spawning salmon abundance influences forest productivity (Kieran et al., 2021), how beaver-modified environments buffer riparian ecosystems against wildfire (Fairfax & Whittle, 2020), and how grazing pressure from migrating bison (*Bison bison*) alters the quality and phenology of the grasses they forage upon (Geremia et al., 2019). Airborne LiDAR has revealed the effects of elephant (*Loxodonta africana*) foraging on the structural diversity, rates of treefall, and vegetation height of savanna woodlands (Asner et al., 2009; Asner & Levick, 2012; Asner et al., 2016; Davies et al., 2018). We add to these studies by demonstrating high-resolution satellite imagery can provide a landscape-scale perspective of animal ecological effects that function at smaller, patch-level scales.

Future directions and concluding remarks

By demonstrating that satellite imagery can be used to detect vegetation patterns on Arctic fox dens, there are several ways this study can be built upon for future research and monitoring efforts. First, we propose satellite-derived information could be used to identify and locate previously unknown dens with similar vegetation characteristics. In particular, the prominence index we employed may be used to identify vegetation hotspots that, in tandem with region-specific den selection preferences, may guide search efforts for dens. Second, as we continue to assess fox occupancy and reproductive success at dens, we will likely gain a better understanding of how fox denning behavior affects plants across space and time. For instance, how long do the changes to plant communities last once a den is abandoned for good? After a new den is constructed, how long until major changes to plants are detectable? Finally, as Sentinel-2 and other comparable satellites continue to collect high-resolution spatiotemporal imagery, these data can be used to regularly monitor temporal patterns in plant productivity and phenology on dens and assess how climate change may affect these patterns across multiple spatial scales.

Effective species conservation and management often requires employing efficient ways to monitor and measure animal-habitat relationships. This is especially true when

resources are limited, when studies are conducted across large spatial or temporal scales, or when the species are imperiled or have important ecological effects, like top predators do. Remote sensing data offer unique avenues to advance these objectives (Pettorelli et al., 2014; Schulte to Bühne & Pettorelli, 2018), provided the data remain affordable and accessible (Turner et al., 2015). Our study validates the utility of such data by demonstrating how free and easily accessible satellite imagery can provide a cosmic view of animal ecological effects, and ultimately advance our understanding of the intricate functional role predators play in ecosystems.

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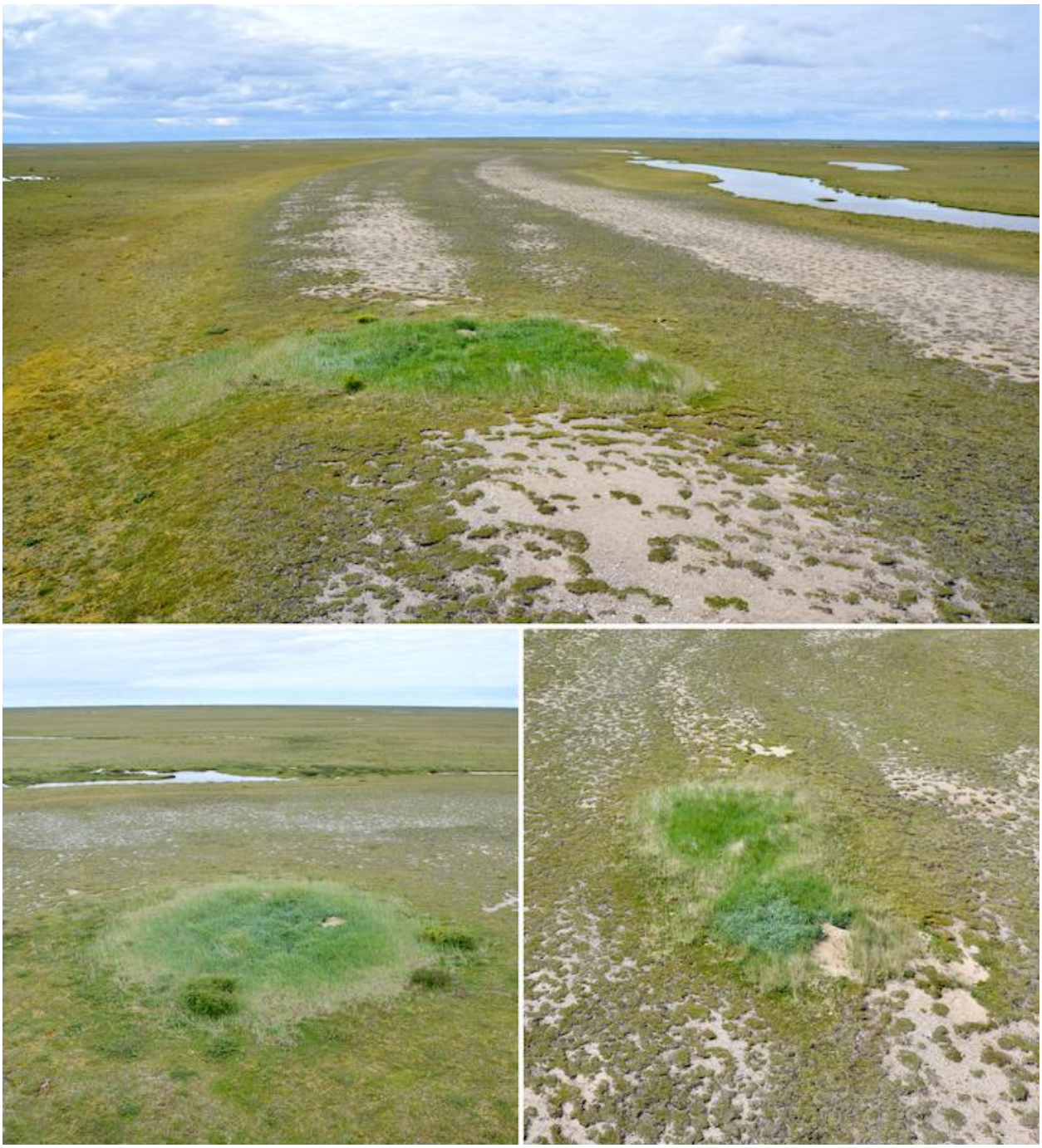

Figure 3.1. Photos of typical Arctic fox dens in Wapusk National Park, Manitoba, Canada taken during an aerial survey. Dens are generally constructed on relatively elevated ancient beach ridges and are characterized by unique plant characteristics relative to the surrounding landscape.

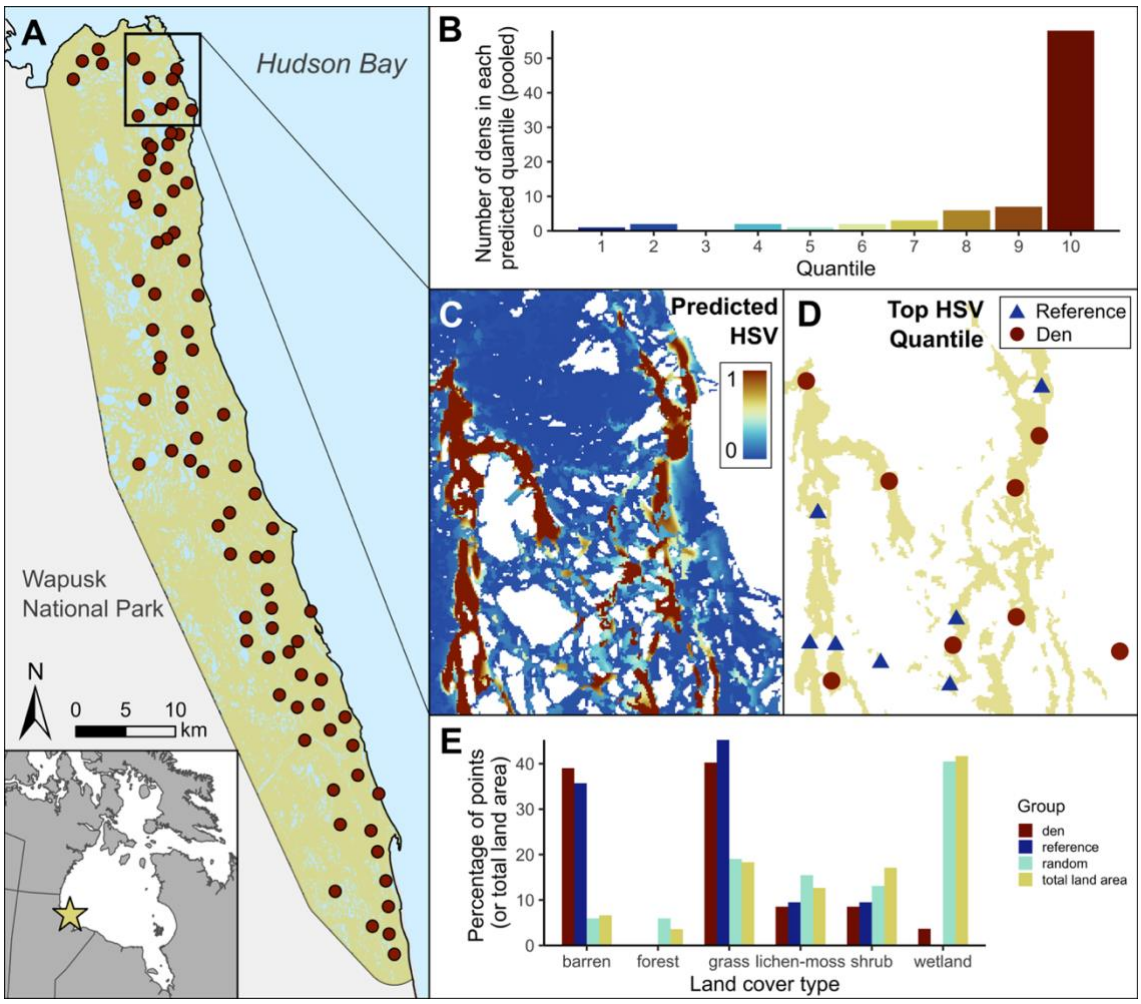

Figure 3.2. Map of the study area in Wapusk National Park, Manitoba, Canada, and results related to our den habitat selection analysis. Panel A shows the study area and all 84 known Arctic fox den locations therein. Panel B shows the number of Arctic fox dens predicted to be within each quantile (1–10) pooled across all five folds of the cross-validation procedure; Spearman's rank correlation (*r*) on the pooled quantiles was 0.86 (*p*=0.002). Panel C shows the predicted habitat selection map generated from the den selection model fit to the full data set, where habitat selection values (HSV) closer to 1 (red) represent areas more likely to be selected by Arctic foxes for denning. Panel D shows the same region with only the reclassified top quantile (10%) of cells present, overlaid with den (red circles) and randomly generated reference sites (blue triangles) used in this study. The study area region shown in Panels C and D is depicted within Panel A. Panel E shows the percentage of den, reference, and random points categorized by each of the six land cover types, along with the percentage of the total study area comprised of each cover type (not pictured: percent 'open water', which comprises ~15% of the total study area).

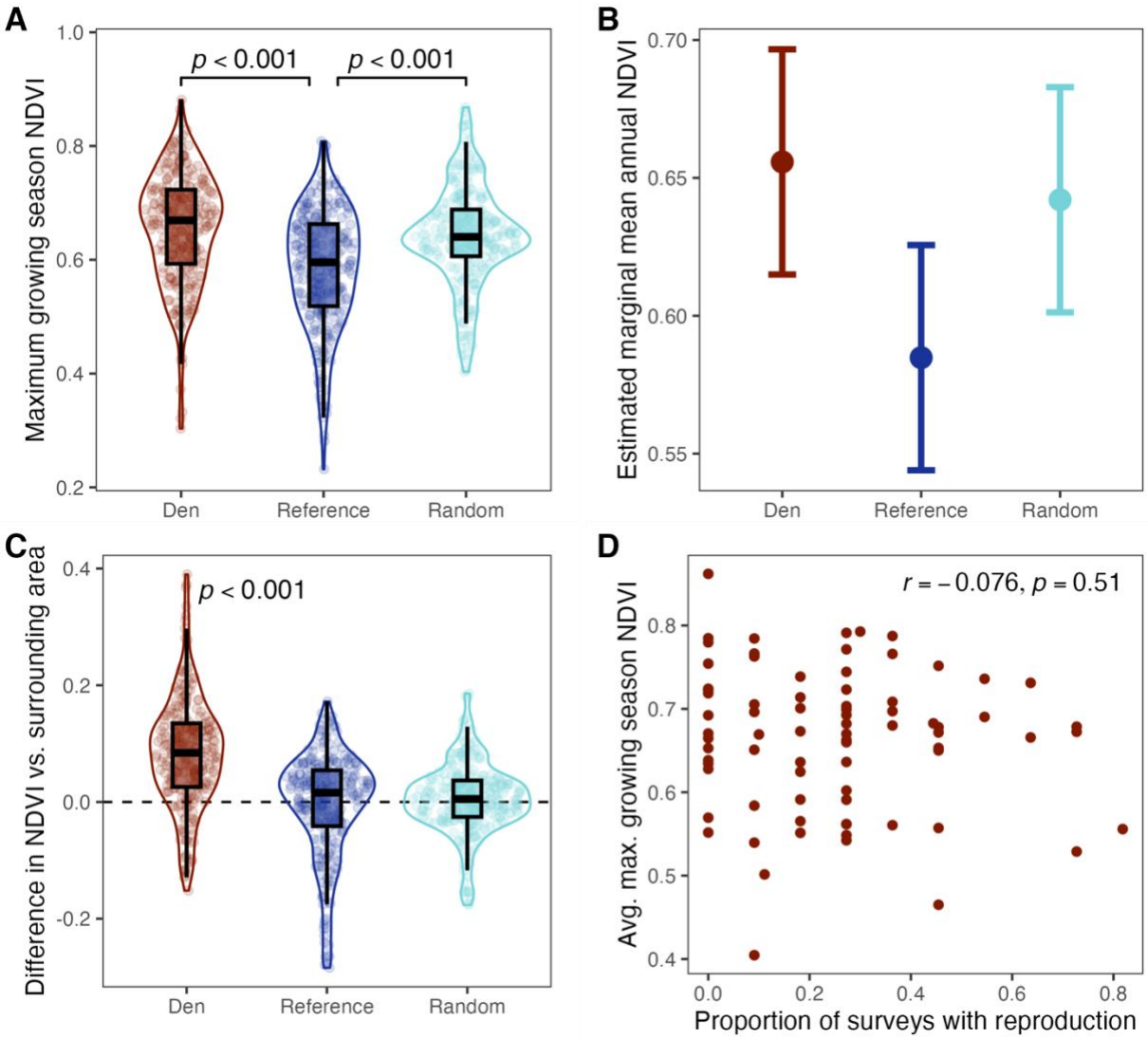

Figure 3.3. Results related to maximum plant productivity analyses on Arctic fox dens in Wapusk National Park, Manitoba, Canada. Panels A and B show the observed values (A) and estimated marginal mean (+/- 95% confidence intervals; B) of maximum growing season NDVI for dens, reference sites, and random sites, where reference sites represent preferred denning habitats based on a habitat selection model and random sites are representative of total habitat availability in the study area. Panel C shows the observed difference between annual average NDVI values within 20 and 250 m buffers, with differences only found for dens. Panel D shows the lack of relationship between fox reproductive success and average maximum growing season NDVI on dens. Sample size for panels A-C was 84 for each category, and 78 dens for panel D.

