Integrating predator energetic balance, risk-taking behavior and microhabitat in functional response: Untangling indirect interactions in a multispecies vertebrate community

Andréanne Beardsell [1,*], Frédéric Dulude-De-Broin [1], Gilles Gauthier[1], Dominique Gravel [2], Pierre Legagneux [1], John P. DeLong [3], Dominique Berteaux [4], and Joël Bêty [4,*]

December 20, 2024

1. Département de biologie and Centre d'études nordiques, Université Laval, Québec, Québec, Canada;
2. Département de biologie and Centre d'études nordiques, Université de Sherbrooke, Sherbrooke, Québec, Canada;
3. School of Biological Sciences, University of Nebraska- Lincoln, Lincoln, Nebraska, USA;
4. Chaire de recherche du Canada en biodiversité nordique, Centre d'études nordiques and Centre de la science de la biodiversité du Québec, Université du Québec à Rimouski, Rimouski, Québec, Canada;

∗ Corresponding authors; Andréanne Beardsell (email: abeardsell@hotmail.com) and Joël Bêty (email: Joel_Bety@uqar.ca)

Author's contributions

A.B.: conceptualization, methodology, formal analysis, investigation, software, visualization, writing—original draft, writing—review and editing;
F.D.-D.-B: conceptualization, visualization, writing—review and editing;
G.G.: funding acquisition, investigation, project administration, writing—review and editing;
D.G.: conceptualization, writing—review and editing;
P.L.: funding acquisition, conceptualization, supervision, writing—review and editing;
J.D.: visualization, writing—review and editing;
D.B.: funding acquisition, investigation, project administration, writing—review and editing;
J.B.: conceptualization, methodology, visualization, funding acquisition, project administration, supervision, writing—review and editing.

Acknowledgments

We are grateful to the many people who helped us with field work over the years, to the Mittimatalik Hunters and Trappers Organization, and to Park Canada staff for their assistance. The research relied on the logistic assistance of the Polar Continental Shelf Program (Natural Resources Canada) and of Sirmilik National Park of Canada. The research was funded by (alphabetical order): Arctic Goose Joint Venture, the ArcticNet Network of Centers of Excellence, the Canada Foundation for Innovation, the Canada Research Chairs Program, the Canadian Wildlife Service (Environment Canada), the Fonds de recherche du Québec-Nature et technologies, the International Polar Year program of Indian and Northern Affairs Canada, the Kenneth M Molson Foundation, the Natural Sciences and Engineering Research Council of Canada, the Northern Scientific Training Program, Polar Knowledge Canada, Université du Québec à Rimouski, and Université Laval.

1 Abstract

1. Predator-prey interactions are universal, governing the flow of energy between trophic levels and shaping ecological communities. Despite >70 years of research, our knowledge of the mechanisms modulating the strength of these interactions is limited.

2. To untangle proximate mechanisms governing species interactions and improve our ability to quantify interaction strength, we developed a mechanistic model that integrates predator risk-taking behavior, predator energetic balance and anti-predator refuges in a natural vertebrate community.

3. Our model, based on species traits and behavior, was inspired by the Arctic tundra, where the main predator (the arctic fox) feeds primarily on cyclic small rodents (lemmings) and eggs of various tundra-nesting bird species such as sandpipers eggs(non-risky prey) and gulls eggs (risky prey). We confront the model predictions with 20 years of data on species density and reproductive success.

4. According to the energetic model, lemmings are the most important contributor to the energetic balance of foxes, with a threshold density of 89 lemmings per km^2 required to switch to a positive energetic balance. When the fox energetic balance goes from positive (high lemming density) to negative (low lemming density), the acquisition rate of gull eggs increases 1.7 times on shores and 9.5 times on islands, a partial refuge and riskier habitat for the predator. Variation in gull hatching success generated by the mechanistic model aligned with empirical observations for both habitat.

5. Our results show that changes in predator energetic balance, translating into a change in attack and capture probabilities, can be a major mechanism underlying predator-mediated effect of lemmings on gulls hatching success.

6. This study is a critical step towards the integration of energetic and landscape characteristics into predator-multiprey models and presents one of the rare mechanistic models parameterized in a natural vertebrate community. Such a model can strongly improve our ability to quantify interaction strengths in multi-species communities.

Keywords: Multi-species functional response, predator-prey interactions, predation sequence, energetic, apparent mutualism, prey refuges, Arctic tundra.

2 Introduction

Predator-prey interactions are the building blocks of food webs and are central to community ecology, from classical predator-prey theory to its application in wildlife management (DeLong, 2021; Guiden et al., 2019). Decades of research show that the strength of predator-prey interactions varies dynamically with predator and prey behavior (e.g. predator group hunting; Fryxell et al. 2007), species traits (e.g. presence of defensive structure), total prey availability (Chan et al., 2017), predator energetic state and landscape characteristics creating small scale prey refuges (Forrester and Steele, 2004). Despite these complexities, many studies on predator-prey interactions have relied on simple proxies for predation risk (e.g., spatial overlap between predators and prey; Suraci et al. 2022), typically focusing on a single predator-prey pair and often under controlled laboratory or field enclosure conditions (reviewed by Pawar et al. 2012; Rall et al. 2012). A growing number of studies call for a better integration of these complexities in natural systems using more mechanistic modeling approaches (Beardsell et al., 2023; Cherif et al., 2024; Guiden et al., 2019; Prokopenko et al., 2023; Suraci et al., 2022; Wheatley et al., 2020; Wootton et al., 2021).

Predator–prey interactions are the culmination of a sequence of events that begins with spatial overlap between predator and prey and progresses through encounter, detection, attack and capture (Fig. 1). Probabilities and duration associated with each component allow the formulation of the functional response (Holling, 1959; Lima and Dill, 1990; Wootton et al., 2021). The predation sequence is highly flexible and can be modulated by various factors, including the presence and abundance of other prey species, the predator energetic balance, and landscape characteristics such as refuges (Fig. 1). Consequently, any change in one factor can alter the predation sequence, potentially resulting in a change in the interaction strength and influencing population dynamics (Beardsell et al., 2023). By disentangling the various components of predation, this modular approach allows identification of the main mechanisms influencing interaction strength. As pointed out by Wootton et al. (2021) and Cherif et al. (2024), there is a need for more mechanistic approaches to better quantify interaction strengths in multispecies communities.

Predators often forage on diverse prey species in natural ecosystems, with variable trade-offs between energy gain and risk of mortality and injury for the predator. Predator injury while foraging can arise from the physical context (steep slopes, strong currents, thorny vegetation) as well as from prey defensive structures (horns, beaks, claws, quills, teeth) combined with aggressive behavior (mobbing, biting, kicking) (see Mukherjee and Heithaus (2013) for review). Predator foraging behavior can vary with the risk of injury, and their energetic state can modulate the propensity to take risks (e.g. Berger-Tal et al. 2009; Embar et al. 2014; Perlman and Tsurim 2008). This short-term behavioral adjustment can be particularly pronounced in endothermic predators, as they generally cannot reduce their metabolic rate to conserve energy when prey abundance is low (unlike ectotherms; Kiørboe et al. 2018). When predators can easily meet their energetic needs, risky foraging activities should be reduced, which can benefit prey that use partial refuges or anti-predator behavior (Embar et al., 2014). Conversely, predators facing energetic deficits may take greater risks, as the probability of mortality from not acquiring enough prey increases (Blecha et al., 2018). For instance, European starlings (*Sturnus vulgaris*) increase their attack rates on chemically defended insect larvae when their energetic state (body masses and fat stores) is reduced (Barnett et al., 2007). Although such mechanisms can modulate interaction strength, they have been rarely integrated in predator-prey models (see Prokopenko et al. 2023 for a review on the subject) and their impact on interaction strengths is unknown in multi-prey systems.

Beardsell et al. (2023, 2022) previously developed a mechanistic model of predation in a multi-prey system in the Arctic, grounded in detailed empirical observations from a long-term ecological study (Gauthier et al., 2024*a*). Here, we extend this model to integrate predator risk-taking behavior, predator energetic balance and the presence of prey refuges in the landscape. While we lack empirical data to fully parameterize the model, it extends the framework proposed by Cherif et al. (2024) to a multispecies community and provides an integrated mechanistic framework to quantify interaction strengths in the wild. We confront the model predictions with long-term data on Arctic wildlife densities and demographic parameters. The originality of this study lies in our ability to integrate the effect of energy acquisition rates on critical components of predation while considering the main prey available in a heterogeneous landscape.

The model was developed for the arctic fox (*Vulpes lagopus*), a predator of the tundra ecosystem. Lemmings and various bird species (mostly eggs and juveniles) are the main components of the summer diet of arctic foxes in most tundra ecosystems (Angerbjörn et al., 1999; Giroux et al., 2012). Lemmings exhibit population cycles (Gauthier et al., 2024*b*), and the fox predation pressure on tundra ground-nesting birds is typically released at high lemming density (Beardsell et al., 2022; Gauthier et al., 2015; Summers et al., 1998). Foxes generally avoid crossing water to access bird nests (Lecomte et al., 2008) and hatching success of glaucous gulls (*Larus hyperboreus*) is higher on islands than on shores (Gauthier et al., 2015). Islands are thereby acting as partial refuges from foxes for some nesting birds (Corbeil-Robitaille et al., 2024). Gulls are large birds with strong beaks, defending their nests by harassing potential predators from distance, bomb-diving on them to scare them away (mobbing; Clode et al. 2000). In our model, we therefore assumed that microhabitats used by nesting gulls (islands vs shore) and prey defensive behavior modulate attack and capture probabilities of foxes. We also assumed that fox risk-taking propensity should be higher when the predator energetic balance is negative. Including these two main assumptions in the mechanistic model, we simulated multispecies predator-prey dynamics at varying prey densities. We hypothesized that the energetic balance of foxes should be strongly influenced by variation in lemming density. We also hypothesized that the interplay between microhabitats used by nesting gulls and changes in fox risk-taking behavior, triggered by changes in their energetic balance, can generate the strong variation observed in gull breeding success.

