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ARTICLE

A mechanistic model of functional response provides new insights into indirect interactions among arctic tundra prey

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Abstract

Prey handling processes are considered a dominant mechanism leading to short-term positive indirect effects between prey that share a predator. However, a growing body of research indicates that predators are not necessarily limited by such processes in the wild. Density-dependent changes in predator foraging behavior can also generate positive indirect effects but they are rarely included as explicit functions of prey densities in functional response models. With the aim of untangling proximate mechanisms of species interactions in natural communities and improving our ability to quantify interaction strength, we extended the multi-prey version of the Holling disk equation by including density-dependent changes in predator foraging behavior. Our model, based on species traits and behavior, was inspired by the vertebrate community of the arctic tundra, where the main predator (the arctic fox) is an active forager feeding primarily on cyclic small rodent (lemming) and eggs of various tundra-nesting bird species. Short-term positive indirect effects of lemmings on birds have been documented over the circumpolar Arctic but the underlying mechanisms remain poorly understood. We used a unique data set, containing high-frequency GPS tracking, accelerometer, behavioral, and experimental data to parameterize the multi-prey model, and a 15-year time series of prey densities and bird nesting success to evaluate interaction strength between species. We found that (1) prey handling processes play a minor role in our system and (2) changes in arctic fox daily activity budget and distance traveled can partly explain the predation release on birds observed during lemming peaks. These adjustments in predator foraging behavior with respect to the main prey density thus appear as the dominant mechanism leading to positive indirect effects commonly reported among arctic tundra prey. Density-dependent changes in functional response components have been little studied in natural vertebrate communities and deserve more attention to improve our ability to quantify the strength of species interactions.

KEYWORDS

arctic fox (*Vulpes lagopus*), indirect effects, lemmings, multi-prey, nonlinear species interactions, passerines, predation, predator–prey interactions, sandpipers

INTRODUCTION

Interactions between predator and prey in natural communities are difficult to describe quantitatively. Various mathematical models have been used to quantify prey acquisition by the predator and to investigate the nature and the strength of species interactions within food webs (Abrams et al., 1998; Baudrot et al., 2016; Chan et al., 2017; Pawar et al., 2012). Several studies have compared how a predator acquisition rate varies with prey density using statistical approaches (reviewed by Novak and Stouffer 2020), but few of them explicitly tackled the underlying mechanisms. Although empirical data may be consistent with various functional response models, this does not provide clear insight into the mechanisms underpinning interaction strengths. Moreover, the sample size is often insufficient to obtain the statistical power needed to properly discriminate between different models (Novak & Stouffer, 2020). Process-based mechanistic models (hereafter referred to as mechanistic models) may help in untangling proximate mechanisms of species interactions (Connolly et al., 2017; Griffen, 2021) and can improve our ability to adequately quantify the strength of interactions in natural communities (Beardsell et al., 2021; DeLong et al., 2021; Spalinger & Hobbs, 1992).

The multi-species version of the Holling (1959) disk equation (Murdoch & Oaten, 1975) is widely used to model predation rates in multi-prey systems and assumes a saturation of predator acquisition rates with increasing prey availability due to rate-limiting handling processes (Barraquand et al., 2015; Brose et al., 2005; McLellan et al., 2010; Serrouya et al., 2015). The summation of the handling time of all prey items is a critical component of this equation and can generate indirect interactions among prey. Increasing abundance of one species saturates the predator because of its limited prey handling capacities (which includes the time needed to pursue, catch, and manipulate a prey item; Jeschke et al. 2002) and thereby indirectly releases predation pressure on other prey. This equation is often at the core of more complex food web models (Barrios-O'Neill et al., 2019; Schneider et al., 2016; Tyson & Lutscher, 2016) and handling time is considered a dominant mechanism inducing short-term positive effects among prey (Abrams, 1987; Abrams et al., 1998; Abrams & Matsuda, 1996). However, the role of handling processes in predator-mediated interactions lacks definitive evidence in the wild and a growing body of research indicates that predators are not necessarily limited by handling processes at the highest prey densities observed in natural systems (Beardsell et al., 2021; Chan et al., 2017; Jeschke et al., 2002; Novak, 2010; Preston et al., 2018).

It is unlikely that predators simply acquire more prey at a rate proportional to their abundance. Non-linearities in functional responses are capable of influencing predation

rates via several mechanisms. For instance, the density of a prey may modulate the predator state (e.g., hunger level, reproductive status), which in turn could have an impact on other prey consumed by that predator. Although a dependence of some components of the functional response to prey density have long been recognized as biologically plausible (Abrams, 1982; Hassell et al., 1977), its potential importance for predator acquisition rates has been little studied empirically (but see Okuyama 2010, 2012), and it is rarely included as explicit functions of prey density in functional response models (Stouffer & Novak, 2021). Yet, changes in predator foraging behavior according to prey density can generate positive effects between prey species (Abrams & Matsuda, 1993; Abrams & Matsuda, 1996) and warrant additional attention in natural predator-prey systems (Stouffer & Novak, 2021).