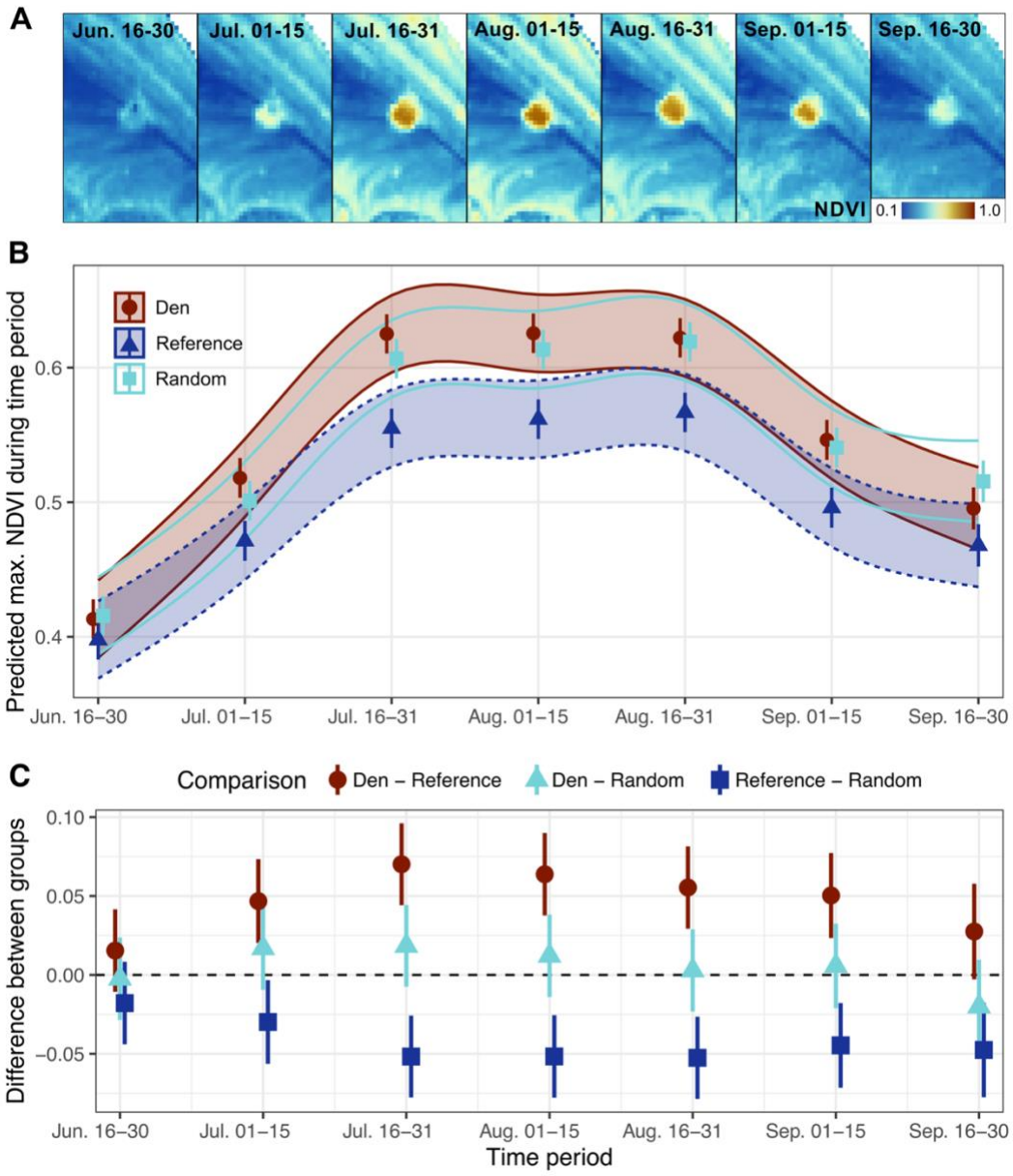

Figure 3.4. Results related to the plant phenology analysis on Arctic fox dens in Wapusk National Park, Manitoba, Canada. Panel A shows the intra-annual change in plant productivity (assessed from NDVI values) across seven time periods on a single Arctic fox den. Each subpanel shows the NDVI values created from the greenest pixel mosaic from each time period. The den is at the center of each panel, the outline of which can be most clearly seen in the middle subpanels. Panel B shows the point and standard error NDVI estimates for den, reference, and random sites predicted from the generalized additive model. The ribbons are the predicted NDVI 95% confidence intervals (CI) for each group. Panel C shows the pairwise differences (point +/- 95% CI) in smooth estimates between each group at each time period. Comparisons where the 95% CIs do not overlap 0 (the dashed horizonal line) are significant.

Chapter 4: Predator activity, proactive anti-predator strategies, and nesting phenology produce a dynamic landscape of risk to tundra goose reproduction

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Abstract

Birds generally rely on proactive anti-predator strategies when selecting nest sites, as they have limited options to adapt to changing levels of risk once incubation begins. Arctic waterfowl often nest colonially as an anti-predator strategy but dispersed-breeding species may use other proactive strategies, such as nesting in less risky areas. However, empirical links between spatial patterns of predation risk and nest habitat selection or success are needed to better understand how predator activity shapes Arctic waterfowl reproduction. Using activity data from the main cursorial nest predators, Arctic and red foxes (*Vulpes lagopus*, *V. vulpes*), and activity data from aerial predators, we evaluate the influence predator activity has on Canada goose (*Branta canadensis interior*) nest habitat selection and success, and how nesting phenology mediates these effects. By comparing habitat selection models fit to i) goose nest locations and ii) fox locations obtained from GPS-collars, we show that geese and foxes display nearly opposite patterns of selection for the same landscape traits. Geese selected sites that appeared to minimize their probability of encountering foxes while also maximizing their ability to detect foxes. Spatial predictions of fox activity revealed nests located in areas with higher probability of fox use had lower nest success, indicating fox space-use patterns reflect predation risk. Nests initiated earlier had a greater probability of nest success, but these patterns strongly depended on location; the benefits of nesting early were largely lost in areas of high fox activity. We also found a negative relationship between clutch size and incubation date, suggesting nests incubated later had higher rates of failure likely due, in part, to geese being in poorer body condition. Although nest success was lower in areas with high aerial predator activity, fox activity likely has a greater influence on goose nest spatial patterns due largely to movement constraints imposed by tundra landscape features on foxes but not aerial predators. Our study demonstrates the mechanisms by which nesting phenology and predator activity interact to

shape bird reproduction, and provides an empirical demonstration of the value of incorporating temporal dynamics into the “landscape of fear” framework.

Keywords: anti-predator behavior; Arctic fox; Canada goose; landscape of fear; movement ecology; nest success; predation risk; predator-prey interactions

Introduction

Responses to predation risk range from “reactive responses” of immediate, short-term risk to “proactive responses” to risk that occur before interacting with predators (Creel et al., 2014; Creel, 2018). Reactive responses typically involve actions that promote the prey’s escape from an attacking predator, such as fleeing or exhibiting reciprocal aggressive behavior (Bêty et al., 2002; Courbin et al., 2016). Proactive responses are decisions that reduce the probability of interacting with predators, or increase the probability prey will survive an expected encounter (e.g., responses in areas of high predator activity). One way that prey proactively mitigate predation risk is by changing their space use patterns based on perceived patterns of risk (Lima, 2002). These behavioral responses of prey to predation risk underlie the “landscape of fear” concept, whereby the landscape interacts with predator space use and prey perception of risk to generate expected levels of predation risk across space and time (Laundré et al., 2010; Gaynor et al., 2019). While mobile prey may readily adapt their proactive antipredator responses to changing levels of risk, immobile prey have fewer options once they are anchored to a location.

Predation is a major source of failure and mortality for bird nests, and birds often use proactive strategies to manage risk when selecting nest sites. Proactive antipredator responses require knowledge of, or direct experience with, predation risk, and birds rely on numerous information sources to gauge risk (Lima, 2009; Chalfoun & Schmidt, 2012). For example, birds can obtain information on predation risk while moving throughout the breeding grounds (Reed et al., 1999) or gaining information from previous breeding attempts (Schmidt, 2001; Hoover, 2003). They can then incorporate this information into their nest site decision-making, such as by choosing nest sites in areas of low predator activity (Schmidt et al., 2006) or sites that promote other antipredator responses (e.g., characteristics that enhance predator detection; Amat & Masero, 2004; Keyel et al., 2013). Despite widespread recognition that predation is a strong selective pressure on bird nesting biology, empirical evaluations linking spatial patterns of risk to nest site selection and survival remain sparse (Lima, 2009; Clermont et al., 2021).

In tundra ecosystems, Arctic birds have adapted proactive antipredator responses that can cope with relatively high exposure to predators due to the short vegetation. Smaller Arctic birds can mitigate nest predation by having cryptically colored nests/eggs or concealing their nests in the short vegetation (e.g., Liebezeit et al., 2009; Ims et al., 2019), but these strategies are harder for larger species like waterfowl. Consequently, Arctic waterfowl commonly nest in large, dense colonies that offer antipredator benefits like predator swamping (Baldwin et al., 2011; Iles et al., 2013), and mutual vigilance and mobbing responses (Burger, 1981; Samelius & Alisauskas, 2001). However, some species, like the Canada goose (*Branta canadensis interior*), breed more dispersed. Although Canada geese nest in clumps at broader spatial scales, they exhibit strong territoriality and distance themselves from neighbors at smaller scales (Reiter & Andersen, 2013). This spacing strategy may help geese reduce encounters with predators by dispersing themselves throughout the landscape, while still being close enough to neighbors to obtain information on attacking predators. When available, Canada geese may select nest sites in microhabitat refuges that restrict terrestrial predators' access, such as on small islets, or within colonies of other species to presumably exploit the antipredator benefits these colonies offer (Baldwin et al., 2011). However, when these antipredator features are limited, geese often select nest sites in open areas that likely promote visual detection of predators (Miller et al., 2007).

Predation risk varies across time as well as space, indicating that an integrated spatiotemporal perspective may better characterize risk (Palmer et al., 2022). For instance, accounting for diel behavioral patterns revealed vicuñas (*Vicugna vicugna*) forage in areas of high predation risk from pumas (*Puma concolor*) during times they have learned are less risky (Smith et al., 2019). For Arctic waterfowl, clear temporal patterns in nesting success often emerge based on the date waterfowl begin nesting, with usually greater rates of nest survival the earlier nesting is initiated (Baldwin et al., 2011; Ross et al., 2017; Clermont et al., 2018). Thus, nesting phenology could potentially mediate spatial patterns of predation risk to breeding waterfowl by affecting spatial patterns of nest predation across the nesting period.

The over-arching objective of this study was to evaluate how predator activity affects nest habitat selection and nesting success of a dispersed-nesting goose, and whether these effects are mediated by nesting phenology. To our knowledge there has been no direct evaluation assessing spatial patterns of predation risk on Canada goose nesting ecology, much less how the timing of nesting affects these dynamics, obscuring our understanding of the degree to which predation risk acts as a constraining influence and selective pressure on

Canada goose reproduction. We first evaluated whether predator activity constrains the spatial distribution of Canada goose nests in the low-Arctic tundra by comparing habitat selection preferences from models—incorporating the same predictor variables—fit to (1) goose nest locations and (2) Arctic (*Vulpes lagopus*) and red fox (*V. vulpes*) locations obtained with GPS-collars. We hypothesized that geese select for nest sites in areas with a low probability of fox use to minimize encounters with foxes, and therefore predicted that habitat selection patterns would be nearly opposite for goose nest and fox locations. We then evaluated whether spatial patterns of predator activity (fox movement data and aerial predator counts) can predict the reproductive success of geese (i.e., evaluating whether nest success was lower in areas of high predator activity), and how nesting phenology affects nest survival rates across varying levels of expected predation risk. Together, this approach allowed us to evaluate to what degree predator activity acts as a selective pressure on goose reproduction by generating expected spatial variation in predation risk, and how incorporating temporal dynamics into these spatial patterns, characterized by nesting phenology, may improve our understanding of this predator-prey relationship.

Methods

Study area

Our study was conducted in Wapusk National Park in northeastern Manitoba, Canada, along the coast of Hudson Bay (Fig. 4.1). The Wapusk tundra is typified by large swaths of fen, lakes and ponds, and elevated beach ridges formed by isostatic rebound that run approximately parallel to the coastline (Ritchie, 1956; Sella et al., 2007). There are 85 known fox dens within the Wapusk tundra, nearly all of which are located on beach ridges (Roth, 2003; Johnson-Bice et al., 2023, Chapter 3).

The most common goose species are the lesser snow goose (*Chen caerulescens caerulescens*) and the Canada goose. These two species exhibit somewhat different nesting strategies: lesser snow geese nest in large colonies, while Canada goose nests are dispersed. The Wapusk lesser snow goose population dramatically increased in abundance from the 1960s through the 2010s, causing well-documented and widespread changes in tundra vegetation throughout the area (e.g., Cargill & Jefferies, 1984; Jano et al., 1998; Jefferies et al., 2006). During spring, snow geese grub for roots and rhizomes, causing vegetative losses and alterations to the soil sediments (Kerbes et al., 1990). These vegetation changes are most

pronounced near the La Pèrouse Bay snow goose colony ~12 km west of our core study area, but parts of our study area were also altered by goose foraging. Approximately 95% of goose nests in our core study area are Canada goose nests, so we excluded snow goose nests here for simplicity.

Arctic and red foxes are the primary cursorial (i.e., ground-based) goose nest predators in the area, along with occasional predation from polar (*Ursus maritimus*) and grizzly (*U. arctos*) bears. Red fox presence in the study area has increased in recent years as Arctic fox abundance has declined, in part due to climate change (Moizan et al., 2023; Verstege et al., 2023). Herring gulls (*Larus argentatus*) are the most common aerial nest predator, but other aerial predators like glaucous gulls (*L. hyperboreus*), parasitic (*Stercorarius parasiticus*) and long-tailed (*S. longicaudus*) jaegers, common ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and sandhill cranes (*Grus canadensis*) are also relatively common.