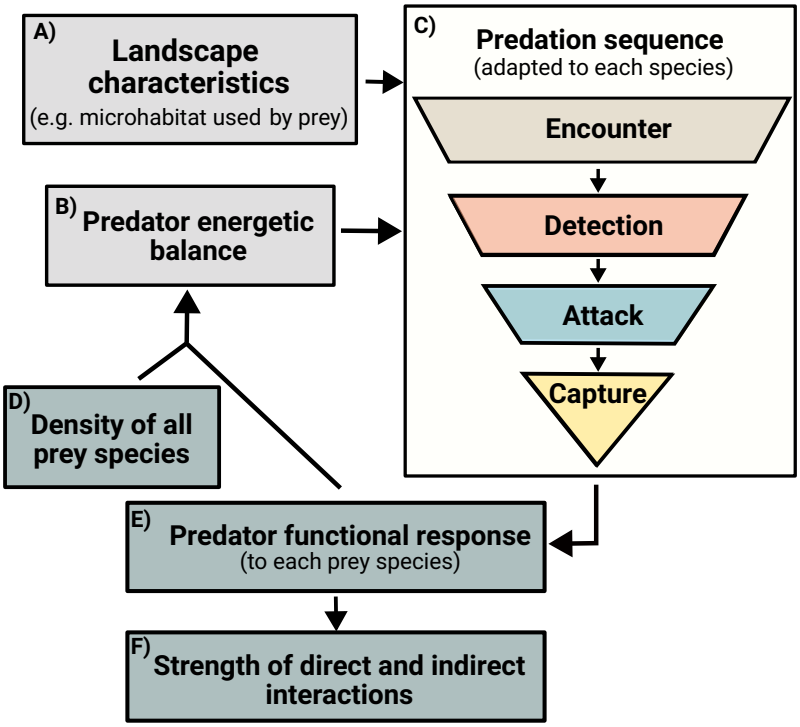

Figure 1: Schematic diagram of the mechanistic model including the effects of landscape characteristics (**A**) and predator energetic balance (**B**) on the predation sequence (**C**). The quantitative outcome of the predation sequence, the functional response (**E**), combined with prey density (**D**), enables calculation of the energetic balance of the predator, which in turn can influence components of the predation sequence (through changes in predator risk-taking behavior). **F)** Finally, a change in functional response can modulate the strength of direct and indirect interactions.

3 Methods

3.1 Study system

We built the mechanistic model of predation using detailed empirical data from a long-term ecological study on Bylot Island, Nunavut, Canada (Gauthier et al., 2024*a*). The monitoring area of lemmings, sandpipers and gulls is located in a 35 km^2 portion of the Qarlikturvik Valley (73° 09'N; 79° 56'W). The valley is dominated by a mosaic of mesic tundra, wet polygons, small lakes and ponds. Wetlands are predominantly used by nesting glaucous gulls, cackling geese (*Branta hutchinsii*), red-throated loons (*Gavia stellata*) and occasionally snow geese (*Anser caerulescens*). The snow geese nesting in the valley are generally associated with nesting snowy owls (*Bubo scandiacus*), whose presence reduces predation by foxes (Bêty et al., 2001). Ground-nesting birds present include passerines (Lapland longspur, *Calcarius lapponicus*), long-tailed jaegers (*Stercorarius longicaudus*), and sandpipers (primarily Baird's Sandpiper (*Calidris bairdii*) and White-rumped Sandpiper (*Calidris fuscicollis*)). Two species of small mammals are present: brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings (Gauthier et al., 2013). The brown lemming is the most abundant species and shows large-amplitude fluctuations of abundance every 3-5 years, whereas collared lemmings show weak amplitude population fluctuations (Fauteux et al., 2015; Gruyer et al., 2008). The nest density of gulls and sandpipers in the study area was relatively constant between years (Beardsell et al., 2022; Gauthier et al., 2015). Some species nesting at low densities (e.g., loons and geese) were not included in the mechanistic model, as their presence is unlikely to significantly impact the energetic balance of foxes. The arctic fox is an active searching predator that travels long distances daily within its territory during the summer (Poulin et al., 2021).

3.2 Multi-prey mechanistic model of predation

The functional response model, inspired by the theoretical framework of Holling (1959) and Wootton et al. (2021), was derived by breaking down predation events into a maximum of 4 steps: (1) encounter, (2) detection, (3) attack and pursuit, (4) capture and manipulation (Fig. 1C). At the core of this modular framework is the adaptation of the model to different prey species according to their anti-predator behavior and the predator hunting behavior (Beardsell et al., 2021, 2022; Cherif et al., 2024; Wootton et al., 2021). We built upon the mechanistic model of predation by Arctic foxes on lemmings and sandpiper nests previously developed in the same study system (Beardsell et al., 2021, 2022). Remarkably, functional responses derived from the model were consistent with field observations for various prey species, including lemmings and the nests of geese, passerines, and sandpipers (Beardsell et al., 2021). We expand here the model to include predation on glaucous gull nests. Figure 2A provides an overview of the multi-prey mechanistic model including the three prey species.

While the parameters needed to fully define the relationship between predator energetic balance and its attack and capture probabilities of gull nests remain unknown, we have hypothesized this relationship based on the following considerations. Unlike passerines and sandpipers, gulls actively defend their nests with dive attacks, posing a potential risk of serious eye, skull or limb injury to foxes (see Fig. S7 for images of interactions between gulls and foxes). Since foxes attacking island nests must swim, they cannot achieve the same speed or adopt the same attack and defensive positions as they would on the shore when harassed by gulls. Therefore, we assumed that both attack and capture probabilities (steps 3 and 4) are lower for nests located on islands (Fig. 3). An experimental study at our site shows that fox predation measured with artificial nests is 5-9 % lower on islands than on the shore, supporting the assumption that microhabitat influences fox hunting behavior (Beaudoin, 2025). This study justified the difference in intercept values shown in Fig. 3. Finally, we assumed that attack and capture probabilities decrease linearly with the net energy acquired by the predator at time t - 1 (Fig. 3). Specifically, attack and capture probabilities should be higher when the predator energetic balance is negative (increased risk-taking behavior) and lower when the energetic balance is positive (Fig. 2B). Given the limited empirical data on this relationship, we generated three functions (Fig. S8A). The model outputs obtained with one function are presented in the results and all other simulations are presented in Fig. S8B.

An attack by the predator on a gull nest (prey 3) can occur when the predator is at a distance (d_3), being defined as the maximum distance at which the predator will attack a nest (in 2D, detection region = $2d_3$; Pawar et al. 2012). As gulls are highly conspicuous, we assumed that within the attack distance, the detection probability is 1. As not all nests within the searched area may be attacked and captured by the predator, we introduced the attack and capture probabilities. Capture efficiency of a gull nest (α_3; km^2 day^{-1}) is thus expressed as the product of the distance traveled by the predator when active (s; km day^{-1}), the attack distance (d_3; km), and attack and capture probabilities ($f_{3,3,is}$ and $f_{3,3,sh}$ for nests located on island and on the shore, respectively):

$$\alpha_{3,is}(N_1, E_{net}(N_1, N_2, N_3)_{t-1}) = s(N_1) \cdot (2 \cdot d_3) \cdot f_{3,3,is}(E_{net}(N_1, N_2, N_3)_{t-1}) \tag{1}$$

$$\alpha_{3,sh}(N_1, E_{net}(N_1, N_2, N_3)_{t-1}) = s(N_1) \cdot (2 \cdot d_3) \cdot f_{3,3,sh}(E_{net}(N_1, N_2, N_3)_{t-1}) \tag{2}$$

Where $E_{net}(N_1, N_2, N_3)_{t-1}$ is the net energetic balance of the predator at time t-1, which determines attack and capture probabilities (Fig. 3). Parameter values used in the predator model for gulls and other prey (lemmings, prey 1, and sandpiper, prey 2) and their source can be found in Supplementary methods.

Gull nest density (N_3, nests km^{-2}) is calculated for each microhabitat ($N_{3,sh}$, $N_{3,is}$). At the study site, 75% of nests were located on islands ($n = 264$ nests, from 2004 to 2023). We therefore introduced the probability of a nest being located on an island (p_r) to distribute the overall nest density, N_3, between island and shore nests:

$$N_{3,sh} = N_3 \cdot (1 - p_r) \tag{3}$$

$$N_{3,is} = N_3 \cdot p_r \tag{4}$$

The number of gull nests acquired (nests per fox day $^{-1}$) is expressed as the sum of gull nests acquired from both habitats:

$$\begin{aligned} FR_3(N_1, N_2, N_3, E_{net}(N_1, N_2, N_3)_{t-1}) = & (\phi_{active}(N_1) \cdot \alpha_{3,is}(N_1, E_{net}(N_1, N_2, N_3)_{t-1}) \cdot N_{3,is}) \\ & + (\phi_{active}(N_1) \cdot \alpha_{3,sh}(N_1, E_{net}(N_1, N_2, N_3)_{t-1}) \cdot N_{3,sh}) \end{aligned} \tag{5}$$

Where ϕ_{active} is the proportion of time the predator is active in a day and N is the density of each prey (prey item km^{-2}). The values of ϕ_{active} and s are correlated and are a function of lemming density (N_1). This function was partially obtained from empirical data (GPS-tracking of 16 foxes (7 females and 9 males) during summers 2018 and 2019; Fig. S9, Beardsell et al. 2022). Changes in Arctic fox movement (ϕ_{active} and s) have been identified as important mechanisms driving the positive effects of lemmings on non-risky prey, such as sandpipers, generating up to 31% variation in their absolute nesting success (Beardsell et al. 2022; Fig. S10).

For simplicity, prey handling was not included in the predation model as these processes (time associated with pursuit and manipulation per prey item) play a minor role in our system (Beardsell et al., 2021, 2022). Very similar results were obtained with predation models including prey handling parameters. As arctic foxes can capture more prey than they consume in the short-term (Careau et al., 2008; Samelius and Alisauskas, 2000), prey digestion time was not included in the model as a potential limit on acquisition rate. For more details on construction of the model for sandpipers and lemmings see Beardsell et al. (2022). The next section describes the integration of the predator energetic balance into the model.