Our objectives were twofold. First, we developed a mechanistic model of acquisition rates that includes a dependence in both predator handling time and foraging behavior on the main prey density. Second, we illustrated this model using the predator-prey dynamics of a multi-prey system in the arctic tundra to identify the proximate mechanisms of the well-known short-term positive indirect effects of cyclic rodents on nesting birds. This type of predator-mediated effect is widespread between prey sharing a predator and can affect species abundance and coexistence in various ecosystems (Bonsall & Hassell, 1997; Duchesne et al., 2021). We evaluated three hypotheses that could explain such indirect interactions (Table 1 and Figure 1). The first hypothesis was based on the multi-prey version of the Holling (1959) disk equation, in which prey handling processes reduce the time available to search for other prey and result in positive indirect effects between prey. The second and the third hypotheses extended the multi-prey model to include prey density-dependent effect on prey handling time and on predator foraging behavior, respectively (Table 1).

We developed the multi-prey mechanistic model for the arctic fox, an active-searching top predator of the arctic tundra that feeds primarily on lemmings, as well as on bird eggs during the summer (Angerbjörn et al., 1999; Giroux et al., 2012). Within this predator-prey system, lemmings are the most abundant prey and show population cycles with a maximum density occurring every 3–5 years (Fauteux et al., 2015). Fox predation pressure on eggs of ground-nesting birds is generally released when lemming density is high, leading to short-term positive indirect effects of lemmings on bird nesting success (McKinnon et al., 2014; Nolet et al., 2013; Summers et al., 1998). This classic example of predator-mediated effects among vertebrates was studied across the circumpolar arctic but the underlying proximate mechanisms remain unclear (McKinnon et al., 2014; Nolet et al., 2013; Summers et al., 1998; Underhill et al., 1993). We parameterized the model using a combination of behavioral,

TABLE 1 Three hypothesized mechanisms underlying the short-term positive effects of a cyclic prey (prey 1; lemmings) on two prey species (prey 2 and 3; passerine and sandpiper nests, respectively) through a common predator (arctic fox)

Predation component	Density-dependent component	Hypothesized mechanism	Application to a multi-prey community in the Arctic
Prey handling time	None	Constraints on predator foraging such as the time required to handle (chasing, manipulating) prey may lead to positive indirect effects because time spent handling one prey reduces the time available for searching other prey (Holt, 1977). The average handling time per prey is independent of prey density	As lemming density increases, foxes spend more time handling lemmings, reducing the time available to search for passerine and sandpiper nests
Prey handling time through prey delivery	Positively related to prey density	Prey density commonly influences predator investment in reproduction (Gilg et al., 2003; Terraube et al., 2015). Central place foragers must often return to a specific location (e.g., nest, den) to feed their offspring. Prey delivery is therefore part of handling time, and as investment in reproduction increases (e.g., litter size, which may depend on prey abundance), the probability of prey delivery increases. This process results in a relationship between prey handling time and prey density	The breeding probability of a fox pair increases with summer lemming density (Juhasz et al., 2020). During breeding, which overlaps with the nesting period of birds, foxes primarily bring lemmings back to their dens, which increases the time spent handling the retrieved prey. Thus, the time foxes spent handling lemmings increases with lemming density through prey delivery
Predator activity time and distance traveled	Both parameters negatively related to prey density	Predators adjust the amount of time devoted to foraging, resting, and reproductive behaviors with prey availability (Busdieker et al., 2019; Harding et al., 2007). This behavioral flexibility may result in reduced foraging effort as prey density increases (Harding et al., 2007) or in increased time-consuming behaviors associated with reproduction (e.g., parental care)	There are two non-exclusive processes. First, when lemming densities increase, foxes can decrease their foraging effort. Second, when lemming densities are high enough, foxes breed and females can increase time spent near the den (for lactation/parental care before cubs emerge). This period overlaps with the nesting period of birds. At high lemming densities, those processes can translate into a decrease in fox distance traveled and activity time during the bird nesting period

demographic, and experimental data acquired over 20 years in the high arctic tundra. As a previous mechanistic single-prey model indicated that the arctic fox is not limited by handling processes at the highest lemming densities observed in our study system (Beardsell et al., 2021), we expected changes in the predator foraging behavior in relation to lemming density to be the dominant mechanism of the short-term positive effects of lemmings on arctic bird nesting success.

METHODS

Study system

The mechanistic model of multi-prey functional response was developed using data from a long-term ecological

monitoring on Bylot Island, Nunavut, Canada (73° N; 80° W). Two cyclic species of small mammals are present, the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings. Ground-nesting birds present include passerines (mostly Lapland Longspur, *Calcarius lapponicus*) and sandpipers (primarily Baird’s Sandpiper (*Calidris bairdii*) and White-rumped Sandpiper (*Calidris fuscicollis*)). The monitoring area of lemmings, and passerine and sandpiper nests is located within the Qarlikturvik Valley (72°85’ N, 78°85’ W). Sandpipers and passerines nest at relatively low densities (2 and 7 nests/km² on average, respectively). During the breeding season (June–July), passerines and sandpipers lay an average of five and four eggs, which they incubate for 12 and 21 days, respectively (Gauthier et al., 2013; Hussell & Montgomerie, 2020; McKinnon et al., 2014). Sandpiper