Goose nest surveys and assessing nest fate

We conducted goose nest surveys between June 8 and 18, 2014–2023 (excluding 2020) using line-transect methods. Each year, we located goose nests along 15 2-km long transects spaced 1 km apart (7 transects in the west portion of the study area, 8 transects in the east, offset by 500m; Fig. 4.1). The transects were oriented east-west, generally perpendicular to the beach ridges. The northing value of the northernmost transect was randomly generated each year, resulting in slightly different transects to obtain full coverage of the study area across all study years.

During surveys, 3–5 observers walked along each transect and searched for goose nests using binoculars. Once a nest was detected, we slowly approached the nest until the goose flushed, then recorded the clutch size and nest location using a handheld GPS unit. Nest processing was done as rapidly as possible (usually <2 min) to minimize disturbance. If eggs were present we recorded float stage, reflecting development age, which we later used to estimate incubation initiation date (hereafter “incubation date”) assuming a 28-day incubation period (Reiter & Andersen, 2008). If eggs were pipped or goslings were present, we assumed incubation began 28 days prior to the survey date. If a nest encountered on the survey contained fresh down but no eggs, we assumed the nest had either been depredated or the eggs had already hatched. We determined the fate of nests, including empty nests encountered on surveys, from the presence (hatched) or absence (depredated) of large pieces of membrane (corresponding to at least one hatched egg) in or near the nest (Reiter & Andersen, 2011).

Nests were revisited in late July to early August to assess nest fate, although nest fate data was sporadically collected until 2021. Nest survival estimates should be conservative as some membranes may have disappeared from the nest area between hatching and revisiting. We also recorded the number of aerial predators observed on each transect as an index of aerial predator activity.

Fox capture, collaring, and home range analysis

We captured Arctic and red foxes during 2017–2023 using padded leghold and Tomahawk live traps (for details on captures and collaring see Warret Rodrigues & Roth, 2023a, b). Foxes were fit with GPS collars that recorded locations every 1.5 or 2 h during the goose nesting season (Iridium satellite collars #4170 or 4270, Telonics, Mesa, Arizona, USA). Foxes captured during 2022–2023 (*n*=5) were fit with collars that recorded locations every 15 min (0.25 hr) during one 6-hr period each day, with the 6-hr period changing daily to ensure locations were recorded across the full 24-hr diel period. We thinned the locations obtained from these foxes to one location every 1.5 hr to match fix rates of the other foxes. For this study, we included only foxes with home ranges near the goose nesting study area (*n*=10 foxes; 2 red and 8 Arctic, Fig. 4.1) during the primary nesting period. All handling procedures were approved by the University of Manitoba Animal Care Committee (Protocol F17-012). Research permits were obtained from Parks Canada (WAP-2017-25781, WAP-2018-27938), Manitoba Wildlife (WB18911, WB20226, WB21856, WB25383, WB25857), and Environment and Climate Change Canada (14-MB-SC002, 21-MB-SC001).

We constructed home ranges for each collared fox to delineate boundaries within which ‘available’ locations would be generated for the used–available habitat selection analysis. We first retained only GPS locations collected during the goose nesting period (defined as May 15–June 30), and then generated 95% autocorrelated kernel density home ranges for each fox following guidelines from the *ctmm* R package (see Calabrese et al., 2016 for details).

Goose nest and fox habitat selection study design

We compared fox and goose nest habitat selection by fitting two separate models incorporating the same landscape variables in a used–available study design. For both models, we randomly generated 100 available locations for every used (observed) location. Fox available locations were generated within each fox’s home range. Goose nest available locations were generated within 300 m of the survey transects (~97% of nests found during surveys were located within this threshold). Some nests were used in multiple years, so only the

first observation of a nest was included in the habitat selection model. We excluded all nests categorized as ‘open water’ from the land cover data set (~12%), as these nests were largely located on small islets within lakes/ponds and the spatial resolution of our habitat data precluded evaluating whether/how geese select for islets. Although islets can be refuges from terrestrial predators (Clermont et al., 2021; Duchesne et al., 2021), our data indicated there was likely no substantial difference in nest success (0.56 vs. 0.51 average success).

We used the same four variables for both habitat selection models to allow for direct comparison: land cover type, distance to nearest patch of open water, distance to nearest beach ridge, and an index of terrain ruggedness. Since geese should select for areas that reduce the likelihood of nest depredation, we predicted geese select nest sites that were close to open water, which would reduce the number of directions from which foxes could approach the nests and also limit the distance females needed to travel to drink. We also predicted geese would nest in relatively flat areas, to aid in visual detection of predators, and far from beach ridges that contain almost all of the fox dens in the area and also function as wildlife corridors (beach ridges are one of the few dry habitats).

We used a 5-m resolution data set developed for Wapusk National Park as our land cover data (Ponomarenko et al., 2014), reclassified into 7 different categories (Appendix 4, Table S4.1): ‘Fen’, ‘Goose-affected’, ‘Dryas heath’, ‘Shallow water/sedge fen’, ‘Unvegetated’, ‘Shrub/willow’, and ‘Open water’. Goose-affected areas were generally ‘Fen’ cover types that had been altered by goose foraging, typically characterized with sparse vegetation interspersed with mudflats. Since geese nest on land, we excluded ‘Open water’ areas from the goose nest analyses but retained it for the fox model, as lakes/ponds are often still frozen during parts of the nesting period and foxes can theoretically swim in these features when unfrozen. Land cover type was then extracted for each used/available point. We also calculated the Euclidean distance (in meters) between each point and the nearest open water patch and beach ridge (*Appendix 4*). We used the 30-m resolution FABDEM elevation data set (Hawker et al., 2022) to create a 5x5 window terrain ruggedness index (TRI) raster using the ‘tri’ function from the *spatialEco* R package (Evans & Murphy, 2021). Lower TRI values indicate relatively flat areas, whereas higher TRI values indicate relatively uneven (“rugged”) areas.

Statistical analyses

Habitat selection models

We compared fox movement and goose nest locations with random (available) locations using binomial generalized linear mixed effects models (GLMMs) with a logit link. Available locations were assigned a weight of 5000, while used locations a weight of 1 (Fieberg et al., 2021). In each model, we log+1 transformed the continuous variables (distance to water, distance to beach ridge, TRI) due to the data being heavily skewed and having some values of 0. 'Fen' was the reference land cover type (categorical variable) as it is the most common cover type in the study area. For the fox movement model, we included a random intercept for 'fox ID' and random slopes to allow all continuous covariates to vary by 'fox ID' (Muff et al., 2020). For the goose nest model, we included a random intercept term for 'year'; model fitting issues precluded also including random slopes (likely due to a negligible effect of 'year' or resolution of our data). We verified each fitted model had no collinearity issues (variance inflation factors were <2 for each variable). We evaluated the importance of individual covariates with an α=0.05 and whether the 95% confidence intervals overlapped 0. We used spatial (goose nest model) and individual (fox model) blocking cross-validation methods (n=5 folds) to evaluate the fit of each habitat selection model (Boyce et al., 2002; Roberts et al., 2017; see *Appendix 4* for full details).

We visualized and compared model results by calculating the relative selection strength (RSS) for each continuous variable from each model (Avgar et al., 2017; Fieberg et al., 2021). RSS is a quantitative measure of the relative magnitude of selection of a given location in relation to another location(s) (Avgar et al. 2017; Fieberg et al. 2021; Northrup et al. 2022), calculated as $\exp(\beta_1 \times X_1 + \beta_2 \times X_2 + \beta_3 \times X_3 + \ldots)$ from each fitted model, where β_1 is the coefficient estimate of variable X_1, β_2 is the coefficient estimate of variable X_2, etc. (i.e., exponentiated model predictions without the intercept term). We calculated RSS scores across a range of values for each covariate relative to the mean value of that covariate from the goose nest data set, with all other variables fixed. This approach allowed us to make direct comparisons of selection strength between the two models under identical conditions. We used the natural log of RSS values for plotting the effects. Log-RSS values >0 show selection for those conditions relative to the mean, whereas values <0 show avoidance relative to the mean.

Nest fate and clutch size analyses

We tested the relationship between goose nest success and relative probability of fox use at each nest site using a binomial GLMM with a logit link (hatched nests=1, failed nests=0). Throughout the study area, we generated estimates of log-RSS values predicted from the fitted fox movement model, and then used the estimated log-RSS value from each nest location as a

predictor variable in the nest success model. We included incubation date as another predictor variable, plus an interaction term between incubation date and log-RSS value. Including incubation date meant we excluded depredated clutches that were detected during surveys (~13%). However, given the importance of nesting phenology from previous research, we elected to focus our analysis on nests for which we could estimate incubation date. To evaluate how aerial predator activity influenced nest fate, we included the number of aerial predators observed on the transect as another predictor variable (log-transformed). We included 'year' as a random intercept term; model fitting issues precluded also including random slopes (likely due to a negligible effect of 'year'). We did not include a random intercept term for 'nest ID' (to account for clutches at the same site from multiple years) due to the low number of repeated nest sites in our data (<10%).

We also investigated whether clutches incubated later in the breeding season have smaller clutch sizes, which could be an indirect sign that geese are in worse body condition and likely more vulnerable to depredation. Since we were primarily interested in the over-arching pattern, rather than intra-annual patterns, of how clutch size changes with incubation date, we pooled all years of data and evaluated the relationship between clutch size and incubation date (ordinal day) using a generalized linear model. Clutch size is non-zero integer count data and the data also showed a left skew, so we used a truncated Conway-Maxwell Poisson distribution to obtain a suitable model fit. We performed residual diagnostic checks using the *DHARMa* R package (Hartig, 2022).

All models were fit using the *glmmTMB* R package (Brooks et al., 2017), and we estimated and visualized the marginal effects of predictor variables from the nest fate and clutch size models using the 'ggemmeans' function from the *ggeffects* R package (Lüdecke, 2018). All analyses were carried out using R version 4.3.1 (R Core Team, 2023).

Results

During 2014–2023, we detected 697 Canada goose clutches from 559 unique nesting sites. Of the 559 sites, 69 were classified as "open water" and were subsequently excluded from the analyses, leaving 490 sites for the remaining analyses. We assessed the hatching fate (successful/failed) of 422 clutches from these sites, 311 of which we also estimated incubation date and recorded the number of aerial predators observed during the survey. The majority of

nests with a known hatch fate but unknown incubation date were nests that were already depredated when detected during surveys (n=56).

We collected 2,048 locations from 10 different GPS-collared foxes (range: 78–397 locations per fox) in the goose nesting study area and nearby vicinity. We detected an average of 14.3 avian predators along each transect (SD=10.8, range: 1–58).

Habitat selection analysis

Overall, Canada geese selected nest sites (n=490) in areas that were predicted to be less used by foxes. Geese selected sites that were close to open water (β=–0.233, z=–6.03, p<0.001). Although foxes showed no significant response to water (β=0.045, z=0.60, p=0.552), the 95% confidence intervals of the coefficient estimates and log-RSS predictions did not overlap between the two models (Fig. 4.2a). Goose nests tended to be farther from beach ridges (β=0.272, z=6.94, p<0.001), whereas foxes selected for areas close to beach ridges (β=–0.134, z=–2.37, p=0.018; Fig. 4.2b). Geese selected nest sites located in relatively flat areas (i.e., lower terrain ruggedness index values; β=–0.755, z=–5.97, p<0.001), whereas foxes selected for relatively uneven areas (β=0.579, z=3.82, p<0.001; Fig. 4.2c).

Foxes and geese also showed different selection preferences for land cover types. Nests were disproportionately located within areas affected by goose foraging (i.e., goose-affected areas; Fig. 4.2d,e). Geese tended to avoid building nests in Dryas heath, unvegetated, and shrub/willow cover types (Fig. 4.2d,e). Foxes tended to select land cover types in similar frequencies to their availability, with the notable exception of shrub/willow land cover types and open water (Fig. 4.2d). The random intercept/slope terms of ‘fox ID’ were influential in the fox movement model, whereas the random intercept term of ‘year’ in the goose nest model had no effect (Table 4.1).

When comparing spatial predictions of areas likely to be used by foxes and geese, the generally opposite patterns of selection become evident (Fig. 4.3). There was a strong negative correlation between fox movement log-RSS values and goose nest log-RSS values from across the goose nest study area (R^2=0.45, p<0.001).

Cross-validation results indicated both habitat selection models were excellent fits to the data. Across testing folds, the fox movement model had an average Spearman’s r value of 0.896 (range: 0.802–0.964) and the goose nest model had an average Spearman’s r value of 0.926 (range: 0.878–0.976).

Nest fate and clutch size analyses

Annual Canada goose nest success averaged 0.51 (SD=0.25, range: 0.18–0.93). Average incubation date across all nests was May 28, with the average annual start of incubation date ranging from May 19 (2023) to June 5 (2021).

Both avian predator activity and fox activity affected nest success (*n*=311 nests). Predicted fox activity, represented by the estimated log-RSS value from the fox movement model at each nest location (mapped in Fig. 4.3), was negatively related to the probability of nest success (β=–21.02, *z*=–2.07, *p*=0.038; Table 4.2). Incubation date had the greatest relative influence on nest success, with clutches incubated earlier having a greater probability of success (β=–0.180, *z*=–6.10, *p*<0.001). However, these results depended on nest location, as there was a significant interaction between fox log-RSS value and incubation date (β=0.142, *z*=2.09, *p*=0.037): the benefits of nesting earlier dissipated in areas of high fox activity (Fig. 4.4a,b). We also found a negative relationship between aerial predator activity (i.e., the number of aerial predators observed during the survey transect) and the probability of nest success (β=–0.372, *z*=–2.11, *p*=0.035; Figs. 4.4c, 4.5).

Results from the clutch size analysis showed a significant negative relationship between incubation date and clutch size (β=–0.011, SE=0.003, *z*=–4.29, *p*<0.001, 95% CI: [–0.017, –0.006]; Fig. 4.6).

Discussion

Using movement data from the dominant cursorial nest predators, Arctic and red foxes, plus aerial predator activity data obtained during nest surveys, we demonstrate that predator activity has a strong effect on the spatial distribution and reproductive success of a dispersed-breeding goose on the Arctic tundra. As expected, habitat selection preferences of Canada geese were nearly opposite those of foxes, indicating that geese select nest sites in areas that minimize interactions with foxes. Goose nest success was lower, on average, in areas with a greater probability of use by foxes, although these effects were strongly mediated by the date geese started incubation. Our study provides a novel spatiotemporal perspective on how predator activity influences the reproduction of prey in a heterogenous tundra landscape.