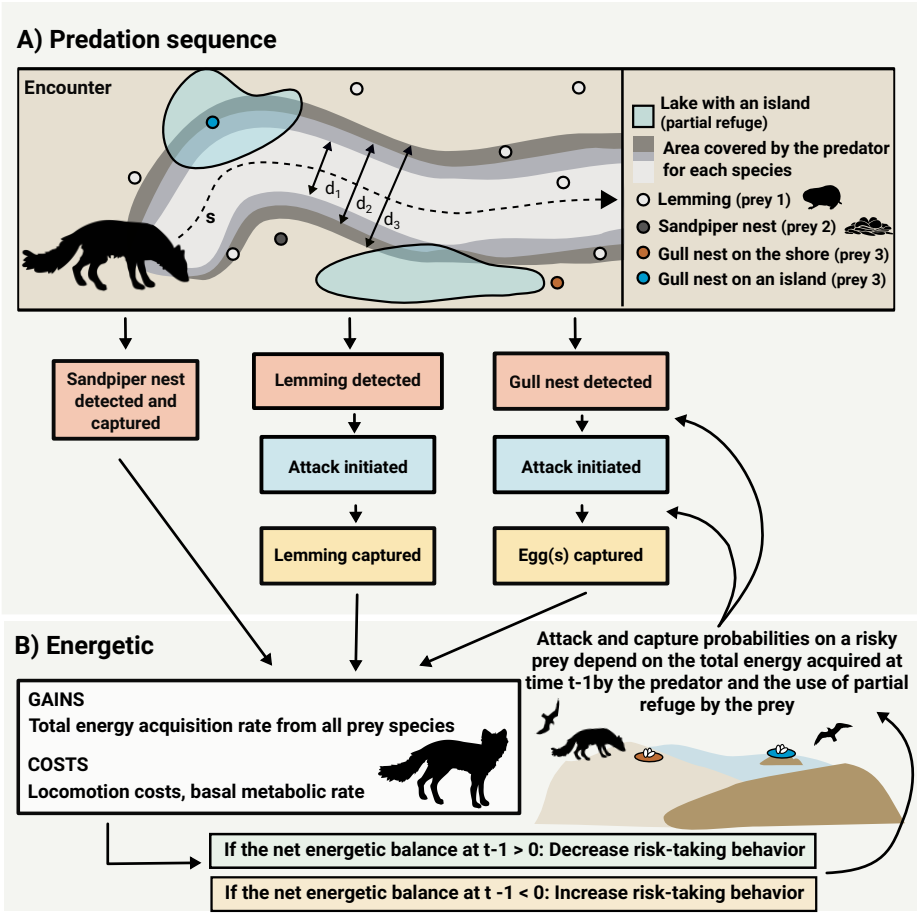

Figure 2: **A)** Conceptual mechanistic model of arctic fox functional response to density of lemmings, sandpiper nests (non-risky prey) and glaucous gull nests (risky prey). Each box represents one or more components of predation (search, prey detection, attack decision and capture). Arrows represent the probability that the predator reaches the next component. **B)** Schematization of the integration of the energetic component in the predation model. The attack and capture probabilities of a gull nest by the arctic fox varies according to whether the nest is located in a partial refuge and the net energetic balance of the predator at time t-1.

3.3 Integrating energetics into the predation model

The daily energy gain rate from all prey per individual fox ($ER_i(N_1, N_2, N_3, E_{net}(N_1, N_2, N_3)_{t-1})$) is expressed as the product of the predator acquisition rate (for instance Eq. 5 for prey 3) and the energetic content of a prey item (E_i , KJ per prey item). The net energy gain rate from all prey acquired ($E_{net}(N_1, N_2, N_3)$; per fox day^{-1}) is expressed as:

$$E_{net}(N_1, N_2, N_3) = \sum_{i=1}^{3} ER_i(N_1, N_2, N_3, E_{net}(N_1, N_2, N_3)_{t-1}) - E_{loc}(N_1) - E_b \tag{6}$$

where the total energy gain rate from all prey species is reduced by the energetic costs of locomotion (E_{loc}; KJ day^{-1}) and basal metabolic rate (E_b; KJ day^{-1}). Considering that movement is a substantial portion of daily energy expenditure in canids (Garland, 1983; Gorman et al., 1998) and that handling time of all three prey species is very low (e.g., 250 sec. to consume or hoard a sandpiper nest and 125 sec to pursue, consume or hoard a lemming; Beardsell et al. 2022), we assumed that short-term energy costs associated with the time spent pursing prey (including running and swimming) and handling prey are negligible, and that a portion of these costs is already included in locomotion costs.

The energetic costs of locomotion (E_{loc}; KJ day $^{-1}$) was estimated by the product of the energetic cost per kilogram

per unit distance (COT, KJ kg^{-1} km^{-1}), the average predator body mass (M; kg), the predator speed (km day^{-1}; s) and proportion of time spend active (ϕ_{active}):

$$E_{loc} = COT \cdot M \cdot s(N_1) \cdot \phi_{active}(N_1) \tag{7}$$

COT was estimated using the following allometric equation from Taylor et al. (1982):

$$COT = 10.7 \cdot M^{-0.316} \tag{8}$$

This equation was derived using an energy conversion of 20.1 J ml^1 O_2 and assumes a negligible contribution from anaerobic glycolysis (Taylor et al., 1982). We estimated the energetic cost of locomotion at 23.8 KJ km^{-1} for an average fox body mass (3.2 kg), which is consistent with an estimate from the kit fox (*Vulpes macrotis*) in natural settings (15.6 kJ km^{-1}; Girard 2001). The energetic cost of locomotion estimated here is also consistent with Fuglei et al. (2003), who used indirect calorimetry to measure the metabolic rate of an Arctic fox running on a treadmill. From their reported values, we calculated an energetic cost of 35.7 kJ km^{-1} for an average body mass of 3.2 kg. To estimate basal metabolic rate (E_b), we used the equation presented in Careau et al. (2008) based on arctic fox body mass:

$$E_b = -507 + 303 \cdot M \tag{9}$$

Which leads to an average basal metabolic rate of 472 KJ per day. Parameter values of the energetic model are summarized in Table 2 and details on the estimation of parameter values can be found in Supplementary Methods.

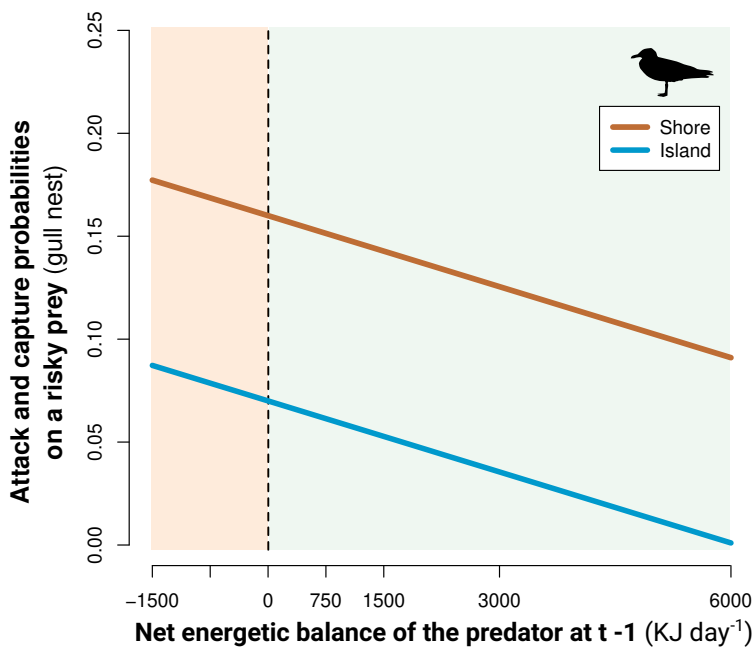

Figure 3: Hypothetical relationships between attack and capture probabilities on a risky prey (gull nest) by the arctic fox as a function of the net energetic balance of the predator at time t-1. Attack and capture probabilities of a nest located on the shore (orange line) are expected to be higher than those of a nest located in a partial refuge (island; blue line). Areas where the net energetic balance is >0 are in green and <0 in orange.

3.4 Estimating gulls hatching success from the mechanistic model

The number of prey items acquired by the predator population per day for each prey species (i = 1,2,3) is given by the product of the functional response and the predator density (NR, ind. km^{-2}):

$$P_i(N_1, N_2, N_3, E_{net}(N_1, N_2, N_3)_{t-1}) = FR_i(N_1, N_2, N_3, E_{net}(N_1, N_2, N_3)_{t-1}) \cdot NR \tag{10}$$

In the study area, arctic fox home ranges are generally stable throughout the summer. Thus, predator density was estimated based on average home range size (18.2 km^2 based on 57 home ranges from 2008 to 2016) and the average proportion of overlap (0.18; see Beardsell et al. 2023; Dulude et al. 2023 for more details). Eq. 10 allowed us to estimate annual hatching success of gulls (prey 3) for the whole range of lemming density measured at the study site. For each value of lemming density, we calculated the number of nests acquired for 28 days (the average duration between the gull laying date and hatching date), while considering that the density of nests decreases each day due to predation by foxes. To estimate hatching success, we assumed that the nesting period of gulls occurs simultaneously across individuals, that fox predation is the only cause of nest failure, and that predated nests are not replaced.

3.5 Field evaluation of the model

We evaluated the model output (gull hatching success) using 20 years (2004 to 2023) of glaucous gull nest monitoring in the study area (Gauthier et al., 2015). Nests are dispersed throughout the landscape and typically located on small islands or on the shore of ponds and small lakes in wetlands. The gull incubation period extends from early June to mid-July. We systematically searched the entire study area for gull nests in June of all years. Nests are conspicuous and gulls typically reveal their presence from a relatively long distance with alarm calls and behavioral displays. Most nests were revisited at 1to 2-week intervals to check their contents and to look for signs of predation. A nest is considered to have successfully hatched if at least one egg has hatched. We estimated lemming density using live trapping from 2004 to 2023 (see Fauteux et al. 2018 for methods). To obtain an estimate of total lemming density during the gull incubation period, we summed the density of the two lemming species and averaged the June and July estimates.

The relationships between hatching success, nest microhabitat (shore, island) and lemming density were fitted using a generalized linear mixed model based on the logistic-exposure method (Shaffer, 2004). The method estimates daily nest survival and explicitly accounts for variation in the length of nest monitoring period. Exposure time was computed by determining the number of days between the date of nest discovery and one of the following dates: (1) for successful nests, the observed or estimated hatching date or the date of the last visit if no information on hatching date was available, (2) for failed nests, the observed predation date or the midpoint between the date on which fate was determined and the last date the nest contained eggs. Nests with undetermined fate were not included in the analysis. The model was fitted with survival as a binary response variable (1: success, 0: failed), lemming density and nest microhabitat as fixed effects and the year as a random variable. All analyses and modeling were conducted in R version 4.4.0 ({R Core Team}, 2024).