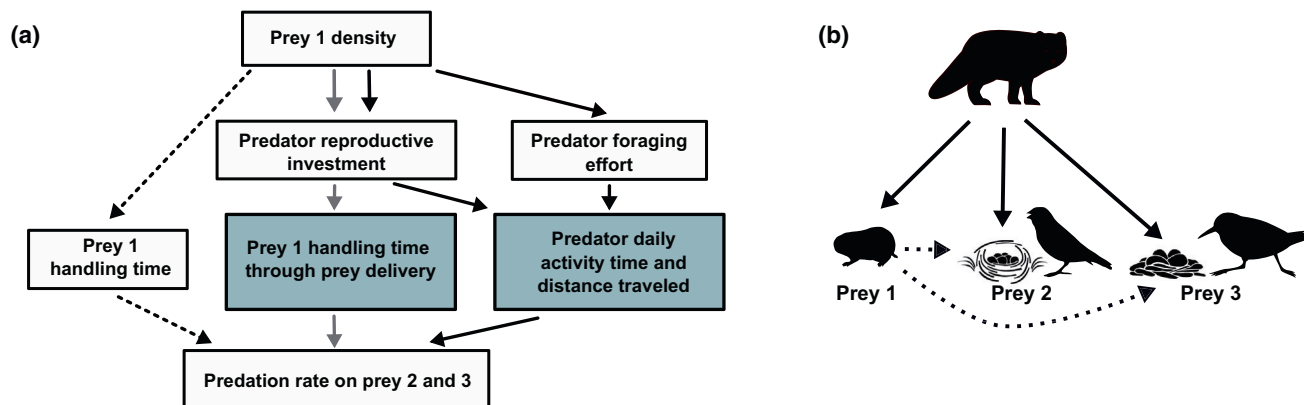


FIGURE 1 (a) Schematic representation of three hypothesized mechanisms underlying the short-term positive effect of a cyclic prey (prey 1, lemmings) on two prey species (prey 2 and 3, passerine and sandpiper nests, respectively) through a common predator (arctic fox). Different arrows (dotted, gray, and black) correspond to each hypothesis described in Table 1. The blue boxes indicate the parameters where prey density-dependence was included. (b) Diagram of a simplified arctic food web indicating the direct (solid arrows) and indirect (dotted arrows) links between the predator (arctic fox), prey 1 (lemmings), prey 2 (passerine nests), and 3 (sandpiper nests)

chicks typically leave the nest within 24 h of hatching (McKinnon et al., 2014), while passerine chicks remain in the nest for 9–10 days (Hussell & Montgomerie, 2020).

The arctic fox is the main egg predator of ground-nesting birds on Bylot Island (McKinnon & B ty, 2009; Royer-Boutin, 2015). The nesting period for birds (typically mid-June to early mid-July) overlaps with the lactation period for foxes. Fox gestation period is around 52 days and births usually occur in late May on Bylot Island (Audet et al., 2002; Morin, 2015). Fox cubs are weaned after 6–7 weeks (Audet et al., 2002). Arctic foxes maintain summer territories (averaging 10 km²) with little overlap (Grenier-Potvin et al., 2021), which limits interference between foxes within territories. Also, foxes rarely encounter and interact with other individuals while foraging within their summer territory (Beardsell et al., 2021). The number of territorial adult foxes remains relatively constant between summers, even if the breeding success of foxes is strongly influenced by lemming cycles (Juhasz et al., 2020; Royer-Boutin, 2015). Like many other animals (Vander Wall, 1990), arctic foxes generally predate more prey than they immediately consume (with associated food hoarding behavior) and thus hide a large proportion of the prey they capture (Careau et al., 2007; Samelius & Alisauskas, 2000).

The monitoring area of passerine and sandpiper nests is located ~30 km away from a colony of Greater Snow Geese (*Anser caerulescens atlanticus*). We excluded geese from the model since they are virtually absent and isotopic studies confirmed that the contribution of goose eggs to the fox diet was limited in the monitoring area (Giroux et al., 2012). However, fox movement data (GPS and accelerometer) used to parameterize the model were collected within the goose colony. Snow geese can influence fox habitat selection and

diet within the colony (Giroux et al., 2012; Grenier-Potvin et al., 2021). Such effects could slightly bias the average values of a few parameters used in our models (e.g., daily distance traveled, time spent active). However, we are highly confident that the effect of lemming fluctuations on fox behavior is relatively similar across the landscape because fox reproduction and predation pressure on bird nests are strongly influenced by lemming density both inside and outside the goose colony (Duchesne et al., 2021; Giroux et al., 2012; Lamarre et al., 2017).

Deriving mechanistic models of multi-prey functional response

General model description and model without density-dependence (model A)

The multi-prey mechanistic functional response model was derived by breaking down the predation process into steps. Our approach follows the theoretical framework proposed by Wootton et al. (2021) and we built on a mechanistic model that was developed for fox–prey dyads (Beardsell et al., 2021). Fox predation was decomposed into a maximum of six steps depending on the prey species: (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) subjugation, and (6) manipulation. Each step was adapted to each prey species according to their anti-predator behavior and the fox behavior observed during the bird nesting season (Beardsell et al., 2021). Figure 2 provides an overview of the mechanistic model (prey 1 is lemmings, prey 2 is passerine nests, and prey 3 is sandpiper nests).