Geese selected nest sites in areas that would likely minimize their probability of encountering foxes while also maximizing their ability to detect foxes. Goose nests tended to be

located near water, within flat areas, and far from beach ridges (Fig. 4.2a–c). These patterns were generally opposite to fox selection patterns, and also likely reflect landscape traits that would aid in the detection and/or defense of hunting foxes. Nesting close to water limits the range of view incubating geese need to search for predators (i.e., foxes will not attack nests from within a lake) and likely reduces the time that incubating geese spend off nest to drink water (Lecomte et al., 2009). Nesting in relatively flat areas also probably enhances the ability of geese to visually detect incoming predators (Miller et al., 2007). Similarly, beach ridges are the only elevated features in the study area, so geese may avoid nesting near ridges as these features may obscure their ability to detect predators on the far side of ridges. Beach ridges are also home to fox dens and often used as movement corridors for other wildlife (Zhao et al., 2022), so it is probably beneficial to nest farther from predator activity centers. It is also possible that some of the observed selection patterns reflect goose preferences for other resources (e.g., proximity to food or water). However, incubating females typically spend <5% of their time away from nests (Aldrich & Raveling, 1983) and nesting geese in this study showed strong selection for areas with degraded food resources (‘goose-affected areas’), suggesting these other resources likely have a lesser role than predation risk in structuring the spatial distribution of nests.

The negative correlation between fox space use and goose nest locations could suggest foxes devote little time to hunting goose nests. However, our fox habitat selection model included locations of foxes in all behavioral states (including resting or tending to offspring at dens), not just foraging. From the prey’s perspective, this temporal component of predator space use—i.e., where predators spend most of their time, not only where they spend time hunting geese—is likely an important consideration when selecting nest sites. Building nests on or near ridges would be risky since foxes spend so much time there. Even though part of the selection strength for beach ridges and uneven terrain by foxes could be related to hunting other preferred prey like lemmings (McDonald et al., 2017), foxes are generalist predators that could easily switch to hunting geese if they encounter a nest in these areas. Our study did not account for indirect interactions between geese and other prey of foxes, which can influence the reproductive success of geese in tundra ecosystems (e.g., Bêty et al., 2001; Bêty et al., 2002; Juhasz et al., 2020). However, previous work from our study area found no link between rodent abundance and Canada goose nest success (Reiter & Andersen, 2011). Moreover, the negative relationship between goose nest success and the probability of space use by foxes (Fig. 4a,b) indicates our index of fox activity adequately reflects spatial variation in predation risk (Clermont et al., 2021). Fox activity therefore seems to generate predictable spatial patterns in predation

risk that influence goose nesting decisions (i.e., a “landscape of fear”; Laundré et al., 2010; Gaynor et al., 2019).

Although geese appear to favor proactive antipredator strategies when selecting nest sites, it remains unclear what information they use to assess risk. Foxes are already localizing at their dens when Canada geese arrive in early May (Neufeld, 2021; Moizan et al., 2023), indicating geese have time to gather information on fox activity before nesting begins 10+ days later. Canada geese are also a long-lived species that breed for many years and the outcomes of previous breeding attempts can provide information on the relative safety of potential nest sites. Indeed, goose nesting success is lower for young individuals (Raveling, 1981; Rockwell et al., 1993), suggesting geese learn how to better protect their reproductive investments as they age. Geese may also incorporate information from conspecific neighbors when choosing nest sites and assessing risk, as interactions with neighbors can influence the spatial distribution and nesting success of Canada geese (Reiter & Andersen, 2013). We could not adequately evaluate neighbor effects in this study since we used line-transect survey methods rather than full census methods (i.e., not all neighbors were accounted for in our study).

Our study provides a novel perspective on how goose reproductive ecology is affected by the interplay of predator activity and nesting phenology, the latter of which is changing in a warming Arctic. Nest survival decreases the later nests are incubated (Fig. 4.4a,b; Baldwin et al., 2011; Ross et al., 2017; Clermont et al., 2018), likely due in part to geese being in poorer body condition later in the breeding season (as indicated by the observed negative relationship between clutch size and incubation date; Fig. 4.6). Geese that lay nests later tend to be in poorer body condition either due to environmental conditions on the breeding grounds that inhibit energy gain (e.g., late snow cover), because they arrived to the breeding grounds in worse condition and must spend more time acquiring food resources, or some combination of both (Bêty et al., 2003; Madsen et al., 2007). Incubating females in worse body condition tend to leave their nests more frequently, and for longer periods of time, to feed (Aldrich & Raveling, 1983), and geese with smaller clutches also tend to return to their nests slower after being disturbed (Miller et al., 2013), both of which leave their nests more vulnerable to predation (Samelius & Alisauskas, 2001; Bêty et al., 2002). As spring phenology advances in a warming Arctic, geese are also faced with increasing pressure to arrive early enough to acquire sufficient food resources for nesting, and to time their nesting with peak vegetation productivity (Nolet et al., 2020) – a task that is particularly difficult for geese in Wapusk as they are forced to acquire food in a highly degraded landscape. Goslings that hatch later have lower survival rates in large

part because of a mismatch with peak vegetative productivity, which is exacerbated if spring phenology advances faster than reproductive phenology (Ross et al., 2018). Like many Arctic regions (reviewed in Nolet et al., 2020), geese in our study area have advanced their timing of nesting (MacInnes et al., 1990; Rockwell et al., 2011). However, our results suggest a major caveat with these phenological patterns, as we found the importance of nesting phenology on nest survival depended on local levels of cursorial predator activity (Fig. 4.5). Nesting early provided benefits to geese only in areas of low fox activity, whereas predation risk to nests in areas of high fox activity were similar regardless of incubation date (Fig. 4.4a,b). Collectively, this study thus sheds light on how predator activity and nesting phenology interact to shape goose nesting patterns, and provides a valuable case study on how incorporating temporal dynamics into spatial patterns of predation risk can provide a better understanding of predator-prey relationships (Palmer et al., 2022).

Sources of mortality other than fox predation seem to be responsible for the influence of nesting phenology in areas of predicted low fox activity, and we suggest that predation by avian predators likely explains at least part of this pattern. Despite the coarser resolution of avian predator activity data relative to fox activity, we found goose nesting success was lower in areas with more aerial predators (Fig. 4.4c). Predation by migratory avian predators seems a reasonable alternative mortality source (along with e.g., weather conditions; Juhasz et al., 2020) since nests incubated later would be exposed to more predators as birds arrive onto the breeding grounds. However, regardless of their influence on nest success, avian predators likely have a lesser influence on Canada goose nest habitat selection in this system than foxes. If avian predator activity strongly affected nest site selection we may have expected geese to select sites that offer concealment, as previously observed (Miller et al., 2007). However, geese tended to avoid land cover types that would offer the best overhead concealment (i.e., shrub/willow cover types; Fig. 4.2d,e). Prey often adapt antipredator behavior more strongly to one predator over others in multi-predator systems (Relyea, 2003; Morosinotto et al., 2010), and geese appear to respond more strongly to predation risk from foxes than avian predators (Lecomte et al., 2008). Unlike foxes, avian predators generally pose little predation risk to adult geese. Additionally, the distribution of lakes, ponds, wetlands, and beach ridges in the area imposes movement constraints on foxes that are not imposed on avian predators, and this heterogeneity influences where foxes move and spend time. Ultimately, landscape composition and fox locomotion interact to create high spatial variation in perceived predation risk, which geese, in turn, use to inform nesting decisions as they navigate this “landscape of fear”. Our

study thus provides evidence that landscape features can mediate relative predation risk, and responses to perceived risk, from aerial and cursorial predators on the Arctic tundra.

Concluding remarks

Without the ability to easily move nests in response to changing levels of risk, birds often employ proactive antipredator responses to guide nesting decisions and maximize their reproductive success. Using movement data from the dominant nest predators in our system, our study provides an empirical link between predator activity, spatial patterns of predation risk, and the breeding ecology of a tundra-nesting bird. We showed how the landscape interacts with predator movements to create predictable spatial patterns of predation risk, which we validated by demonstrating a relationship between probability of predator use and reproductive success. Our finding that geese preferentially selected nest sites in areas with a low probability of predator use indicates geese perceive these spatial patterns of predation risk and respond proactively by constructing nests in predator activity refuges. However, we also demonstrated nesting phenology mediated the effects of spatial variation in predation risk. Our study provides an empirical demonstration of how integrating time into the “landscape of fear” framework enhances our understanding of the reproductive ecology of birds.

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Table 4.1. Results from the fox movement and goose nest habitat selection analyses. Parameters in bold were significant at the α=0.05 level (excluding the intercept). SE= standard error, LC=land cover type.

	Fox movement HSF						Goose nest HSF					
Term	Estimate	SE	Z	*p*	Conf. low	Conf. high	Estimate	SE	Z	*p*	Conf. low	Conf. high
(Intercept)	–13.22	0.481	–27.46	<0.001	–14.17	–12.28	–13.10	0.315	–41.65	<0.001	–13.72	–12.49
LC: Dryas heath	–0.389	0.091	–4.28	<0.001	–0.567	–0.210	-0.742	0.301	-2.47	0.014	-1.332	-0.152
LC: Goose affected	0.081	0.069	-1.18	0.239	-0.217	0.054	0.870	0.101	8.61	<0.001	0.672	1.068
LC: Sedge fen/water	-1.034	0.583	-1.77	0.076	-2.177	0.110	0.952	0.369	2.58	0.010	0.228	1.676
LC: Unvegetated	-0.507	0.090	-5.64	<0.001	-0.683	-0.331	-1.054	0.587	-1.79	0.073	-2.205	0.098
LC: Water	-2.518	0.209	-12.04	<0.001	-2.928	-2.108	-	-	-	-	-	-
LC: Willow	0.580	0.089	6.55	<0.001	0.406	0.754	-1.518	0.583	-2.61	0.009	-2.661	-0.376
Dist. Water (log)	0.045	0.076	0.60	0.552	-0.103	0.193	-0.233	0.039	-6.03	<0.001	-0.308	-0.157
Dist. Ridge (log)	-0.134	0.057	-2.37	0.018	-0.245	-0.023	0.272	0.039	6.94	<0.001	0.195	0.349
Terrain ruggedness log TRI)	0.579	0.152	3.82	<0.001	0.282	0.877	-0.755	0.126	-5.98	<0.001	-1.003	-0.508
σ_{Fox} / σ_{Year}	1.366	-	-	-	0.758	2.462	<0.001	-	-	-	-	-
σ_{Dist_water}	0.223	-	-	-	0.127	0.389	-	-	-	-	-	-
σ_{Dist_ridge}	0.169	-	-	-	0.103	0.276	-	-	-	-	-	-
σ_{TRI}	0.430	-	-	-	0.250	0.741	-	-	-	-	-	-

Table 4.2. Results from the nest fate analysis model. Parameters in bold were significant at the α=0.05 level (excluding the intercept). SE=standard error.

Term	Estimate	SE	Z	*p*	Conf. low	Conf. high
(Intercept)	28.20	4.444	6.35	<0.001	19.49	36.91
Fox movement log-RSS value	–21.03	10.15	–2.07	0.038	–40.91	–1.14
Incubation date (ordinal day)	–0.180	0.030	–6.10	<0.001	–0.238	–0.122
Avian predator count (log)	–0.372	0.176	–2.11	0.035	–0.718	–0.027
Interaction term: fox movement log-RSS*incubation date	0.142	0.068	2.09	0.036	0.009	0.275
σ_{Year}	<0.001	-	-	-	-	-

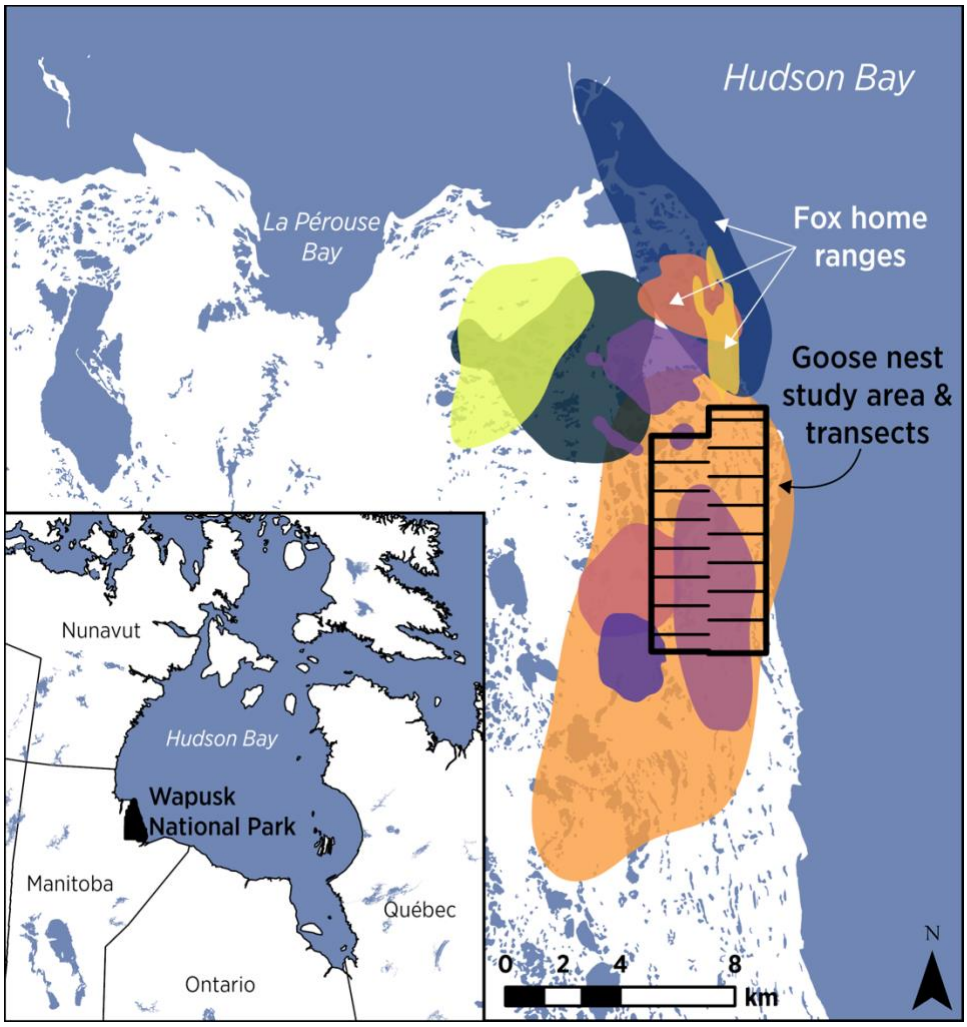

Figure 4.1. Study area within Wapusk National Park, Manitoba, Canada, along the western coast of Hudson Bay. Each of the 10 colored polygons represent the home range of a collared Arctic (*Vulpes lagopus*) or red (*V. vulpes*) fox. The black polygon outline denotes the boundary of the goose nest study area, with the 15 transects from one year shown. (Note: the large home range in orange is from a non-breeding Arctic fox that roamed throughout the study area).