4 Results

The energetic model indicated that lemmings are the most important contributor to the energetic balance of foxes. The model also showed that the energetic balance of foxes switches from negative to positive at a threshold density of 89 lemmings per km^2 (Fig. 4A). Lemmings constituted 83 and 99% of the energy acquired by foxes in a low (50 ind. per km^2) and a high (650 ind. per km^2) lemming year, respectively (Fig. 4B). They represented less than 50% of the energy acquired by foxes below approximately 10 lemmings per km^2. Variations in the density of sandpiper and gull nests (within the variation observed in our system; see Table 2) generated little change in the energetic gain rate of foxes compared to lemmings (346 KJ for gull nests and 417 KJ for sandpiper nests compared to 6652 KJ for lemmings).

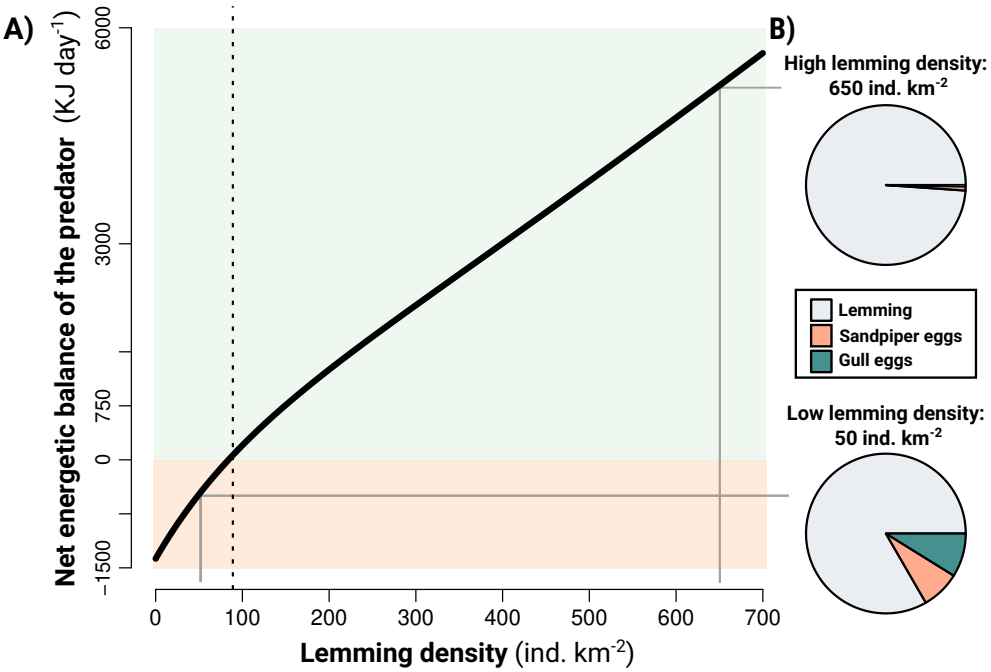

Figure 4: **A)** The black line shows the predator net energetic balance as a function of the density of the fluctuating prey (lemming) for an average-mass fox. Areas where the net energetic balance is >0 are in green and <0 in red. The dashed line shows the lemming density threshold at which the net energetic balance of foxes changes from negative to positive. **B)** Piecharts show the relative contribution of the three prey species to the net energetic balance of foxes at high (650 ind. km^{-2}) and low (50 ind. km^{-2}) lemming densities. Densities of sandpiper and gull nests are set at average densities (respectively 2 and 0.26 nests km^{-2}) over the range of lemming density.

Functional responses of the arctic fox to the risky prey (gull nest) were generated from the multi-prey mechanistic model (Fig. 5). The slope of the functional response (the product of capture efficiency (α; km^2 day^{-1}) and the proportion of time the predator spent active), varied from 0.25 to 0.42 km^2 day^{-1} for nests located on the shore (Fig. 5B) and from 0.02 to 0.19 km^2 day^{-1} for nests located on an island (Fig. 5A). Acquisition rates of gull nests are lowest for nests located on islands when the energetic balance of predators is positive (i.,e. high lemming year), and highest for nests located on the shore when the predator is in deficit (i.e. low lemming year). The variation in predator acquisition rates, generated by the model linking predator risk-taking behavior and energetic balance, is 71% for island nests and 47% for shore nests (Fig. 5). The remaining variation, 33% for island nests and 53% for shore nests, is due to changes in predator movement parameters induced by change in lemming density (Fig. 5).

Annual lemming density during the gull incubation period varied from 2 to 710 individuals per km^2 from 2004 to 2023. A total of 155 glaucous gull nests were monitored until hatch during this period (111 located on islands and 44 on shores). Hatching success was positively related to summer lemming density (β = 0.63, 95%CI = 0.25, 1.15) and was lower for nests located on shores compared to islands (β = -3.29, 95%CI = -4.29, -2.43, Fig. 6). Variation in gull hatching success generated by the mechanistic model aligned with empirical observations for both habitat (Fig. 6). For instance, at lemming densities of 50 and 650 ind. per km^2 (which correspond, respectively, to a negative and positive energetic balance of the predator), the mechanistic model estimated gull hatching success probability to vary from 0 to 0.46 on shores and 0.51 to 0.94 on islands, while the statistical model estimated it to vary from 0 to 0.75 on shores and 0.75 to 0.99 on islands.

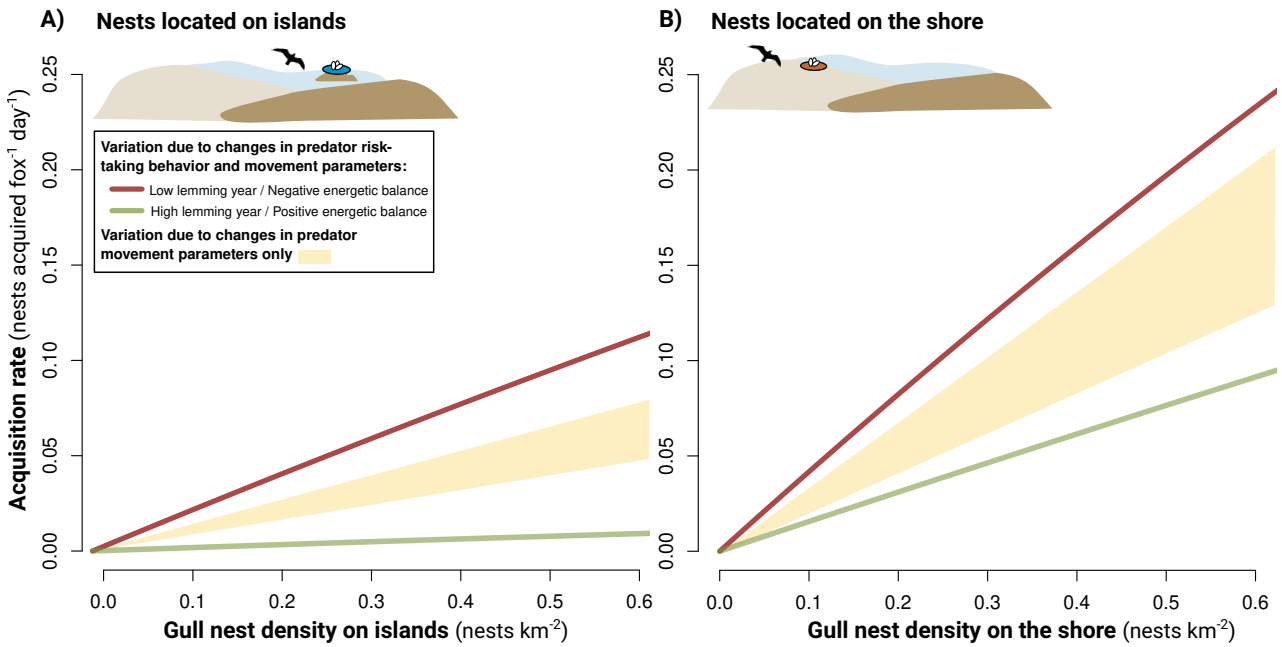

Figure 5: Functional responses of the arctic fox to the risky prey (gull nest) generated from the mechanistic multi-prey model for both habitats (island **(A)** and shore **(B)**), and for a negative (red lines) and positive (green lines) energetic balance of the predator. Positive and negative energetic balance correspond respectively to lemming densities of 650 and 50 ind. per km^2. The shaded area is based on a model that excludes the effect of variations in predator risk-taking behavior and retains only changes in predator movement parameters (as a function of lemming density; Fig. S9) on gull nest encounter rates. Sandpiper density was set at the average value of 2 nests per km^2.

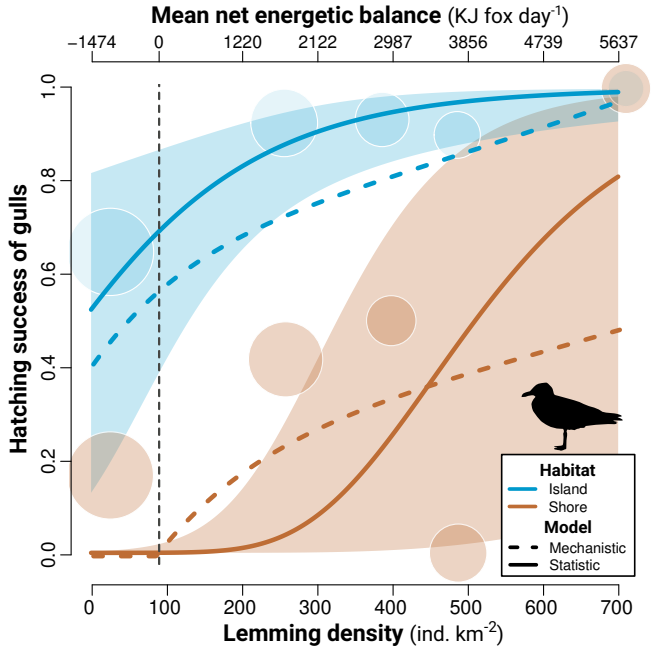

Figure 6: Hatching success probability of glaucous gulls nesting on Bylot Island (Nunavut, Canada) in relation to summer lemming density and nest microhabitat (shores vs. islands) from 2004 to 2023 (continuous color lines). The pale bands represent 95% CI of the regression. Circles illustrate observed data, and circle size is proportional to the number of observations (n = 155 nests). Colored dashed lines show hatching success of gull nests in relation to lemming density and nest microhabitat generated by the mechanistic model. Vertical black dashed line shows the threshold (predicted by the model) at which the net energetic balance of foxes changes from negative to positive.