For the three prey species ($i = 1, 2, 3$), the area searched ($A_{\text{search},i}$, km²) by the predator is expressed by the product

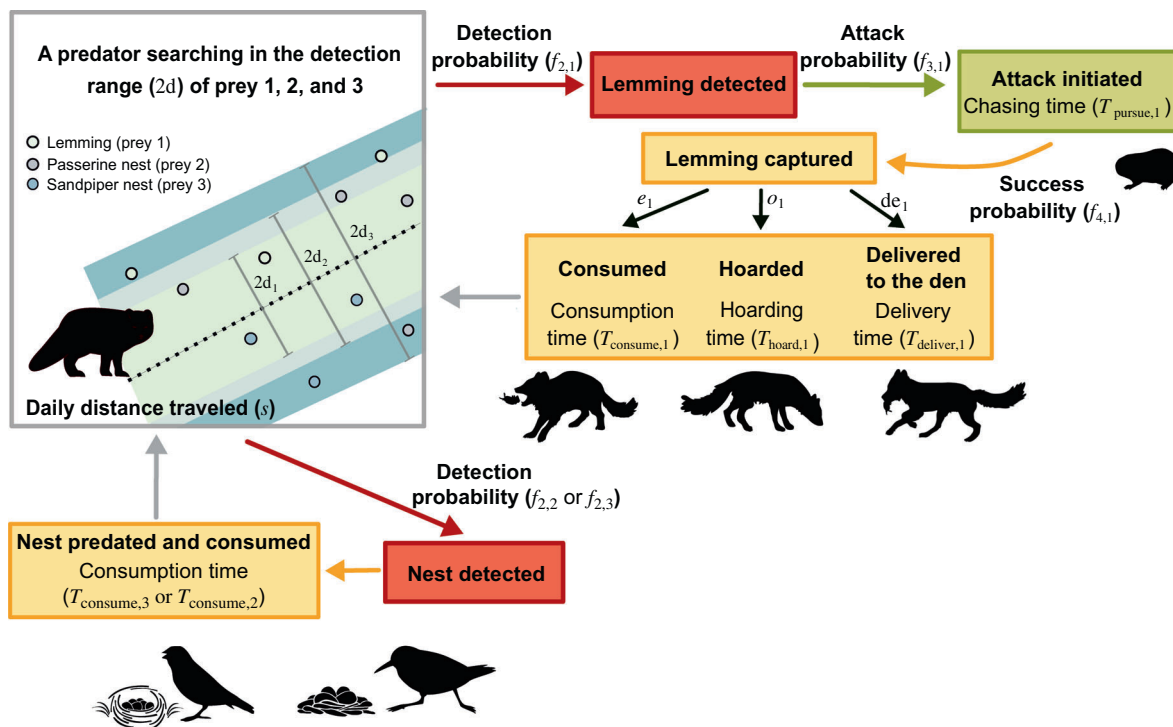


FIGURE 2 Conceptual mechanistic model of predator (arctic fox) functional response to density of a cyclic prey (prey 1; lemmings) and other prey species (prey 2 and 3; ground-nesting birds). The boxes represent the components of predation (search, prey detection, attack decision, pursuit, subjugation and manipulation). Arrows represent the probability that the predator reaches the next component. When there is no parameter near the arrow, the probability to reach the next component is assumed to be 1. The model represented has no prey density dependence in the parameters. Parameters are defined in section “Methods”: “Deriving mechanistic models of multi-prey functional response”: “General model description and model without density-dependence (model A)”

of the daily distance traveled when the predator is active (s , km/day), the reaction distance to a prey item (d_i , km), and the time spent searching (T_{search} , day):

$$A_{search,i} = s \times (2d_i) \times T_{search} \quad (1)$$

A potential encounter occurs between the predator and a prey item i when the predator is at a distance (d_i), being defined as the maximum distance at which the predator can detect a prey item i (in 2D, detection region = $2d_i$; Pawar et al., 2012).

As not all lemmings within the searched area may be detected, attacked, and subdued by the arctic fox, we introduced the detection probability ($f_{2,1}$), the attack probability ($f_{3,1}$), and the success probability of an attack ($f_{4,1}$). Capture efficiency of a lemming (α_1 , km²/day) by the predator is expressed by

$$\alpha_1 = s \times (2d_1) \times f_{2,1} \times f_{3,1} \times f_{4,1}. \quad (2)$$

For passerine (prey 2) and sandpiper nests (prey 3), the capture efficiency is simply the product of s , the reaction distance (d_2 or d_3 , km) and the detection probability ($f_{2,2}$

or $f_{2,3}$), because their nests are always predated when detected (the attack and success probabilities = 1).