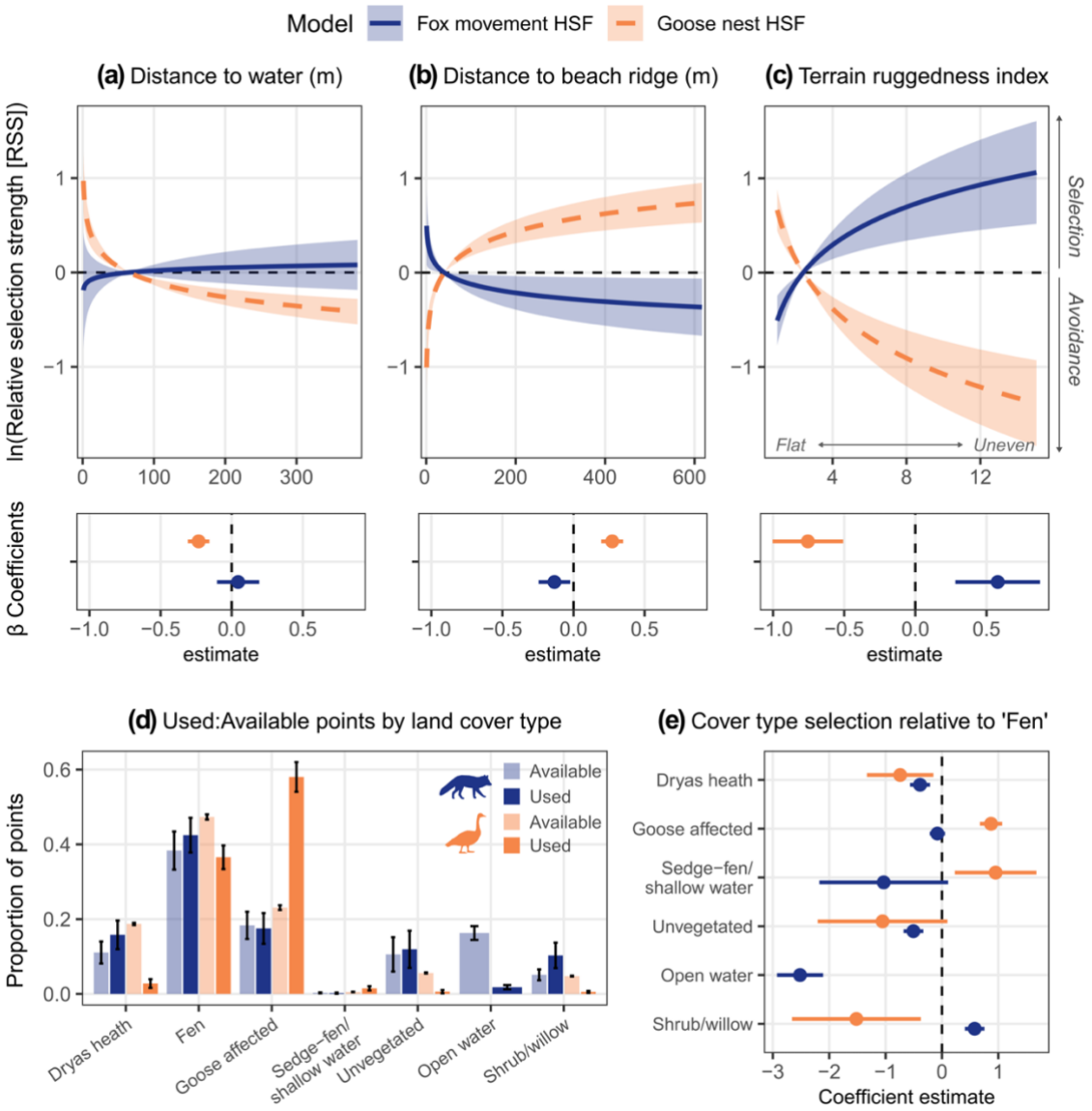

Figure 4.2. Results from the habitat selection models (HSF) demonstrating how foxes (blue) and geese (orange) showed nearly opposite patterns of selection for the same landscape features in Wapusk National Park, Manitoba, Canada. Panels (a–c) show the log-relative selection strength values (+/-95% confidence intervals [CI]) relative to the mean x-covariate value from the goose nest data (all other covariates were fixed at their mean). Values greater than 0 show selection, whereas values less than 0 show avoidance (model predictions cross 0 at the mean of each x-covariate). Coefficient estimates (+/-95% CI) are shown below in sub-panels. Panel (d) shows the mean (+/- std. error) proportion of used and available points from each land cover type across all 10 foxes (light/dark blue) and all eight years of goose nests. Panel (e) shows the coefficient estimates (+/-95% CI) of each land cover type relative to 'Fen', the reference level used in both fox movement and goose nest habitat selection models.

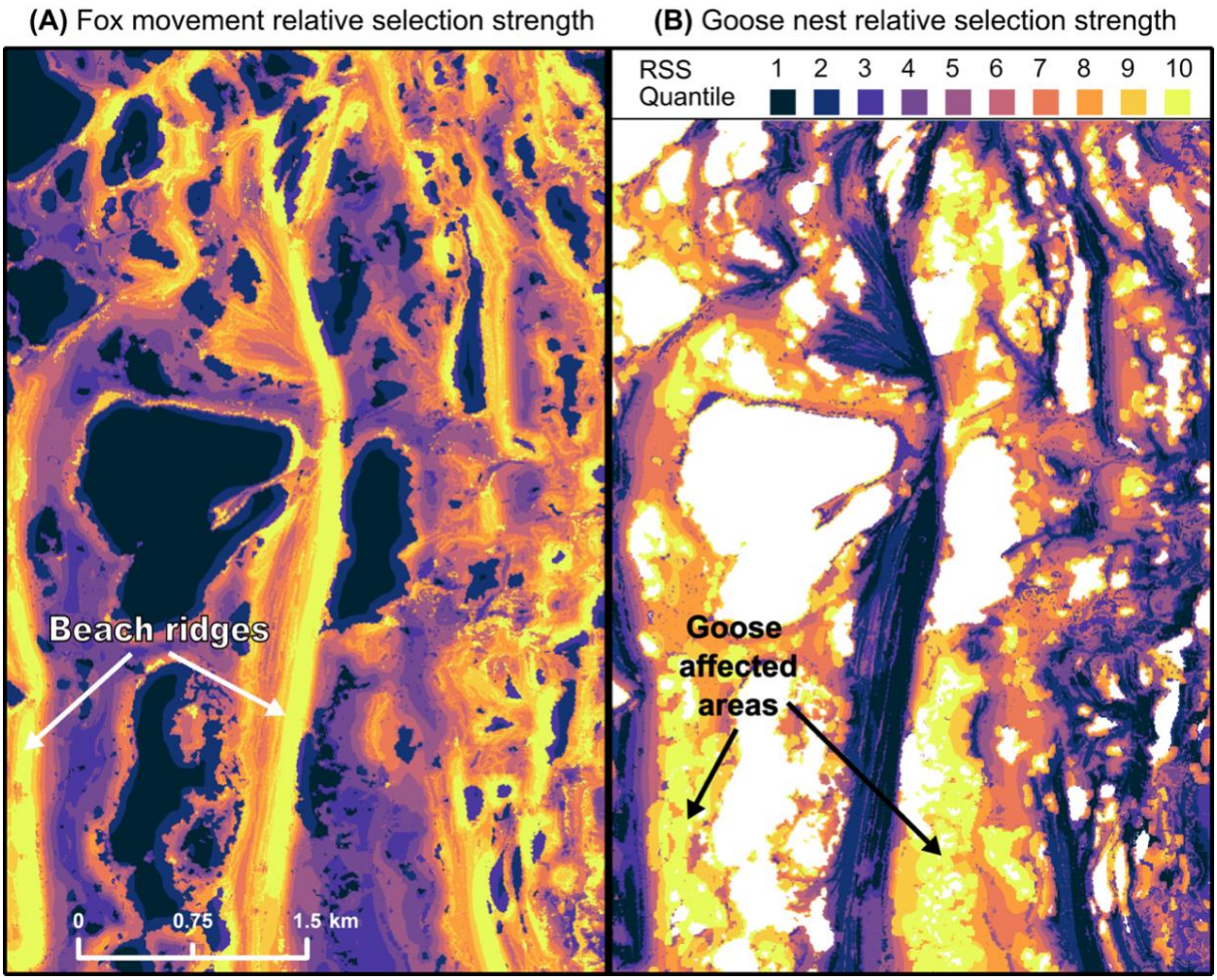

Figure 4.3. Relative probability of use generated from the fox movement (left) and goose nest (right) habitat selection models. Predictions from both models were binned into 10 equal-sized quantiles. Areas with a low relative selection strength (RSS) are shown in blue/purple and areas with a high RSS value are shown in orange/yellow. The plots show how foxes generally select to move along beach ridges, whereas geese avoid beach ridges and select for goose-affected areas (darkest blue areas in left panel/white areas in right panel are open water, which were excluded in the goose nest model).

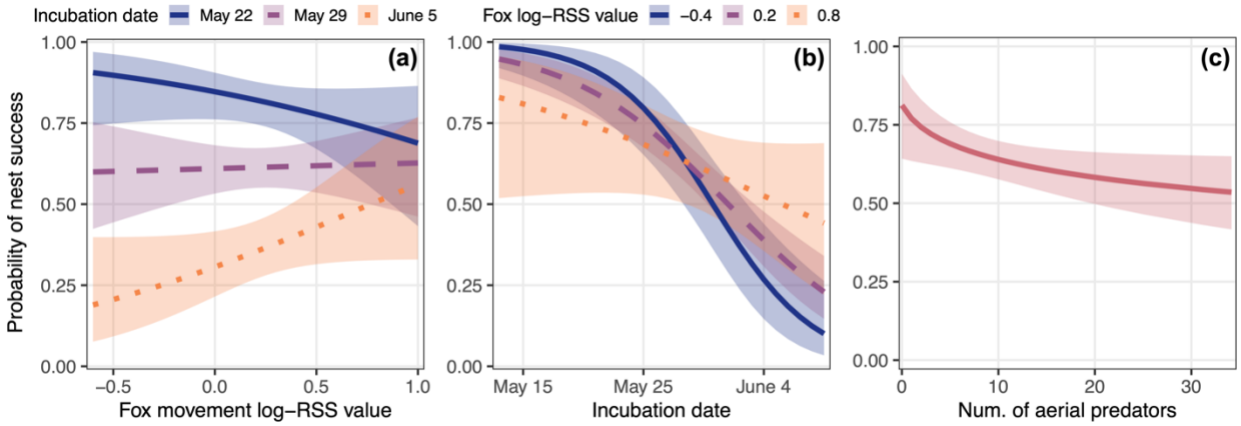

Figure 4.4. Results from the model evaluating Canada goose nest success (*n*=311 clutches) in Wapusk National Park, Manitoba, Canada. Panel (a) shows the effects of fox activity (estimated log-relative selection strength [RSS] values) on the probability of nest success at three different goose incubation initiation dates (mean incubation date: May 29, +/- 1 std. deviation). Panel (b) shows the predicted effects of incubation date on the probability of nest success at three different levels of predicted fox activity (low, medium, high). Panel (c) shows the marginal effects of aerial predator activity on the probability of nest success, predicted from the nest fate model. Ribbons represent +/-95% confidence intervals of each estimate.

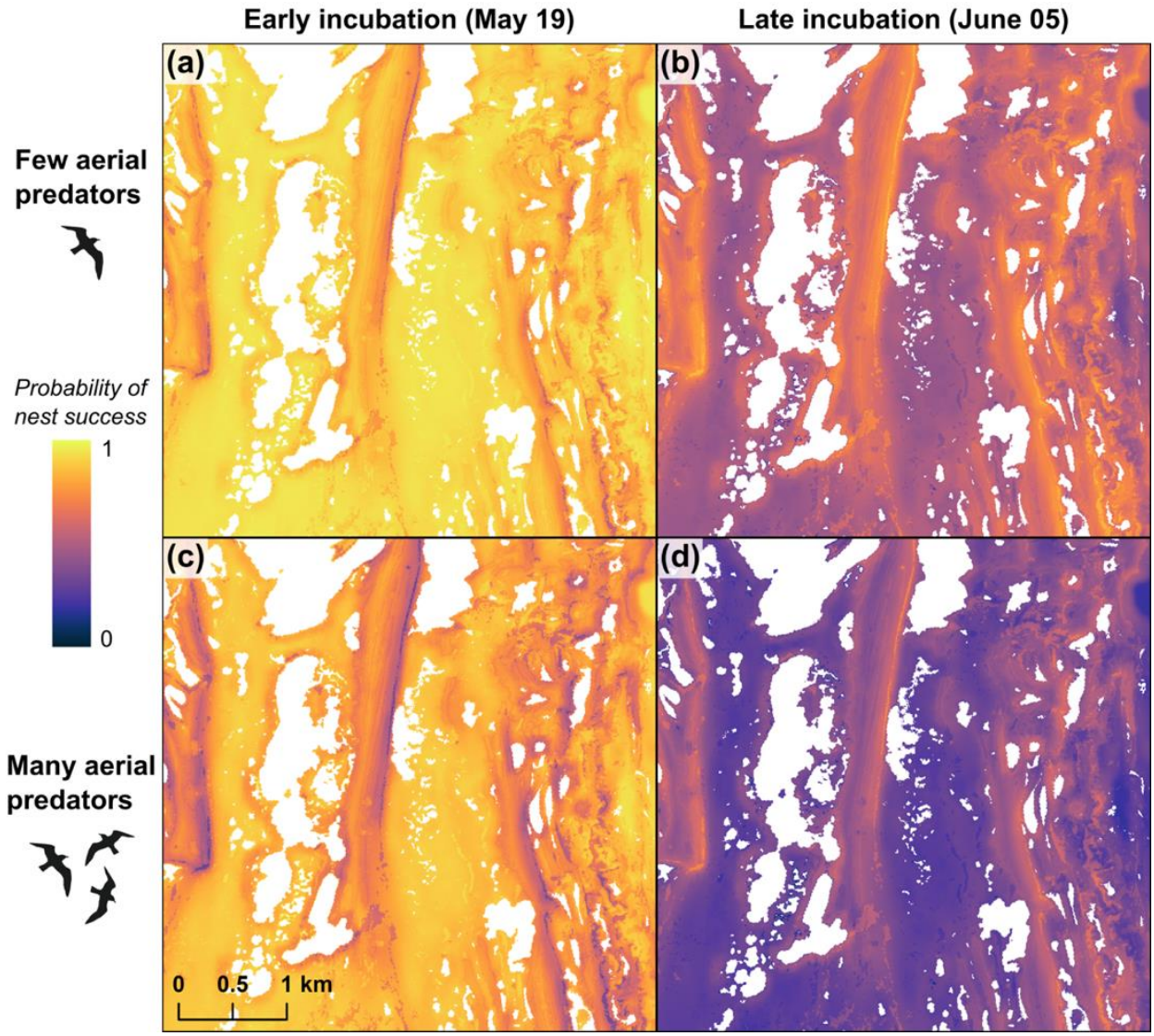

Figure 4.5. Predicted spatial patterns of Canada goose nest success within the study area, demonstrating the dynamic landscape of risk to goose reproduction that is produced by nesting phenology and predator activity (both fox and aerial predators). The figure depicts the probability of nest success under four different scenarios: few aerial predators (mean – 1 std. deviation) with early (a) and late (b) nest incubation, and many aerial predators (mean + 1 std. deviation) with early (c) and late (d) incubation. Incubation dates selected were the earliest (May 19) and latest (June 5) average incubation dates during our study period.