5 Discussion

Our study is a first critical step towards the integration of energetic and landscape characteristics into predator-multiprey models. It also presents one of the rare mechanistic models parameterized in a natural vertebrate community. Such a model can strongly improve our ability to quantify direct and indirect interaction strengths in complex ecological communities. By explicitly incorporating the sequence of events associated with the consumption of different prey species by a predator within an energetic framework, our model disentangles the interplay between the energetic balance of the predator, risk-taking behavior by the predator, and microhabitat heterogeneity. Our results highlight the various mechanisms that can drive indirect interactions among prey and generate strong inter and intra annual variation in prey survival.

Although many empirical studies have demonstrated links between the risk-taking propensity and energetic state of a predator (Barnett et al., 2007; Blecha et al., 2018; Moran et al., 2021), this relationship has rarely been explicitly included in predator-prey models (Prokopenko et al., 2023). The integration of energy is crucial for understanding interaction strengths, since many species traits and behavior, including movement rate, territoriality, home range size, hunting tactics and risk-taking propensity, are highly plastic and can be strongly influenced by the energetic balance (e.g., Blecha et al. 2018; Lyon et al. 2018). The model developed here is innovative because it uses multispecies functional responses to estimate the total energy acquired by a predator in the wild and it integrates feedback loops generated by changes in the predator energetic balance on the acquisition rate of each prey. Hence, changes in total prey density (all species combined) can drive changes in the behavior of the predator and subsequently generate heterogenous cascading effects on the survival of different prey species, depending on their traits and use of microhabitats. The model can be adapted to other communities, and emerging biologging technologies —such as high-frequency GPS tracking, acoustic recording, and accelerometry—should further facilitate the development of such models (Studd et al., 2021; Williams et al., 2014). This approach should strongly enhance our understanding and quantification of interaction strengths in free-ranging animals.

The energetic model indicated that lemmings are the primary contributors to the energetic balance of Arctic foxes, comprising an average of 92% of their energy gain rate across the range of lemming densities observed in the study area. This finding aligns with the results of Angerbjörn et al. (1999) and Elmhagen et al. (2000), who reported that small rodents accounted for an average of 87% of the Arctic fox diet in Siberia (based on the analysis of 751 fresh scats) and 85% in Sweden (based on the analysis of 796 scats). However, the main contributors to fox energetic balance could shift if other abundant prey, such as migratory birds or carrion, are present in their home range. The lemming density threshold at which the energetic balance of foxes changes from negative to positive (i.e., 89 ind. per km^2) is also consistent with previous research conducted at our study site indicating a very low occurrence of fox reproductive activity when lemming density is below 100-170 individual per km^2 (Bergeron et al., 2025; Juhasz et al., 2020). In our model, movement parameters (distance traveled and time spent active) of foxes were functions of lemming density (see Beardsell et al. 2022). Although these relationships were not the focus of the study, these two parameters are - like the risk-taking behavior - likely to be related to predator energetic balance. Linking energetic balance to key components of predation, such as predator travel rate, detection, attack and capture probabilities of the prey by the predator, could strongly improve our ability to develop general mechanistic models of predation.

Predators foraging on diverse prey species are common in natural ecosystems. A classic hypothesis in ecology is that predators can stabilize prey populations by adjusting their ”preferences” according to the relative abundance of prey (the concept of prey switching; Murdoch 1969). The term “preference” encompasses a wide range of mechanisms, including the probability of detecting, attacking, and capturing a prey item (Chesson, 1984). However, in most cases, the parameter that induces prey switching in predator-prey models does not have an explicit mechanistic interpretation (DeLong, 2021). This parameter is typically integrated through the type III functional response, where the space clearance rate (or capture efficiency) is squared. One mechanism often suggested for prey switching is predator learning or experience (Real, 1977). While these cognitive processes can be important, our model illustrates that changes in attack

probability on a given prey species can be driven by changes in the energetic state of the predator per se (not by the relative abundance of prey). Our approach based on dynamic multi-species functional responses, combined with total prey densities, allows the integration of such important energy-dependent mechanisms in predator-multi-prey models.

In our model, predator decisions are modulated by short-term energy acquisition rates at time t-1 (the previous day). However, energetic balance over a longer time scale may also play a role in decision-making, particularly if the predator can store energy, either through caching or endogenous reserves. This could become especially important when a pulse of abundant prey is available (e.g., a bird colony or carcasses available to foxes in the Arctic tundra) and used by the predator to cover its energetic needs during periods of low prey availability. Moreover, predators experiencing long-term energy deficits may adjust their spatial behavior, shifting from residency to migration or nomadism. For instance, Arctic foxes can increase extra-territorial excursions during periods of low prey abundance (Lai et al., 2017). Identifying the appropriate time scale for linking predation components (such as attack probability) to the predator energetic balance is essential, as it could influence predator behavior and interaction strengths.

The positive indirect effect of lemmings on tundra-nesting birds due to shared predators was reported decades ago (Summers et al., 1998; Underhill et al., 1993) and has been studied across the Arctic since then. Changes in the daily activity budget and distance traveled by arctic foxes have been identified as important mechanisms leading to positive indirect effects of lemmings on non-risky prey like sandpipers and passerines (Beardsell et al., 2022). Unlike passerines and sandpipers, gulls can defend their clutches against arctic foxes and we show that changes in predator energetic balance, translating into a change in attack and capture probabilities, could be a major mechanism underlying the positive effect of lemmings on gulls hatching success. However, we recognize that the relationship between attack and capture probabilities and predator energetic balance was based on very limited empirical data. Further refinement of these functions (Fig. 3 and Fig. 9) is needed to strengthen our conclusions on the relative importance of changes in movement parameters versus changes in attack and capture probabilities on gull hatching success. Overall, this study highlights how species traits and behaviors can lead to different mechanisms underlying similar indirect interaction outcomes (short-term apparent mutualism) between species sharing the same enemy.

Although landscape characteristics are known to modulate the strength of predator-prey interactions (Barrios-O'Neill et al., 2015; Englund et al., 2011), few studies have explicitly included their effects in functional response models (see the review by Cherif et al. 2024). The mechanistic model showed that changes in nest microhabitat generated variations in gull hatching success of 50% (for an average lemming density). In the Arctic, wetland degradation is anticipated to accelerate with global warming potentially leading to the formation of new refuges (islands), while some existing refuges may disappear (Corbeil-Robitaille et al., 2024). Although the net impact of these changes in refuge availability remains unknown, they could affect Arctic biodiversity by modulating the strength of predator-prey interactions. Accurately anticipating ecosystem responses thus depends on reliable estimates of predation rates and on a mechanistic understanding of these interactions. As emphasized by Cherif et al. (2024) and DeLong (2021), the development of accurate mechanistic models of predator-prey interactions is crucial for improving predictions of how food webs will respond to environmental changes.

6 Supplementary Methods

6.1 Parameter values used in the mechanistic model of predation

Table 1: Symbol definition and parameter values used in the multi-prey mechanistic model of fox predation as a function of the density of lemmings (prey 1), sandpiper nests (prey 2) and glaucous gull nests (prey 3). Parameter values for foxes, lemmings and sandpipers as well as methods used to obtain the values can be found in Beardsell et al. (2022) unless mentioned otherwise.

Parameter name	Symbol	Value(s) and unit	Additional information
Arctic Fox			
Daily proportion of time the predator spent active	ϕ_{active}	See Fig. 9	The value is function of N_1. Based on accelerometry data (23 summer foxes, 2018-2019).
Daily distance traveled when active	s	See Fig. 9; km day^{-1}	The value is function of N_1 and correlated to ϕ_{active}. Based on high-frequency GPS data (23 summer foxes, 2018-2019).
Average fox density	NR	0.13 ind. km^{-2}	Based on the average fox home range size in the study area (Beardsell et al., 2023).
Lemmings			
Lemming density	N_1	216 ind. km^{-2}	Average 216 ind. km^{-2} (range from 2 to 710 ind. km^{-2})
Maximum reaction distance	d_1	0.0075 km	Estimated distance from 29 observed attacks (from 1996-1999, 2019)
Average detection and attack probability within the reaction distance	$f_{2,1} \cdot f_{3,1}$	0.15	-
Capture probability	$f_{4,1}$	0.51	Direct observations of the outcome of 268 attacks (from 1996-2019)
Sandpiper nests			
Sandpiper nest density	N_2	2 nests km^{-2}	Average 2 nests km^{-2} (range from 0.25 to 4.25 nests km^{-2}) from 2005 to 2019.
Maximum reaction distance	d_2	0.085 km	Based on flushing distance (Smith and Edwards, 2018)
Average detection probability within the reaction distance	$f_{2,2}$	0.029	Based on flushing probability (Beardsell et al., 2021)
Glaucous gull nests			
Gull nest density	N_3	0.26 nests km^{-2}	Average 0.26 nests km^{-2} (range from 0.05 to 0.54 nests km^{-2}) from 2008 to 2016.
Proportion of nest in partial refuge (island)	p_r	0.75	From 262 nests monitored from 2004 to 2023.
Average clutch size	CS_3	2.6	From 175 nests monitored from 2004 to 2023.
Reaction distance (attack distance)	d_3	0.03 km	
Attack and capture probabilities of a nest on the shore	$f_{3,3_{sh}}$	See Fig. 3A	-
Attack and capture probabilities of a nest on an island	$f_{3,3_{is}}$	See Fig. 3A	-

6.1.1 Glaucous gull nest density

We calculated the average density of glaucous gull nests within Arctic fox home ranges monitored in the study area from 2008 to 2016 (n = 18 home ranges; data from Dulude et al. 2023; total area of 481 km^{-2}). Average nest density is 0.26 nests km^{-2} and ranges from 0.05 to 0.54 nests km^{-2}.

6.1.2 Reaction distance

The reaction distance on a gull nest was defined as the distance at which an attack can be initiated by the predator. We used the same value as for the greater snow goose (*Anser caerulescens atlanticus*) since glaucous gulls are similar in mass and color. The body mass of glaucous gull ranges from 1.25 kg to 2.7 kg and from 1.6 kg to 3.3 kg for the greater snow goose. This parameter was estimated from direct observations of foraging foxes on snow goose nests in summer 2019 (μ = 0.0328, se = 0.007, n = 25 attacks; Beardsell et al. 2021).