Handling time per lemming (h_1 , day/prey item) sums the time spent chasing (means of successful and unsuccessful attacks) and the time spent manipulating a lemming once subdued. The average chase time for a successful and a failed attack is slightly different (110 and 70 s, respectively [$n = 230$ attacks]). Adding this source of variation in handling time to the model had negligible effects on predator acquisition rates. The manipulation time of lemmings is divided in three mutually exclusive behaviors: the lemming is either (1) consumed, (2) hoarded, or (3) delivered (Careau et al., 2007). The handling time of lemmings is hence expressed as follows:

$$h_1 = \frac{T_{pursue,1}}{f_{4,1}} + (T_{consume,1} \times e_1 + T_{hoard,1} \times o_1 + T_{deliver,1} \times de_1) \quad (3)$$

where e_1 , o_1 , and de_1 are respectively the probability that a lemming is consumed, hoarded, or delivered to the den. The sum of e_1 , o_1 , and de_1 equals 1. $T_{consume,1}$, $T_{hoard,1}$, and $T_{deliver,1}$ are the average amount of time each behavior

lasted. As many other carnivores (Jeschke, 2007), arctic foxes probably often meet or exceed their daily energy requirements during the summer. However, there is no evidence that short-term energy needs influence arctic fox behavior since they can harvest more prey than they consume in the short term and also cache prey for later consumption (e.g., during winter; Careau et al., 2007). Hence, prey digestion time was not included in the model. As passerines and sandpipers are unable to defend their clutches against arctic foxes (Hussell & Montgomerie, 2020; Smith & Edwards, 2018), their nests are always predated when detected (negligible chasing time) and consumed immediately upon detection (Beardsell et al., 2021). Thus, the handling time of passerine and sandpiper nests (h_2 and h_3) includes only the time spent consuming the nest ($T_{\text{consume},2}$ and $T_{\text{consume},3}$).

The number of prey captured ($V_{\alpha i}$) is the product of the time spent searching (T_{search} , day) and the prey density (N_i , number of i km²):

$$V_{\alpha i} = \alpha_i \times T_{\text{search}} \times N_i. \quad (4)$$

The total time available in a day (T_{total}) is multiplied by the proportion of time spent active by the predator in a day (φ_{active}) and by the time spent handling prey 1, 2, and 3 if subdued:

$$T_{\text{search}} = T_{\text{total}} \times \varphi_{\text{active}} - V_{\alpha 1} \times h_1 - V_{\alpha 2} \times h_2 - V_{\alpha 3} \times h_3. \quad (5)$$

Substituting T_{search} from Equation 5 into Equation 4 and by dividing it by T_{total} to express the number of prey 1 acquired per predator per day ($\text{FR}_1(N_1, N_2, N_3)$), we obtain the following final formulation:

$$\text{FR}_1(N_1, N_2, N_3) = \frac{\varphi_{\text{active}} \times \alpha_1 \times N_1}{1 + \alpha_1 \times h_1 \times N_1 + \alpha_2 \times h_2 \times N_2 + \alpha_3 \times h_3 \times N_3} \quad (6)$$

An equivalent equation for the predator acquisition rate on prey 2 and 3 can be obtained by substituting all 1 for 2 (or 3) in Equation 6 and vice versa. Equation 6 is the basic model, without density dependence in the predation components (model A). In model A, positive indirect effects between prey species can be generated only through prey handling processes. Below, we provide details on the inclusion of prey density dependence on some components in models B and C.

Models including prey density-dependence (models B and C)

We added a dependence on lemming density in the probability that a lemming is delivered to the den (model B; see Table 1) by modifying Equation 3 as follows:

$$h_1 = \frac{T_{\text{pursue},1}}{f_{4,1}} + (T_{\text{consume},1} \times e_1 + T_{\text{hoard},1} \times o_1 + T_{\text{deliver},1} \times de_1(N_1)). \quad (7)$$

We added a dependence on lemming density in the daily distance traveled (s), and proportion of time spent active (φ_{active} ; model C; see Table 1) by modifying Equations 2 and 5 as follows:

$$\alpha_1 = s(N_1) \times (2d_1) \times f_{2,1} \times f_{3,1} \times f_{4,1} \quad (8)$$

$$T_{\text{search}} = T_{\text{total}} \times \varphi_{\text{active}}(N_1) - V_{\alpha 1} \times h_1 - V_{\alpha 2} \times h_2 - V_{\alpha 3} \times h_3. \quad (9)$$

Although φ_{active} and s can be expressed as a function of all prey species densities, we have only considered lemming density as sandpipers and passerines nest at low densities (7 and 2 nests/km² on average, respectively). As arctic foxes cache a large proportion of prey they capture (Careau et al., 2007), we also assume that the proportion of time spent active is not affected by the rate of prey capture in the previous days.

Parameter values

From June to August 2018 and 2019, 16 foxes (seven females and nine males) were fitted with high-frequency GPS collars and triaxial accelerometers (95 g, 2.6%–3.3% of body mass; Radio Tag-14, Milsar, Romania) to monitor their movements and behaviors. Of these, seven were equipped in both years, for a total of 23 summer foxes (eight foxes in 2018 and 15 in 2019). Foxes were captured using cage traps (Tomahawk Live Trap Company, USA) or Softcatch #1 padded leghold traps (Oneida Victor Inc. Ltd., USA). GPS fix intervals were set to 4 min (360 fixes/day) and the location error was 11 m (Poulin et al., 2021); 30-s bursts of accelerometry data were collected every 4.5 min at 50 Hz (320 bursts/day; Clermont, Gagné, and Berteaux 2021). We extracted the daily activity budget of foxes from accelerometry data (Clermont, Gagné, & Berteaux, 2021). We estimated the proportion of time spent active by subtracting the proportion of time spent resting from 1. We estimated an average proportion of time spent active using a linear mixed model with year and individual-fox as random effects. The average proportion of time spent active in a day (φ_{active}) was 0.50 ($n = 371$ fox-days; 95% CI [0.40–0.60]; Table 2) and ranged from 0.29 to 0.64.