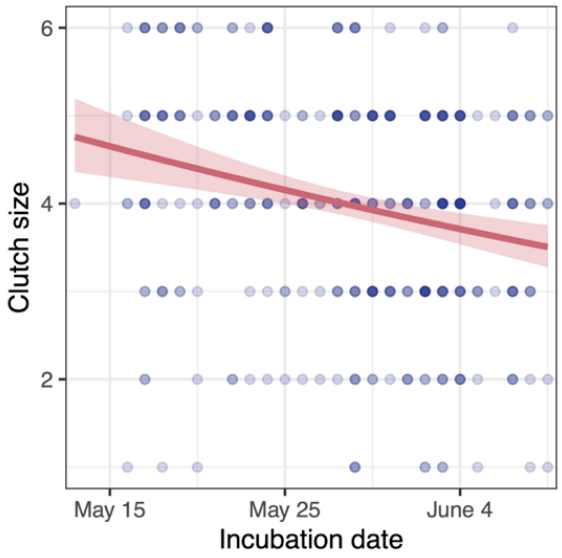

Figure 4.6. Negative relationship between incubation date and size of clutches laid by Canada geese. The red line and ribbon depict the effects of incubation date on clutch size estimated from a generalized linear model (+/- 95% confidence interval), and the blue points are the observed data (darker points = more clutches; *n*=351 clutches).

Appendix 4

Supplemental information for: "Predator activity, proactive anti-predator strategies, and nesting phenology produce a dynamic landscape of risk to tundra goose reproduction"

Additional details on landscape traits used for the habitat selection analyses

Distance to nearest open water (m) was calculated as the Euclidean distance between each point and the nearest water feature >0.001 km^2 (as determined from the land cover data set). To assess the effect of proximity to beach ridges on fox movement and goose nest selection, we first defined the boundaries of beach ridges using the land cover data set, such that contiguous areas >0.01 km^2 comprised of 'Unvegetated' and/or 'Dryas heath' cover types were classified as beach ridges. We then calculated the Euclidean distance (meters) from each point to the nearest beach ridge. The areas used to define water patches and beach ridges were informed based on our expert knowledge of the study area: water patches <0.001 km^2 in area are typically tiny ponds/puddles on the landscape that likely have a negligible influence on wildlife space use, while no fox dens occur on beach ridges <0.01 km^2 in area.

Full details on how land cover types were re-classified are presented in Table S1.

Table S4.1. Land cover types used in the fox movement and goose nest habitat selection analyses, re-classified from (Ponomarenko et al., 2014).

Original land cover type	Re-classified cover type
Coastal fen	Fen
Poor sedge fen	Fen
Ridge sedge fen	Fen
Shrub sedge fen	Fen
Emerging sedge fen/shallow water	Emerging sedge fen/shallow water
Coastal tall willow	Shrub/willow
Coastal low willow	Shrub/willow
Riparian tall willow	Shrub/willow
Lichen dwarf shrub	Shrub/willow
Shrub-moss-lichen	Shrub/willow
Spruce larch forest*	Shrub/willow
Lichen spruce woodland*	Shrub/willow
Moist rhododendron-Dryas	Dryas heath
Dry Dryas Heath	Dryas heath
Mild goose affected	Goose affected
Severe goose affected	Goose affected
Unvegetated	Unvegetated
Water	Water

*In our study area, these habitats are functionally shrub height.

Cross-validation methods for habitat selection models

We used cross-validation methods to evaluate the fit of each habitat selection model (Roberts et al., 2017). This process involved fitting 80% of the data to each model, testing model performance on the withheld 20% of data, and repeating that process four more times until all portions had been tested. For the fox movement model, we split the data using a random individual blocking method (i.e., training data sets had data from eight foxes, testing data sets had data from remaining two foxes). We used a spatial blocking method to split the goose nest data into training/testing data sets, whereby the goose nest study area was divided into five equal-sized areas (nests from one area were withheld as each of five testing folds). We then binned predicted results from each testing fold into 10 equal-sized, frequency-adjusted quantiles and performed Spearman-rank correlation analysis on these quantiles (Boyce et al., 2002).

Relationship between survey date and aerial predators observed on the transect

Since aerial predators in our study area are migratory, it is theoretically possible that the number of aerial predators observed along goose nest survey transects could have been influenced by survey date (with likely more predators observed on later transects). However, the relationship between transect survey date and aerial predator counts indicates there was no evidence that aerial predator counts were greater at later survey dates (Fig. S1). Our results should therefore not be affected by the date the survey occurred.

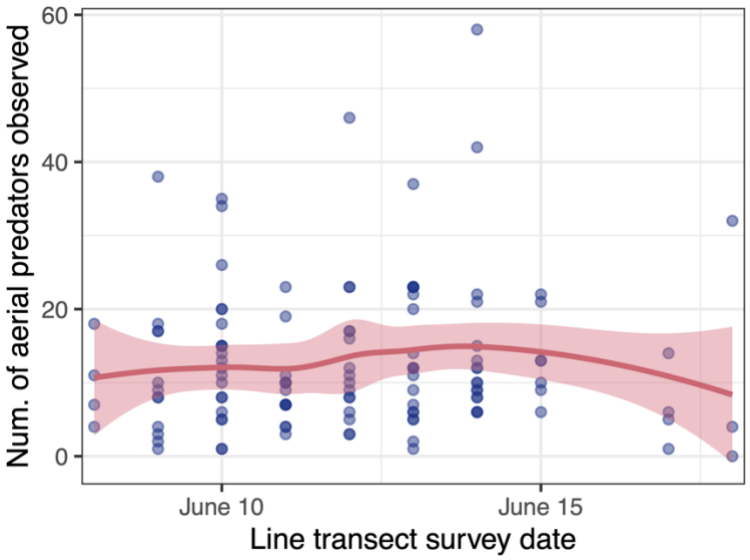

Fig. S4.1. Relationship between the date that goose nest transects were surveyed (range: June 8–18) and the number of predators observed on the transect, fit with a Loess smoother (+/-95% confidence intervals). Each point is a single transect.

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Chapter 5: Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice

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Status: under review at Ecology.

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 readily 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 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, which was positively related to greater snow persistence on the tundra. Arctic fox abundance was positively related to polar bear body condition metrics, which was 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 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 indirectly affects 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 these resources 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 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 and 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 via consumer diet switching (Spiller et al., 2010). Spatial subsidies that are regularly available tend to elicit a numerical response in predator populations (Rose and 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 and 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 these 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 subsidies. 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, weather conditions, predator abundance) (Oli, 2019). Relevant to this study is the observation that deeper snow conditions can positively 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 that are 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 species via their shared predator (foxes) (e.g., Bêty et al., 2001; Bêty et al., 2002; Nolet et al., 2013; 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 and 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 and 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. 5.1). 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 (Chapter 4), 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 5.

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 5 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 Chapter 4 for full details of the 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 slowly approached the nest until the goose flushed. We then counted clutch size and used egg flotation methods to estimate the date incubation was initiated, assuming a 28-day incubation period (Reiter and 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 and Andersen, 2011).

To account for the effects of weather 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 weather and trophic interactions on this coastal tundra food web (models and model formulas listed in Appendix 5). Our regression models assembled test the hypothesized causal (i.e., directed) relationships between each of the variables identified in our conceptual model (Fig. 5.1). 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 can accommodate 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., 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 (Chapter 4). 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 weather 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 5.1, Fig. 5.2a). However, we found only weak evidence for a relationship between polar bear storage energy (MJ) and sea ice break-up date (Table 5.1), 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 5.1), although younger and older bears tended to have lower energy stores (Appendix 5: Fig. S5.1). Total rodent abundance in June was greater during years when snow persisted longer on the tundra in spring (Table 5.1, Fig. 5.2b).

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. 5.2c) and storage energy (Table 5.1), which we used as proxies for marine subsidy availability. The performance of models with energy density and energy storage were very similar (Table 5.1), suggesting the energetic metrics performed equally well in explaining fox den occupancy. Rodent abundance positively affected fox den occupancy (Fig. 5.2d), with similar results between both models tested (Table 5.1).

Effects of weather 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 5.1, Fig. 5.3a). 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 5.1, Fig. 5.3b). As reported previously with this data set (Chapter 4), nests incubated later had lower rates of nest success (Table 5.1). We also found both total precipitation and average daily temperature during the incubation period positively affected individual goose nest success (Table 5.1, Fig. 5.3c-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 (a proxy of) 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 5.1, Fig. 5.2c). 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 5: Fig. S5.2). 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 5.1, Fig. 5.3c-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. 5.3a; Madsen et al., 2007; Lameris et al., 2019), which, in turn, affects goose reproductive success (Table 5.1). Yet, like many Arctic systems, Canada geese in our system are apparently not adjusting their nesting phenology enough to compensate for earlier springs (Appendix 5: Fig. S5.2), 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 5: Fig. 5.S3), 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 5: Fig. 5.S4), 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 (Chapter 4). 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. 5.2c; our proxy for marine subsidy availability), 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 5.1. 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 ($\hat{\beta}$, 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
$\sigma_{\mathrm{TransectID}}$	0.250	0.553	(0.013, 4.660)	-	-

†Estimates are **edf** (effective degrees of freedom) for Models 1a, 1b, and $\hat{\beta}$ for all other terms.
‡Statistics are ***t*** for parametric terms of models 1, 2, **F** for smooth terms of models 1a, 1b, and ***z*** for models 3–5.

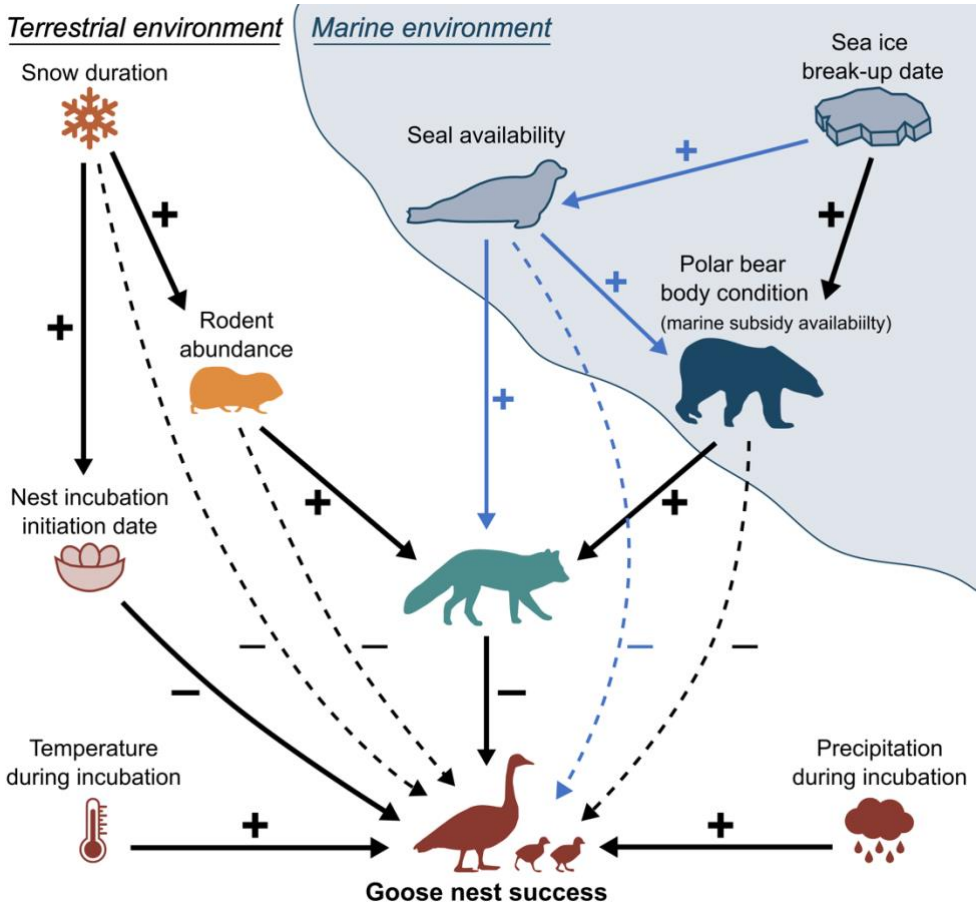

Figure 5.1. Conceptual model depicting our hypotheses on how winter environmental conditions, food abundance/availability, and predator activity interactively shape Canada goose nest success through direct and indirect pathways in a coastal tundra ecosystem. We hypothesized environmental conditions affect 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).