6.2 Parameter values of the energetic model

Table 2: Energetic parameters of the arctic fox and energetical content of all prey species.

Parameter	Symbol	Value(s) and unit
Predator body mass	M	3.231 kg
Predator basal metabolic rate (BMR)	E_b	472 KJ per day
Energetical content of a lemming (prey 1)	E_1	320 KJ per ind.
Energetical content of a sandpiper nest (prey 2)	E_2	262 KJ per nest
Energetical content of a glaucous gull nest (prey 3)	E_3	1965.6 KJ per nest

6.2.1 Predator body mass, M

From 2004 to 2022, the body mass of adult foxes captured at our study site averaged 3.231kg (sd = 0.409, n = 420 foxes).

6.2.2 Predator basal metabolic rate (BMR)

We used the equation presented in Careau et al. (2008) to estimate BMR based on the average fox mass (M):

$$BMR = -507 + 0.303 \cdot M \tag{11}$$

6.2.3 Energetic content of prey

Brown lemming is the most abundant species at our study site and adults weigh on average 51g (sd = 14 g, n = 1 450; from Seyer et al. 2020). Energetic content of a lemming was estimated at 6.276 KJ g^{-1} leading to 320 KJ for an average mass lemming. The energetic content estimate is based on the average of 220 animals (from 5 species of small mammals) analyzed with a calorimetric bomb (Górecki, 1965).

We estimated the energetic content of a sandpiper clutch (prey 2, E_2) at 262 KJ per nest. Eggs of White-rumped and Baird's sandpipers have a similar average mass of 9.32 g (Baird's sandpiper: sd = 0.67, n = 30 eggs from 8 clutches (Moskoff and Montgomerie, 2020) and White-rumped sandpiper: n = 4 eggs from 1 clutch (Parmelee, 2020)). Energetic content was estimated at 7.03 KJ g^{-1} based on the energetic content of *Cortunix* quail eggs (a similar egg size; Prelipcean et al. 2012) leading to 65.58 KJ per egg and 262 KJ per nest (clutch size of 4 eggs; Moskoff and Montgomerie

2020).

We estimated the energetic content of a glaucous gull clutch (prey 3, E_3) at 1965.6 KJ (based on an average clutch size of 2.6 eggs). Glaucous Gull eggs weigh on average 108 g (n = 31; Verboven et al. 2009) and their energetic content was estimated at 7 KJ g^{-1} based on the energetic content of herring gull (*Larus argentatus*) eggs (Hebert et al., 2020).

7 Supplementary Figures

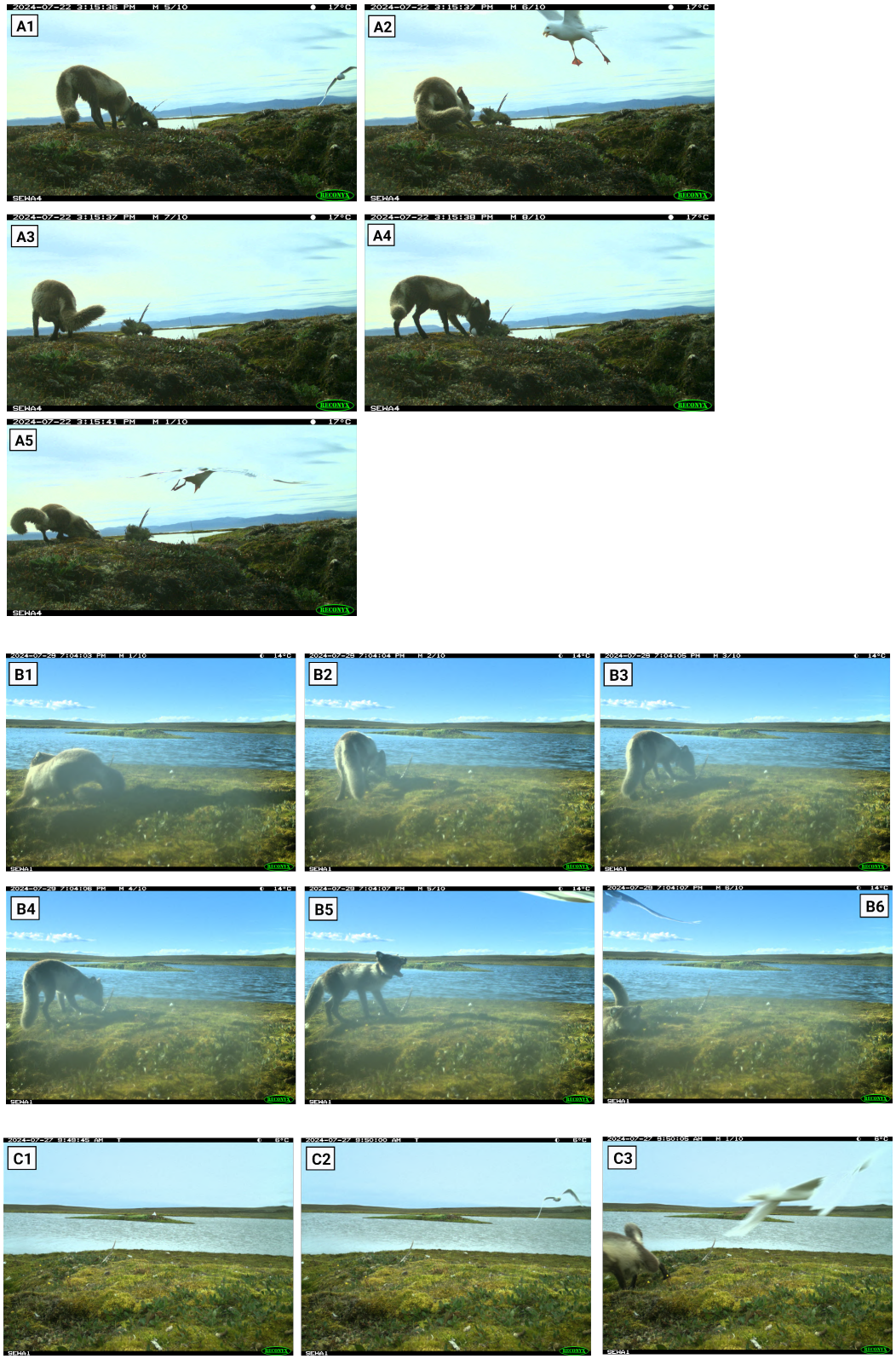

Figure 7: Image sequences (A, B and C) of interactions between foxes and nesting glaucous gulls on Bylot Island in July 2024.

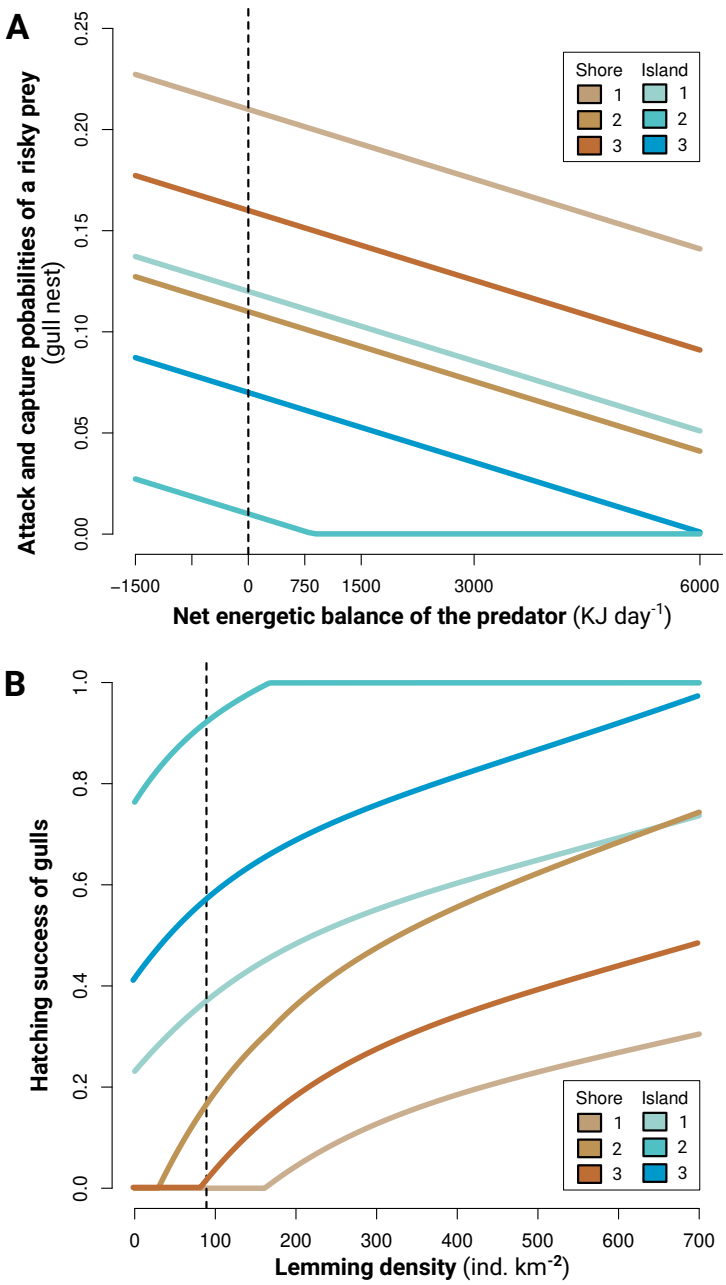

Figure 8: **A**) Simulations of three functions of attack and capture probabilities of a risky prey (gull nest) by the arctic fox in relation to the net energetic balance of the predator for the two habitats. Each colored line represents a different function. **B)** Relationship between hatching success of gull nests and lemming density in the two habitats predicted by the model based on the three functions presented in **A)**. Vertical black dashed line shows the threshold (predicted by the model) at which the net energetic balance of foxes changes from negative to positive.