The distance traveled by foxes each day (km/day) was estimated by adding linear distances between successive GPS locations and was extracted from 5 June to 9 July to

TABLE 2 Values of parameters used in the multi-species functional response model of a mammalian predator (arctic fox) to density of a cyclic prey (prey 1; lemmings) and two other prey species (prey 2 and 3; passerine and sandpiper nests, respectively)

Parameter name	Symbol	Value(s)	Unit
Proportion of time spent active in a day	ϕ_{active}	0.5	–
Daily distance traveled (when $\phi_{\text{active}} = 0.5$)	s	41	km/day
Lemmings			
Lemming density	N_1	0–700	ind./km ²
Maximum reaction distance	d_1	0.0075	km
Average detection and attack probability within the reaction distance	$f_{2,1} \times f_{3,1}$	0.15	–
Success probability	$f_{4,1}$	0.51	–
Chasing time	$T_{\text{pursue},1}$	1.0×10^{-3}	day/ind.
Consumption time	$T_{\text{consume},1}$	3.8×10^{-4}	day/ind.
Consumption probability	e_1	0.48	–
Hoarding time	$T_{\text{hoard},1}$	4.9×10^{-4}	day/ind.
Hoarding probability	o_1	0.32	–
Delivering time	$T_{\text{deliver},1}$	3.9×10^{-3}	day/ind.
Delivery probability	de_1	0.20	–
Passerine nests			
Passerine nest density	N_2	0–15	nests/km ²
Maximum reaction distance	d_2	0.02	km
Average detection probability within the reaction distance	$f_{2,2}$	0.12	–
Consumption time	$T_{\text{consume},2}$	3.6×10^{-4}	day/nest
Sandpiper nests			
Sandpiper nest density	N_3	0–7	nests/km ²
Maximum reaction distance	d_3	0.085	km
Average detection probability within the reaction distance	$f_{2,3}$	0.029	–
Consumption time	$T_{\text{consume},3}$	2.8×10^{-3}	day/nest

Notes: Parameter values were estimated from a combination of high-frequency GPS and accelerometry (23 summer foxes, 2018–2019), behavioral observations ($n = 124$ h, 1996–2019) and camera traps (2006–2016) data. Individuals is abbreviated ind.

cover the incubation period of most birds. Days with <75% of observations (i.e., 270 daily fixes) were excluded from analyses to avoid underestimating daily distances. Since the distance and the proportion of time spent active were closely correlated (Figure 3a), we applied a linear mixed model to estimate the average daily distance with the distance as the response, the proportion of time spent active as a fixed factor, and individual fox and year as random effects. The predicted average daily distance traveled was 41 km ($n = 371$ fox-days; 95% CI [32–49 km]) and ranged from 19 to 62 km while setting the proportion of time spent active on average (i.e., 0.50).

The probability that a lemming captured was either consumed, hoarded, or delivered to the den was estimated based on behavioral observations of foraging foxes

($n = 74$ in 2004–2005; see Careau et al. 2007). Hoarding and consumption time were estimated with the same method and averaged 42 s ($n = 31$) and 32 s ($n = 47$), respectively. Average delivering time was estimated at 337 s on the basis that (1) dens are generally located close to the centroid of the home range, (2) home ranges average 10 km² (Grenier-Potvin et al., 2021), (3) the average speed of an active fox is 3.8 km/h (this study), and (4) foxes return an average of five lemmings per trip to the den (based on 164 lemming deliveries to the den; D. Berteaux, unpublished data).

Values for the remaining parameters of the functional response of foxes to lemmings, passerines, and sandpipers were extracted from Beardsell et al. (2021) and are summarized in Table 2. Parameter values were estimated

using a combination of direct observations of foraging foxes ($n = 124$ h, 1996–2019), camera traps (2006–2016), and information from the literature (see Beardsell et al. 2021 for more details). We conducted simulations for different values of detection probability for the three prey species since there was a high uncertainty in these parameter values (Beardsell et al. 2021). We presented results of all the simulations in Appendix S1: Figures S1, S2, and S3. We used a detection and attack probability of 0.15 (the product of $f_{2,1}$ and $f_{3,1}$) since the number of lemmings captured per day predicted by the model with this value is more consistent with the highest acquisition rate of foraging foxes observed in the field at high lemming densities (i.e., 2.5 lemming/h for active foxes; Beardsell et al. 2021). We used intermediate values of 0.12 ($f_{2,2}$) and 0.029 ($f_{2,3}$) in the results.