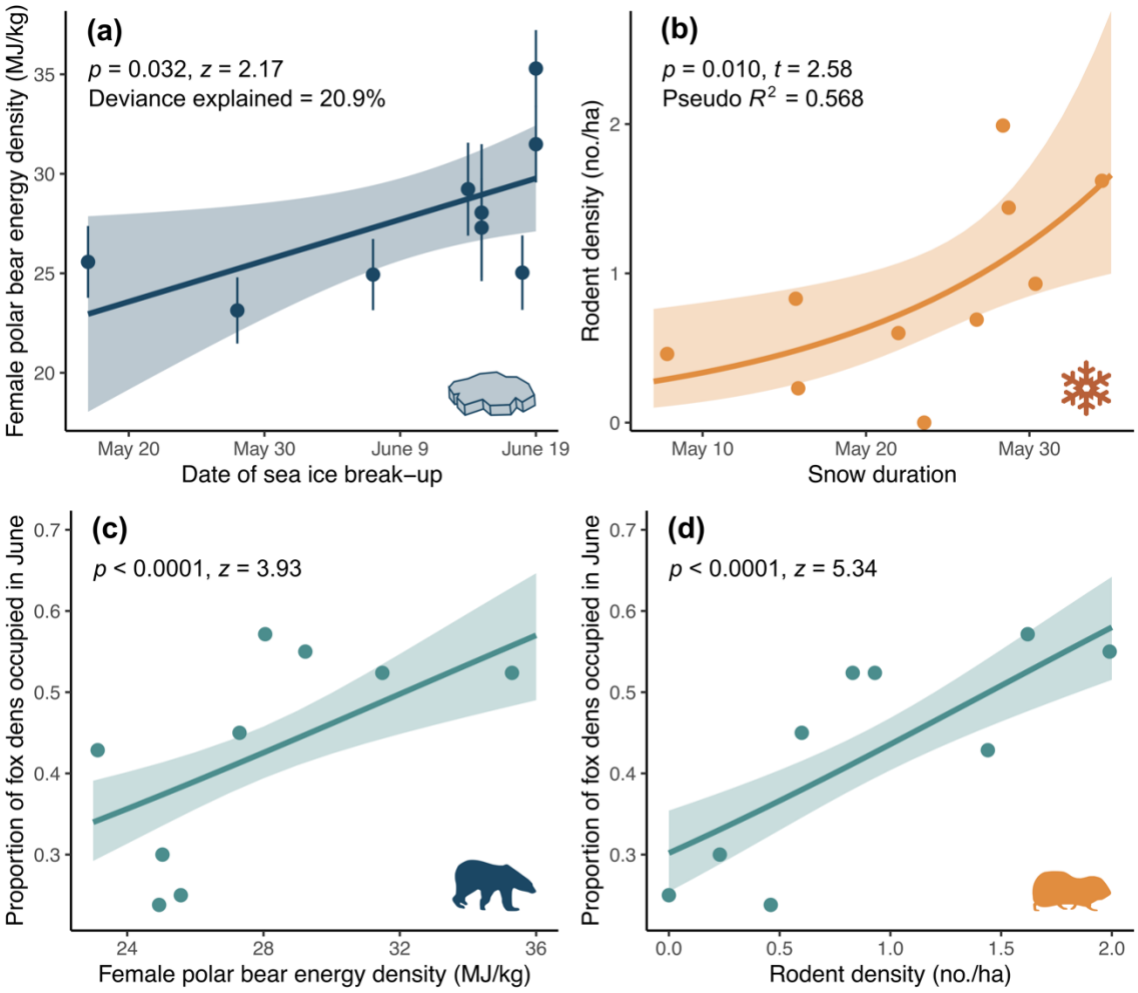

Figure 5.2. Results depicting how winter weather conditions affect the abundance/availability of winter food resources for Arctic foxes, which, in turn, respond numerically to greater food resources. Panel (a) shows the estimated effect of sea ice duration on female polar bear energy density (MJ/kg). 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. 5.1.

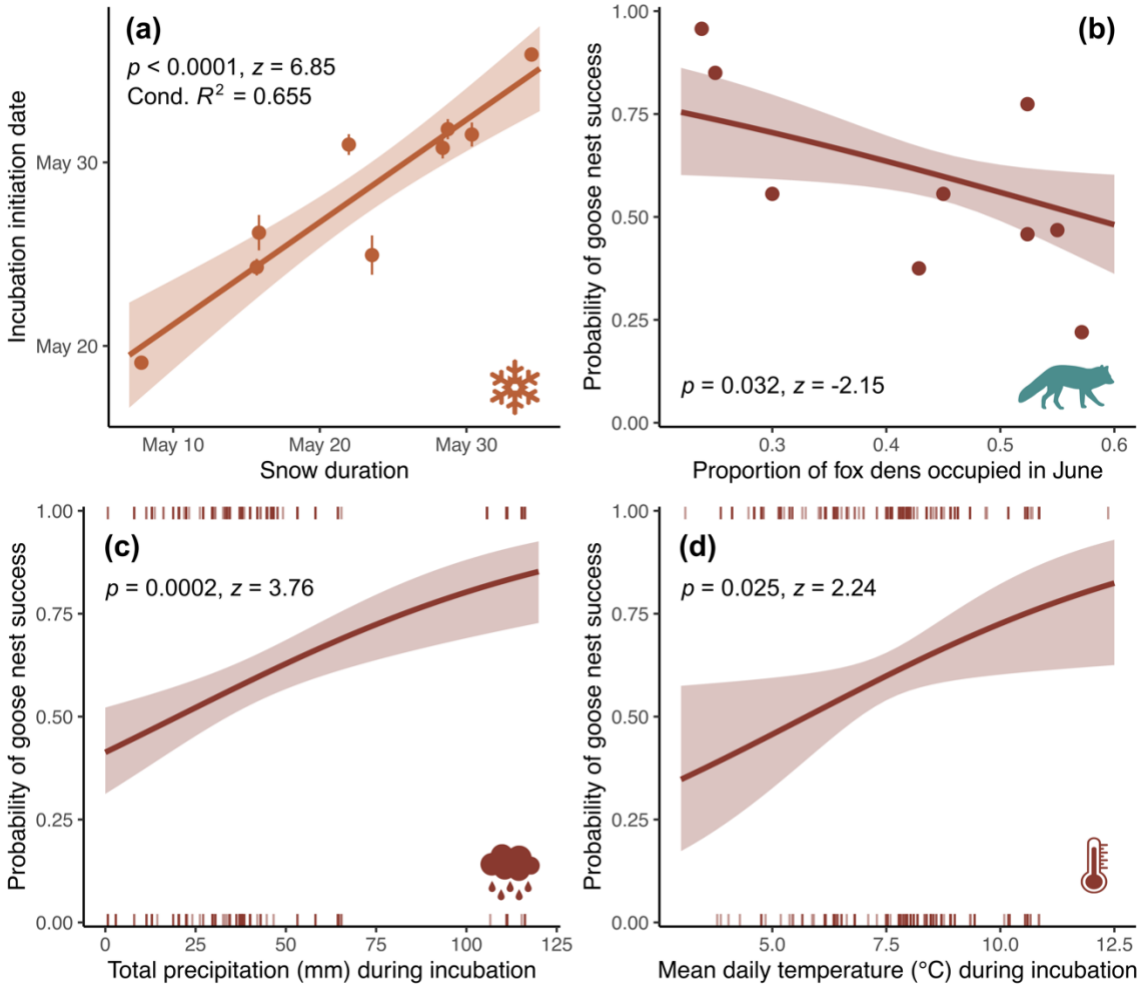

Figure 5.3. Results depicting how weather conditions and fox activity affect Canada goose reproduction. Panel (a) shows the estimated effect of snow duration on incubation initiation date. Individual dots show the annual average values +/- std. error, highlighting the low intra-annual variation in timing 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. 5.1.

Appendix 5

Supplemental information for: “Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice”

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 (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: $EnergyDensity_{ij} \sim N(\mu_{ij}, \sigma^2)$

$\mu_{ij} = SeaIceBreakup_{ij} + f_1(Age_{ij}) + f_2(Year_i)$

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

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 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: $RodentAbundance_i \sim Tweedie(\mu_i, \sigma^2, p)$

$\mathrm{E}(RodentAbundance_i) = \mu_i$

$\mathrm{Var}(RodentAbundance_i) = \theta \mathrm{Var}(\mu_i) = \sigma^2 \mu_i^p$

$\log(\mu_i) = SnowDuration_i$

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*. $RodentAbundance_i$ is assumed to follow a Tweedie distribution with mean μ_i and variance $\sigma^2 \mu_i^p$, θ 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: $PropDenOccupied_i \sim Beta(\mu_i, \phi)$

$\mathrm{E}(PropDenOccupied_i) = \mu_i$

$\mathrm{Var}(PropDenOccupied_i) = \frac{\mu_i(1-\mu_i)}{1+\phi}$

$\mathrm{logit}(\mu_i) = RodentAbundance_i + EnergyDensity_i$

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:
$$IncubationDate_{ij} \sim N(\mu_{ij}, \sigma^2)$$
$$\mu_{ij} = SnowDuration_{ij} + Year_i$$
$$Year_i \sim N(0, \sigma^2)$$

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

Model 5:
$$NestSuccess_{ij} \sim Bernoulli(\pi_{ij}, \pi_{ij}(1-\pi_{ij}))$$
$$\mathrm{E}(NestSuccess_{ij}) = \pi_{ij}$$
$$\mathrm{logit}(\pi_{ij}) = PropDenOccupied_{ij} + Temp_{ij} + Precip_{ij} + TransectID_i$$
$$TransectID_i \sim N(0, \sigma^2)$$

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*. $NestSuccess_{ij}$ 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

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 worse energy density and storage energy (Fig. S5.1).

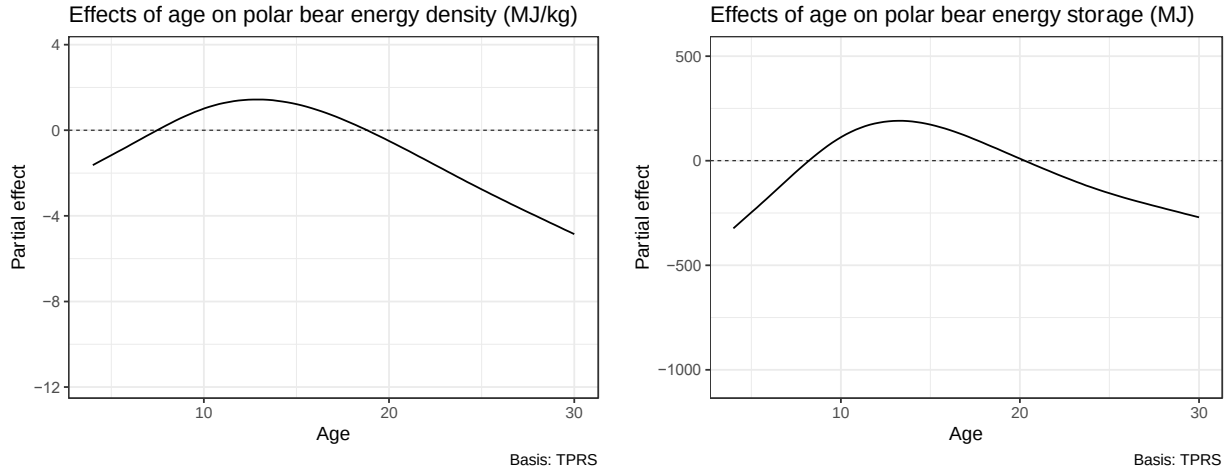

Figure S5.1. Results from the generalized additive mixed-effects models evaluating the effects of polar bear age and sea ice break-up date on the energy density (*left*) and storage energy (*right*) of solitary adult female polar bears from the Western Hudson Bay population. Plots were made using the *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 2000–2023. 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. S5.2). 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 advance 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.

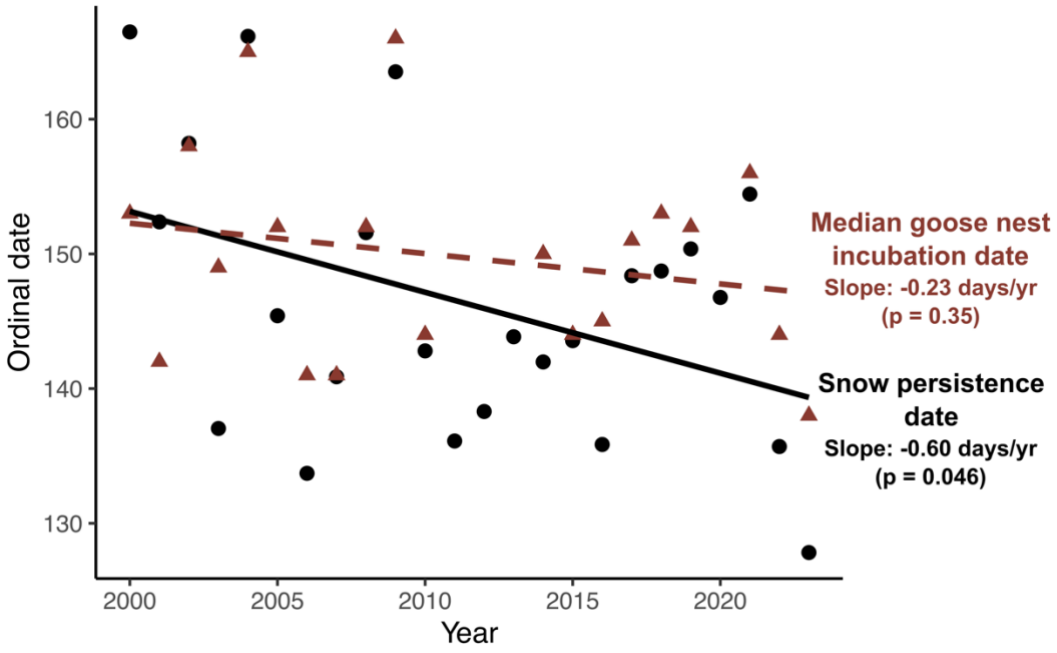

Figure S5.2. Linear trends of Canada goose median nest incubation initiation date (red triangles, red dashed line) and snow persistence date (black circles, solid line) from 2000 to 2023 in Wapusk National Park, Manitoba, Canada. The linear trends show the date that snow disappears from the study area is advancing roughly 2.6 times faster than median nest incubation date, suggesting an ongoing phenological mismatch between goose nesting and snow coverage.

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 that would indicated geese that nest at intermediate dates have higher rates of success. We found no evidence that nest success increases at intermediate incubation dates (Fig. S5.3). 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.

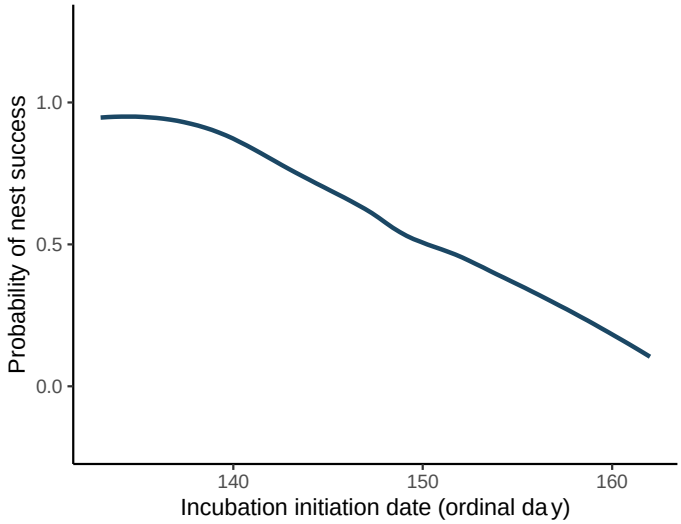

Figure S5.3. The relationship between incubation initiation date (ordinal day) and the probability of Canada goose nest success in Wapusk National Park, Manitoba, Canada, 2014–2023, fit with a Loess smoother. The data suggests no evidence of a non-linear relationship between nesting phenology and Canada goose nest success.