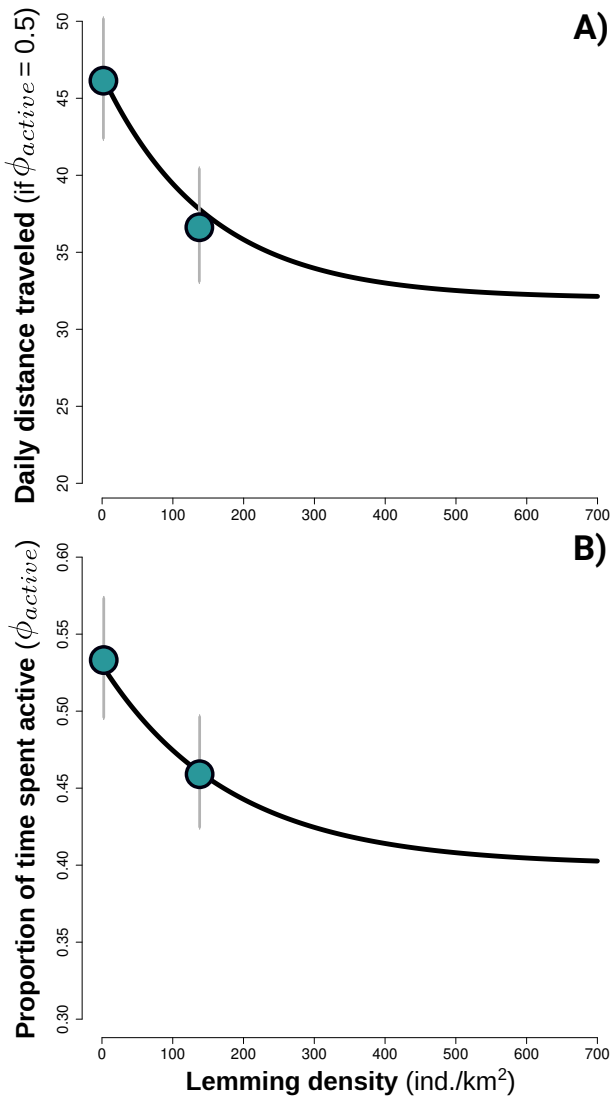

Figure 9: Relationships between lemming density and (A) the daily distance traveled by the arctic fox (when active), and (B) the proportion of time the arctic fox spent active in a day. Both parameters are positively correlated. Points show the predicted proportion of time spent active per day and predicted daily distance traveled by the fox between low and intermediate lemming densities (n = 371 fox-days). Error bars represent 95% confidence intervals. Relationships are from Beardsell et al. (2022) and are partially derived from empirical observations.

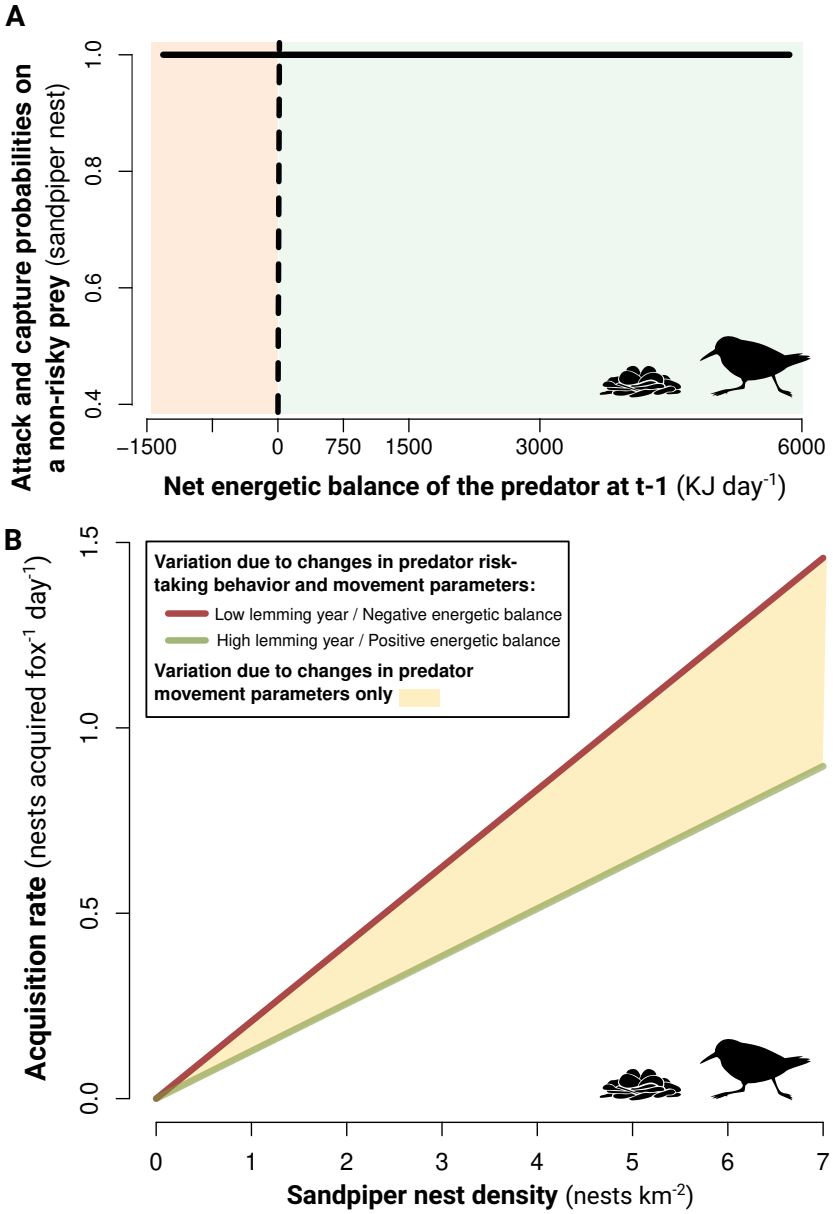

Figure 10: **A)** Relationship between attack and capture probabilities on a non-risky prey (sandpiper nest) by the arctic fox as a function of the net energetic balance of the predator (at time t-1). Areas where the net energetic balance is >0 are in green and <0 in red. **B)** Functional responses of the arctic fox to the non- risky prey (sandpiper nest) generated from the mechanistic multi-prey model for a negative (red lines) and positive (green lines) energetic balance of the predator. Positive and negative energetic balance correspond respectively to a lemming densities of 650 and 50 ind. per km^2. The shaded area is based on a model that excludes the effect of variations in predator risk-taking behavior and retains only changes in predator movement parameters (as a function of lemming density; Fig. S9) on sandpiper nest encounter rates. The density of gulls was set at the average value of 0.26 nests per km^2.

Literature Cited

Angerbjörn, A., M. Tannerfeldt, and S. Erlinge. 1999. Predator-prey relationships: Arctic foxes and lemmings. Journal of Animal Ecology, 68:34–49.

Barnett, C. A., M. Bateson, and C. Rowe. 2007. State-dependent decision making: Educated predators strategically trade off the costs and benefits of consuming aposematic prey. Behavioral Ecology, 18:645–651.

Barrios-O'Neill, D., J. T. Dick, M. C. Emmerson, A. Ricciardi, and H. J. Macisaac. 2015. Predator-free space, functional responses and biological invasions. Functional Ecology, 29:377–384.

Beardsell, A., D. Berteaux, F. Dulude-De-Broin, G. Gauthier, J. Clermont, D. Gravel, and J. Bêty. 2023. Predator-mediated interactions through changes in predator home range size can lead to local prey exclusion. Proceedings of the Royal Society B: Biological Sciences, 290.

Beardsell, A., D. Gravel, D. Berteaux, G. Gauthier, J. Clermont, V. Careau, N. Lecomte, C. C. Juhasz, P. Royer-Boutin, and J. Bêty. 2021. Derivation of predator functional responses using a mechanistic approach in a natural system. Frontiers in Ecology and Evolution, 9:630944.

Beardsell, A., D. Gravel, J. Clermont, D. Berteaux, G. Gauthier, and J. Bêty. 2022. A mechanistic model of functional response provides new insights into indirect interactions among arctic tundra prey. Ecology, e3734.

Beaudoin, M. 2025. Impact des îlots-refuges, de leurs caractéristiques physiques et des fluctuations d'abondance en proies sur le risque de prédation de nids d'oiseaux par le renard arctique. MSc thesis.

Berger-Tal, O., S. Mukherjee, B. P. Kotler, and J. S. Brown. 2009. Look before you leap: Is risk of injury a foraging cost? Behavioral Ecology and Sociobiology, 63:1821–1827.

Bergeron, G., G. Gauthier, F. Lutscher, P. Legagneux, D. Fauteux, J. Bêty, D. Berteaux, C. Hutchinson, and D. Gravel. 2025. Seasonal switches in food web composition unveil the complexity of an arctic predator-prey system. The American Naturalist. In Review.

Blecha, K. A., R. B. Boone, and M. W. Alldredge. 2018. Hunger mediates apex predator's risk avoidance response in wildland–urban interface. Journal of Animal Ecology, 87:609–622.

Bêty, J., G. Gauthier, J.-F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? interplay between nest density and predators. Oikos, 93:388–400.

Careau, V., J. F. Giroux, G. Gauthier, and D. Berteaux. 2008. Surviving on cached foods - the energetics of egg-caching by arctic foxes. Canadian Journal of Zoology, 86:1217–1223.

Chan, K., S. Boutin, T. J. Hossie, C. J. Krebs, M. O'Donoghue, and D. L. Murray. 2017. Improving the assessment of predator functional responses by considering alternate prey and predator interactions. Ecology, 98:1787–1796.

Cherif, M., U. Brose, M. R. Hirt, R. Ryser, V. Silve, G. Albert, R. Arnott, E. Berti, A. Cirtwill, A. Dyer, B. Gauzens, A. Gupta, H. C. Ho, S. M. Portalier, D. Wain, and K. Wootton. 2024. The environment to the rescue: can physics help predict predator–prey interactions? Biological Reviews, 33.

Chesson, P. L. 1984. Variable predators and switching behavior. Theoretical Population Biology, 26.

Clode, D., J. D. S. Birks, and D. W. Macdonald. 2000. The influence of risk and vulnerability on predator mobbing by terns ({Sterna spp.}) and gulls ({Larus spp.}). Journal of Zoology, 252:53–59.

Corbeil-Robitaille, M.-Z., Éliane Duchesne, D. Fortier, C. Kinnard, and J. Bêty. 2024. Linking geomorphological processes and wildlife micro-habitat selection : nesting birds select refuges generated by permafrost degradation in the arctic. Biogeosciences, 21:3401–3423.

DeLong, J. P. 2021. Predator Ecology : Evolutionary Ecology of the Functional Response. Oxford University Press.