Density-dependent functions and simulations

We used data from behavioral observations of foraging foxes to define the density-dependent function of the probability that a lemming is delivered to the den. The probability that a lemming captured was delivered to the den is positively related to lemming density (from 0.04 to 0.22 for a year of low and high lemming density, respectively; Careau et al. 2007). As the probability that a fox pair is breeding increases markedly around a lemming density of 100 individuals/km² (Juhász et al., 2020), we used a sigmoidal function to describe the relationship between delivery probability and lemming density (Figure 3c).

We used a combination of foxes' accelerometry and GPS tracking data to define the parameter space of the density-dependent functions of the daily proportion of time spent active and distance traveled by the predator. These data were available for 2 years contrasted by very low (2 lemmings/km² in 2018) and intermediate (137 lemmings/km² in 2019) lemming densities. We applied a linear mixed model to estimate the distance traveled and the proportion of time spent active for both lemming densities. We included the distance traveled (km/day) as the response, the proportion of time active and lemming density as fixed effects and individual fox as random effect. Predicted proportion of time spent active was higher at low than at intermediate lemming density (Figure 3b1). Predicted daily distance traveled was also higher at low than at intermediate lemming density, even when the proportion of active time was set at 0.5 (Figure 3b2). Based on these results and using the range of values observed for individuals tracked with GPS, as well as the 95% confidence intervals of the average daily distance traveled and the proportion of time spent active recorded over 2 years, we generated three density-dependence

functions for each parameter (Figures 3d1 and 3d2; Appendix S2: Figure S1). The model outputs obtained with one function are presented in the results and all other simulations are presented in Appendix S2.

Field evaluation of models

We evaluated the model outputs (A, B, and C) using a 15-year time series (2005–2019) of prey densities and bird nesting success. Lemming densities were estimated annually using live trapping (see Fauteux et al. 2018 for methods). Sandpiper and passerine nest densities were estimated by the maximum number of nests found in an 8-km² plot systematically searched during the nesting season. Each year, nests were revisited every 2–6 days to determine clutch and brood size and nest status (Gauthier et al., 2013; McKinnon et al., 2014). A nest was considered successful if at least one young left the nest (sandpipers) or fledged (passerines). Average annual daily survival rates of passerine and sandpiper nests were estimated using the logistic exposure method (Shaffer, 2004). It was then converted to nest success by increasing daily nest survival to the power of the average number of days (~24 days) between the laying date and the fledging date (for passerines) or hatching date (for sandpipers). See Royer-Boutin (2015) for more details on these calculations.

To compare model outputs (A, B, and C) to empirical data on bird nesting success, we estimated nesting success of passerines (prey 2) and sandpipers (prey 3) from predator acquisition rates using two differential equations. These equations allow us to calculate predator acquisition rates over the bird nesting period considering that nest density decreases each day. The number of nests predated after 24 days is then divided by the maximum number of nests found in the study plot ($N_{b_{plot}}$), giving us an estimate of annual nesting success. The equation giving the total number of passerine nests predated (P_2) is the product of predator acquisition rate and the number of foxes foraging in the plot ($N_{b_{fox}}$):

$$\frac{dP_2}{dt} = FR_2(N_1, N_2, N_3) \times N_{b_{fox}}. \quad (10)$$

The rate of change in passerine nest density (N_2) is expressed as follows:

$$\frac{dN_2}{dt} = \frac{(N_{b_{plot}} - P_2)}{plot} - N_2 \quad (11)$$

where $N_{b_{plot}}$ is the maximum number of nests found in the study plot, and plot is the plot size (8 km²).