Finally, 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. S5.4).

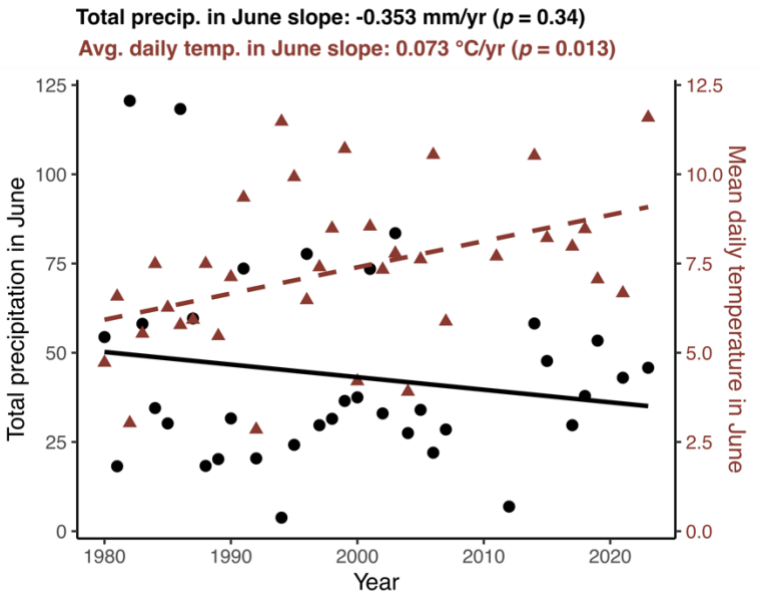

Fig. S5.4. Long-term trends in average temperature and total rainfall from the Churchill, MB weather station, 1980-2023. There has been a significant increase in June temperature (~5.9°C in 1980 to ~9.1°C), and a non-significant decrease in total precipitation.

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Chapter 6: General discussion

Expanding our understanding of the effects of predators within ecosystems

At the time of writing this dissertation, there had already been significant research and synthesis done on the "non-traditional" effects that predators have on ecosystem dynamics (i.e., the effects of predators that are not directly related to how predators alter the abundance or traits of lower trophic levels). Influential syntheses have been published assessing the role that predators play in nutrient cycling and ecosystem biogeochemistry (Schmitz et al., 2010; Monk & Schmitz, 2022); how carrion can influence the behavior and trophic interactions of scavengers (Prugh & Sivy, 2020; Moleón & Sánchez-Zapata, 2021) and be used to assess ecosystem integrity (Newsome et al., 2021); and how animals can act as nutrient vectors within and across ecosystems (McInturf et al., 2019; Subalusky & Post, 2019; Ellis-Soto et al., 2021). Yet, despite the growing recognition that predators have these additional irreplaceable effects within ecosystems, discussions regarding the importance of predators to healthy ecosystems still largely revolve around their ability to alter the abundance and traits of prey and subordinate predators. Part of the reason for this bias is likely due to these "non-traditional" effects being approached and perceived from isolated perspectives. In other words, how predators affect nutrient dynamics and scavenger interactions, for instance, have been considered separate processes, which has hindered the adoption of these effects into the broader discussion of the functional role of predation in ecosystems.

The second chapter of this dissertation was focused on trying to provide a holistic perspective on these "non-traditional" roles that predators have within ecosystems through the lens of a unifying element, a landscape *patch*, which is an area on a landscape with measurable spatial and temporal boundaries that contrasts with the surrounding landscape matrix. I identified three distinct pathways by which predators affect ecosystem dynamics without necessarily altering the abundance or traits of lower trophic levels (creating and distributing prey carcasses, concentrating prey-derived nutrients, and killing ecosystem engineers), all of which have indirect effects on other species limited to the vicinity of a patch. I termed these processes *patchy indirect effects of predation*, with the hope that providing terminology to this group of predator-mediated processes will help with its adoption in the wider literature.

Moreover, the *patchy indirect effects* concept helps to provide a fuller perspective on the irreplaceable roles that predators have within ecosystems. Large predators are one of the most imperiled groups of species worldwide (Ripple et al., 2014), in large part because of persecution

resulting from conflict, whether perceived or definite, with humans (Lennox et al., 2022). Arguments against the recovery or reintroduction of predators are often centered around the notion that humans can effectively replicate the roles that predators play within ecosystems, with the chief role being the limitation or regulation of prey populations (e.g., using recreational hunting to keep prey populations in check). Yet, this perspective ignores the many other important roles predators have within ecosystems that we, as humans, cannot easily replicate, not to mention the numerous differences in how predators and humans tend to harvest prey that may have long-term effects on species' evolution (Lennox et al., 2022). This part of my dissertation, then, will hopefully help advance the conservation and management of predators worldwide by broadening our understanding of their unique and irreplaceable effects within ecosystems.

Resolving animal impacts on ecosystems using remote sensing data and technology

The third chapter of this dissertation was an empirical extension of the *patchy indirect effects of predation concept* centered around using remote sensing data and technology (satellite imagery) to help resolve the ecological effects of Arctic foxes (*Vulpes lagopus*) on tundra ecosystems via their denning activity. Arctic foxes had previously been classified as ecosystem engineers due to their dens having higher plant productivity and enhanced soil nutrient content (Bruun et al., 2005; Gharajehdaghipour et al., 2016), yet we faced some uphill battles in publishing research around this framing due to the potential alternative, yet seemingly less parsimonious, explanation that Arctic foxes chose areas with these traits already present for their den sites. My research aimed to help resolve this dispute by explicitly accounting for landscape traits of their dens through habitat selection modeling, and using these characteristics to develop model-informed reference sites to compare plant productivity metrics against. In doing so, I found support for the hypothesis that Arctic foxes are the main drivers of their dens being ecological hotspots, as the model suggested that they normally construct dens in low-productivity areas. Though not the final nail in the coffin (we hope experimental nutrient additions will provide that), this study is yet another line of evidence that the concentration of nutrients derived from prey in and around their dens causes the unique soil and plant traits.

Looking forward, I see the continued advancement and access of remote sensing data and technology as playing a major role in quantifying how animals impact ecosystems across diverse spatial and temporal scales. Remotely sensed satellite and aerial imagery has been used to quantify how salmon spawning affects forest productivity (Brown et al., 2020; Kieran et

al., 2021); how seabirds enhance plants around their colonies through nutrient deposition (Mosbech et al., 2018); how beavers (*Castor canadensis*) buffer riparian ecosystems against wildfires and promote ecosystem stability (Fairfax & Whittle, 2020; Johnson-Bice et al., 2022; Fairfax et al., 2024); how outbreaks of defoliating insects affect forests (Rullan-Silva et al., 2013; Hall et al., 2016); and how grazing by large herbivores mediate fire and drought conditions across landscapes (Waldram et al., 2008; Barbosa et al., 2020). Light detection and ranging (LiDAR) and ground-penetrating radar systems have revealed how African elephants (*Loxodonta africana*) influence the structural diversity and rates of treefall of savanna ecosystems (Asner et al., 2009; Asner & Levick, 2012; Asner et al., 2016; Davies et al., 2018; Davies & Asner, 2019); the 3-D structure of burrows by digging mammals (Kinlaw & Grasmueck, 2012; Chlaib et al., 2014); and how termite mounds influence ecosystem dynamics by affecting large herbivore grazing activity (Levick et al., 2010). These examples are meant to highlight the variety of ways in which remote sensing data and technology can already be used to advance our understanding of the ecological impacts of animals. The resolution and spatial scale at which these data can be obtained are advancing rapidly, and are poised to become a major tool in the ecologists' toolbox for assessing animal ecological effects across diverse spatial and temporal scales (Pettorelli et al., 2014; Pettorelli et al., 2018; Schulte to Bühne & Pettorelli, 2018).

Novel approaches to assessing "dynamic landscapes of fear"

Research on the "landscape of fear" that predators engender has exponentially increased in recent years (Gaynor et al., 2019), in part because of technological advancements that can better capture predator and prey movements across space and time. Where spatial patterns in predation risk were once presumed to be static through time (or constrained to a static representation of predation risk due to technological limitations), we now understand that the predator-prey space race shows considerable variation through time (Kohl et al., 2019; Smith et al., 2019; Suraci et al., 2022). Places that are risky at one time of day may be comparably safe at another time (Dröge et al., 2017; Kohl et al., 2018), and the "landscape of fear" paradigm has now been extended to account for these temporally dynamic patterns of predation risk (Palmer et al., 2017; Palmer et al., 2022). Yet, most of this research has been limited to evaluating how large mammal predator-prey systems change throughout the diel cycle. The fourth chapter of this dissertation looked to extend this dynamic landscape of fear concept to breeding birds on the tundra.

Birds are under evolutionary pressure to select nest sites in areas that maximize their probability of success, yet few studies have linked spatial patterns in predator activity to bird nest site selection to assess how predation risk shapes bird reproduction (Lima, 2009; Clermont et al., 2021) – much less how these spatial patterns vary across the breeding season. My research revealed that Canada geese (*Branta canadensis interior*) can either perceive spatial risk from Arctic foxes or have learned through experience or from conspecifics where safer areas on the tundra are, and adjust their nesting behavior accordingly. To my knowledge, this is the first time that predator and bird nest habitat selection have been compared in this manner, and I anticipate this general approach of comparing how predator and prey select among the same landscape traits may be used in more systems to assess how predators shape bird reproduction behaviors. But I also showed that these patterns of risk to goose nest success strongly depend on the timing of incubation, thereby providing a rare empirical example that demonstrates how spatial patterns of predation risk to bird nests can vary through time.

Tundra predator-prey interactions in a warming Arctic

The low biodiversity within tundra ecosystems means tundra food web structures are comparably simple, and dominated by a few key players. In particular, rodents (namely lemmings and voles) have historically had an outsized influence on tundra food webs due to their periods of hyperabundance (Elton, 1942; Gilg et al., 2003; Gilg et al., 2006). Indeed, one study estimated that as much as 70% of small mammal production flows up to predators (Krebs et al., 2003). The relative simplicity of tundra food webs means they can provide excellent model systems to investigate theoretical and empirical aspects of predator-prey dynamics. In particular, long-term monitoring of tundra food webs has provided key insights into the prevalence and dominant role that indirect trophic interactions may have in food webs (Gauthier et al., 2023), largely in relation to changes in rodent abundance.

The fifth chapter of my dissertation aimed to expand our understanding of indirect interactions within tundra food webs by incorporating the hypothesized influence of marine subsidies on a major terrestrial predator, Arctic foxes, into the food web analysis. I observed a strong relationship between Arctic fox abundance and polar bear (*Ursus maritimus*) body condition in the same year, which we used as a proxy for marine resource availability under the assumption that conditions that benefit polar bear hunting benefit foxes as the major scavenger of seal carrion. Tying Arctic fox abundance, in turn, to Canada goose reproductive success implied an indirect negative effect of marine resources on goose reproduction on the tundra.

Arctic foxes use the winter sea ice as a secondary source of food when prey is scarce on the tundra, and their ability to cross these ecosystem boundaries provides a mobile link between Arctic marine and terrestrial ecosystems. Arctic foxes generally only show a numerical response to winter foods since they are largely income breeders and mate during late winter, and this asynchronous timing dictates the direction of the indirect effect of marine subsidies on geese; if these subsidies were available during summer, foxes would likely switch toward feeding on the subsidies and reduce their predation pressure on geese, thereby generating a positive indirect relationship between marine subsidies and nesting geese.

Indeed, this prey switching by foxes is generally what leads to short-term positive indirect relationships between rodents and geese in tundra ecosystems (e.g., Bêty et al., 2001; Bêty et al., 2002; McKinnon et al., 2013; Juhasz et al., 2020). Yet, I documented short-term negative indirect effects of rodents on geese in our system (Wapusk National Park), which stands in contrast to pretty much all other studies evaluating rodent–goose–predator interactions. Most prior research was conducted on colonially breeding geese rather than dispersed-breeding geese, like the Canada goose, and I attribute this discrepancy to the different spatial distributions of nests that result from these different breeding tactics. Time spent searching for (or pursuing) prey is a major component of predation (Holling, 1959), and these costs are substantially higher when hunting dispersed vs. clumped prey. Consequently, my hypothesis is that Arctic foxes spend similar amounts of time hunting Canada geese regardless of rodent abundance, in large part because rodent abundance is not high enough even during peak years to sustain foxes. Thus, when evaluating the effect of Arctic foxes on Canada goose nest success, the effects appear linked to the numerical response of foxes to rodents rather than the functional response. With more Arctic foxes on the landscape, encounter rates with goose nests similarly increase, resulting in greater rates of predation.

Climate change sits as the looming backdrop to all these predator–prey relationships. With the Arctic warming substantially faster than other parts of the globe (Rantanen et al., 2022), tundra and sea ice food webs are undergoing rapid and widespread changes (Post et al., 2013; Cooper, 2014), and our system is no exception. I showed that weather conditions play a major role in mediating these food web dynamics in Chapter 5, highlighting the susceptibility of this coastal tundra food web to ongoing and further climate-mediated disruption. In short, despite being a protected area with extremely low direct human pressure, the Wapusk ecosystem is an ecosystem in flux, and we have begun to see the ramifications that climate change is having on the vertebrate food web: climate-related declines in the abundance of

lemmings and Arctic foxes (Verstege et al., 2023), phenological mismatches in goose reproduction (Chapter 5), declines in polar bear survival and abundance due to reduced sea ice duration and extent (Regehr et al., 2007; Lunn et al., 2016), and the expansion and proliferation of boreal forest-associated species onto the tundra (Zhao et al., 2022; Moizan et al., 2023; Johnson-Bice et al., 2024). Exactly what these changes mean for Arctic food webs in the long run remains to be seen. If nothing else, I hope that continued long-term monitoring of this food web will help document and reveal the ways in which we, as humans, have completely re-shaped this ecosystem, and ultimately provide a better understanding of how changes in climate can alter food web dynamics through complex, and often-unforeseen, direct and indirect pathways.

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