Dulude, D. B. F., J. Clermont, A. Beardsell, L.-P. Ouellet, P. Legagneux, J. Bêty, and D. Berteaux. 2023. Predator home range size mediates indirect interactions between prey species in an arctic vertebrate community. Journal of Animal Ecology, pages 1–13.

Elmhagen, B., M. Tannerfeldt, P. Verucci, and A. Angerbjörn. 2000. The arctic fox ({Alopex lagopus}): an opportunistic specialist. Journal of Zoology London, pages 139–149.

Embar, K., A. Raveh, D. Burns, and B. P. Kotler. 2014. To dare or not to dare? risk management by owls in a predator-prey foraging game. Oecologia, 175:825–834.

Englund, G., G. Öhlund, C. L. Hein, and S. Diehl. 2011. Temperature dependence of the functional response. Ecology Letters, 14:914–921.

Fauteux, D., G. Gauthier, and D. Berteaux. 2015. Seasonal demography of a cyclic lemming population in the canadian arctic. Journal of Animal Ecology, 84:1412–1422.

Fauteux, D., G. Gauthier, M. J. Mazerolle, N. Coallier, J. Bêty, and D. Berteaux. 2018. Evaluation of invasive and non-invasive methods to monitor rodent abundance in the arctic. Ecosphere, 9:1–18.

Forrester, G. E. and M. A. Steele. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology, 85:1332–1342.

Fryxell, J. M., A. Mosser, A. R. Sinclair, and C. Packer. 2007. Group formation stabilizes predator-prey dynamics. Nature, 449:1041–1043.

Fuglei, E., N. A. Øritsland, and P. Prestrud. 2003. Local variation in arctic fox abundance on svalbard, norway. Polar Biology, 26:93–98.

Garland, T. J. 1983. Scaling the energetic cost of transport to body mass in terrestrial mammals. American Naturalist, 121:571–587.

Gauthier, G., D. Berteaux, J. Bêty, P. Legagneux, D. Fauteux, D. Gravel, and M.-C. Cadieux. 2024*a*. Scientific contributions and lessons learned from 30 years of ecological monitoring of the bylot island tundra ecosystem. Frontiers in Ecology and Evolution, pages 1–13.

Gauthier, G., J. Bêty, M.-C. Cadieux, P. Legagneux, M. Doiron, C. Chevallier, S. Lai, A. Tarroux, and D. Berteaux. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the canadian arctic tundra. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 368.

Gauthier, G., D. Ehrich, M. Belke-brea, F. Domine, R. Alisauskas, K. Clark, F. Ecke, N. E. Eide, E. Framstad, J. Frandsen, O. Gilg, H. Henttonen, B. Hörnfeldt, T. Oksanen, J. Olofsson, G. Samelius, B. Sittler, and N. M. Schmidt. 2024*b*. Taking the beat of the arctic : are lemming population cycles changing due to winter climate ? Proceedings of the Royal Society: Biological Sciences.

Gauthier, G., P. Legagneux, M.-A. Valiquette, M.-C. Cadieux, and J.-F. Therrien. 2015. Diet and reproductive success of an arctic generalist predator: Interplay between variations in prey abundance, nest site location, and intraguild predation. The Auk, 132:735–747.

Girard, I. 2001. Field cost of activity in the kite fox, vulpes macrotis. Physiological and Biochemical Zoology, 74:191–202.

Giroux, M.-A., D. Berteaux, N. Lecomte, G. Gauthier, G. Szor, and J. Bêty. 2012. Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator. Journal of Animal Ecology, 81:533–542.

Gorman, M. L., M. G. Mills, J. P. Raath, and J. R. Speakman. 1998. High hunting costs make african wild dogs vulnerable to kleptoparasitism by hyaenas. Nature, 391:479–481.

Gruyer, N., G. Gauthier, and D. Berteaux. 2008. Cyclic dynamics of sympatric lemming populations on bylot island, nunavut, canada. Canadian Journal of Zoology, 86:910–917.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator–prey interactions in the anthropocene: Reconciling multiple aspects of novelty. Trends in Ecology and Evolution, 34:616–627.

Górecki, A. 1965. Energy values of body in small mammals. Acta Theriologica, 23:333–352.

Hebert, C. E., D. V. Weseloh, M. T. Arts, S. R. de Solla, D. J. Moore, G. Paterson, and C. Pekarik. 2020. Trends in herring gull egg quality over four decades reflect ecosystem state. Journal of Great Lakes Research, 46:538–548.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist, pages 385–398.

Juhasz, C., B. Shipley, G. Gauthier, D. Berteaux, and N. Lecomte. 2020. Direct and indirect effects of regional and local climatic factors on trophic interactions in the arctic tundra. Journal of Animal Ecology, 89:704–715.

Kiørboe, T., E. Saiz, P. Tiselius, and K. H. Andersen. 2018. Adaptive feeding behavior and functional responses in zooplankton. Limnology and Oceanography, 63:308–321.

Lai, S., J. Bêty, and D. Berteaux. 2017. Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the high arctic. Oikos, 126:937–947. URL http://doi.wiley.com/10.1111/oik.03948.

Lecomte, N., V. Careau, G. Gauthier, and J. F. Giroux. 2008. Predator behaviour and predation risk in the heterogeneous arctic environment. Journal of Animal Ecology, 77:439–447.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology, 68:619–640.

Lyon, S. R., C. A. Sjulin, K. M. Sullivan, and J. P. DeLong. 2018. Condition-dependent foraging in the wolf spider hogna baltimoriana. Food Webs, 14:5–8.

Moran, N. P., A. Sánchez-Tójar, H. Schielzeth, and K. Reinhold. 2021. Poor nutritional condition promotes high-risk behaviours: a systematic review and meta-analysis. Biological Reviews, 96:269–288.

Moskoff, W. and R. Montgomerie. 2020. Baird's sandpiper (calidris bairdii), version 1.0. in birds of the world (a. f. poole and f. b. gill, editors). URL https://birdsoftheworld.org/bow/species/baisan/cur/introduction.

Mukherjee, S. and M. R. Heithaus. 2013. Dangerous prey and daring predators: A review. Biological Reviews, 88:550–563.

Murdoch, W. W. 1969. Switching in general predators : Experiments on predator specificity and stability of prey populations. Ecological Monographs, 39:335–354.

Parmelee, D. F. 2020. White-rumped Sandpiper (Calidris fuscicollis). Cornell Lab of Ornithology.

Pawar, S., A. I. Dell, and V. M. Savage. 2012. Dimensionality of consumer search space drives trophic interaction strengths. Nature, 486:485–489.

Perlman, Y. and I. Tsurim. 2008. Daring , risk assessment and body condition interactions in steppe buzzards buteo buteo vulpinus. pages 226–228.

Poulin, M.-P., J. Clermont, and D. Berteaux. 2021. Extensive daily movement rates measured in territorial arctic foxes. Ecology and Evolution, 11:2503–2514.

Prelipcean, A., A. A. Prelipcean, and V. Teuşan. 2012. Investigations on the structure, chemical composition and caloricity of the quail eggs, deposited at the plateau phase of the laying period.

Prokopenko, C. M., T. Avgar, A. Ford, and E. V. Wal. 2023. Optimal prey switching: Predator foraging costs provide a mechanism for functional responses in multi-prey systems. Ecology, 104:1–15.

{R Core Team}. 2024. R: A language and environment for statistical computing. URL https://www.r-project.org/.

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. Philosophical Transactions of the Royal Society B: Biological Sciences, 367:2923–2934.

Real, L. A. 1977. The kinetics of functional response. American Naturalist, 111:289–300.

Samelius, G. and R. T. Alisauskas. 2000. Foraging patterns of arctic foxes at a large arctic goose colony. Arctic, 53:279–288.

Seyer, Y., G. Gauthier, D. Fauteux, and J. F. Therrien. 2020. Resource partitioning among avian predators of the arctic tundra. Journal of Animal Ecology, 89:2934–2945.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. The Auk, 121:526–540.

Smith, P. A. and D. B. Edwards. 2018. Deceptive nest defence in ground-nesting birds and the risk of intermediate strategies. PLoS ONE, 13:1–12.

Studd, E. K., R. Derbyshire, A. K. Menzies, J. Simms, M. M. Humphries, D. L. Murray, and S. Boutin. 2021. The purrfect catch: using accelerometers and audio recorders to document kill rates and hunting behaviour of a small prey specialist, the canada lynx. Methods in Ecology and Evolution, 12:1277–1287.

Summers, R. W., L. G. Underhill, and E. E. S. JR. 1998. The breeding productivity of dark-bellied brent geese and curlew sandpipers in relation to changes in the numbers of arctic foxes and lemmings on the taimyr peninsula, siberia. Ecography, 21:573–580.

Suraci, J. P., J. A. Smith, S. Chamaillé-Jammes, K. M. Gaynor, M. Jones, B. Luttbeg, E. G. Ritchie, M. J. Sheriff, and A. Sih. 2022. Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. Oikos, 2022:1–15.

Taylor, C. R., N. C. Heglund, and G. M. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion. Journal of Experimental Biology, 97:1–21.

Underhill, L. G., R. P. Prŷs-Jones, E. E. S. JR., N. M. Groen, V. Karpov, H. G. Lappo, M. W. J. V. Roomen, A. Rybkin, H. Schekkerman, H. Spiekman, and R. W. Summers. 1993. Breeding of waders (charadrii) and brent geese branta bernicla bernicla at pronchishcheva lake, northeastern taimyr, russia, in a peak and a decreasing lemming year. Ibis, 135:277–292. Https://doi.org/10.1111/j.1474-919X.1993.tb02845.x.

Verboven, N., J. Verreault, R. J. Letcher, G. W. Gabrielsen, and N. P. Evans. 2009. Differential investment in eggs by arctic-breeding glaucous gulls (larus hyperboreus) exposed to persistent organic pollutants. Auk, 126:123–133.

Wheatley, R., T. P. Pavlic, O. Levy, and R. S. Wilson. 2020. Habitat features and performance interact to determine the outcomes of terrestrial predator–prey pursuits. Journal of Animal Ecology, 89:2958–2971.

Williams, T. M., L. Wolfe, T. Davis, T. Kendall, B. Richter, Y. Wang, C. Bryce, G. H. Elkaim, and C. C. Wilmers. 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. Science, 346:81–85.

Wootton, K. L., A. Curtsdotter, T. Roslin, R. Bommarco, and T. Jonsson. 2021. Toward a modular theory of trophic interactions. Functional Ecology, 00:1–18.