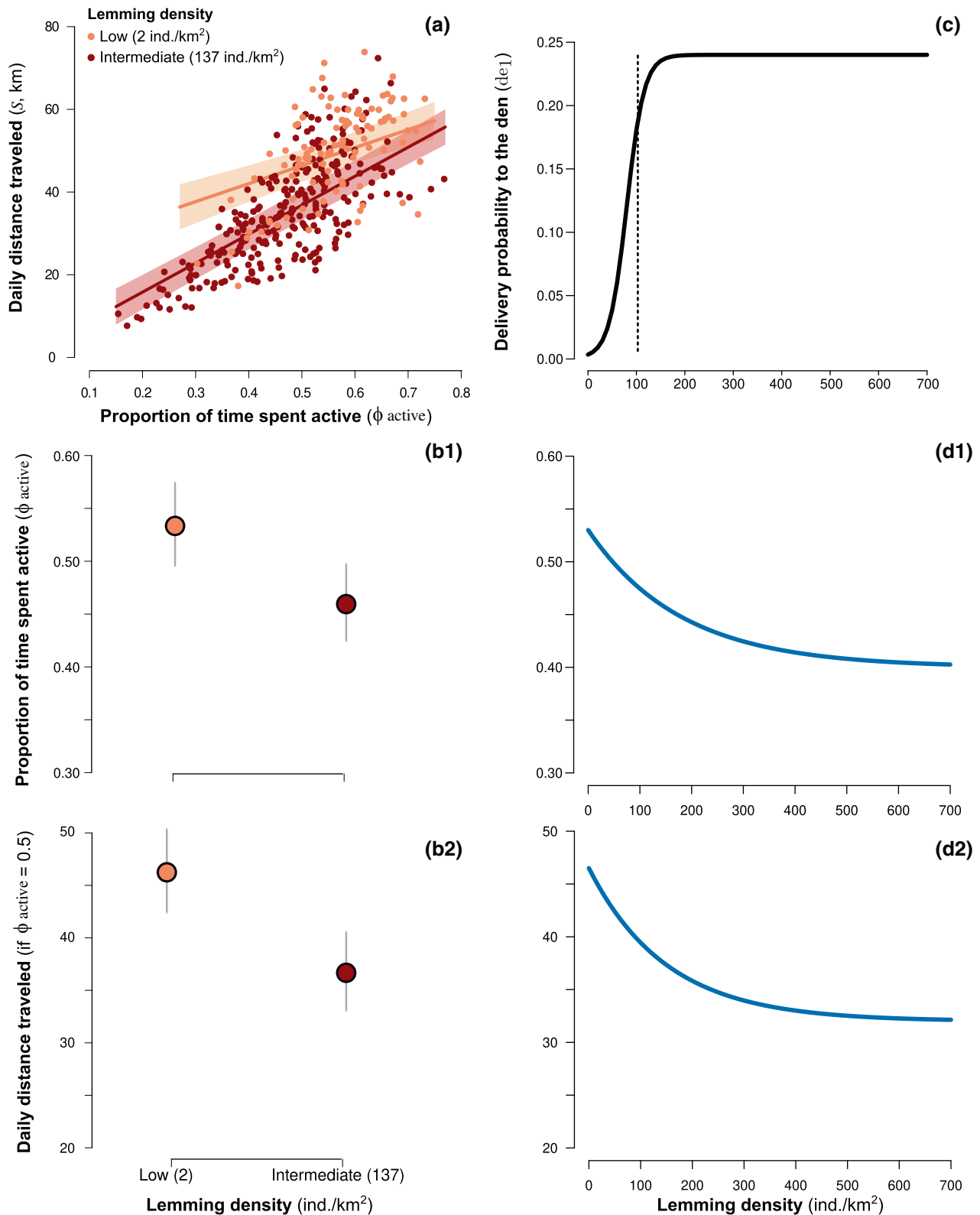


FIGURE 3 (a) Relationship between the daily distance traveled by the arctic fox and the proportion of time it spent active. Colored lines represent predicted relationships and 95% confidence intervals for low and intermediate lemming densities, and dots represent observed data ($n = 371$ fox-days). (b1) Predicted proportion of time spent active per day and (b2) predicted daily distance traveled by the fox between low and intermediate lemming densities. Error bars represent 95% confidence intervals. Density-dependent relationships of the (c) probability that a lemming (prey 1) is delivered to the den, (d1) proportion of time spent active, and (d2) daily distance traveled. The dashed line in (c) indicates a threshold at which the probability that a fox pair is breeding increases markedly (Juhász et al., 2020). Figures c, d1, and d2 are partially derived from empirical observations (see section “Methods”). Individuals is abbreviated ind

Equivalent equations for sandpiper nests can be obtained by substituting all 2s for 3s and vice versa. The model was run for 24 days, which corresponds to the duration between the laying date and the fledging date (for passerines) or hatching date (for sandpipers). We assumed that two foxes were foraging in the study plot since foxes establish territorial pairs with little overlap between neighboring territories (Clermont, Grenier-Potvin, et al., 2021; Grenier-Potvin et al., 2021). The model was implemented in R v. 4.0.4 (R Core Team, 2021).

RESULTS

Multi-prey mechanistic models of functional response

Functional response of the predator (arctic fox) to all prey species were generated for multi-prey models with or without a dependence of some model components on lemming density (Figure 4). According to the model A (based on the multi-prey version of the Holling disk equation), the maximum acquisition rate within the range of lemming densities observed in our study system was 30 lemmings/fox/day (Figure 4a). Including a dependence of lemming handling time on their density through prey delivery (model B) had almost no effect on the functional response of the predator to lemming densities (Figure 4a; maximum acquisition rate remained the same). However, adding a dependence of predator activity time and distance traveled on lemming density (model C) reduced the maximum acquisition rate to 18 lemmings/fox/day (Figure 4a). Over the range of prey densities observed in our study system, the functional response of foxes to lemmings did not reach a plateau for all three models. The use of different density-dependence functions of the predator activity time and distance traveled (either linear or hyperbolic) led to relatively similar functional responses of arctic foxes to lemmings (Appendix S2: Figure S2). Finally, within the range of prey densities observed in our study system, variation in the density of passerine and sandpiper nests had negligible effect on the acquisition rate of lemmings by the predator and, therefore, it was not illustrated in Figure 4a.

Acquisition rate of passerine and sandpiper nests by the predator decreased slightly with increasing lemming density when considering only prey handling processes in the multi-prey model without density dependence (model A). The slope of acquisition rate was 18% lower when comparing a low (0 individuals/km²) and a high (700 individuals/km²) lemming year (Figure 4b,c). Similarly, including a dependence of lemming handling processes on their density (model B) reduced the slope of nests acquisition rate by 19% between a low and high

lemming year. Finally, as illustrated in Figure 4b,c, the models including a dependence of predator activity time and distance traveled on lemming density (model C) had

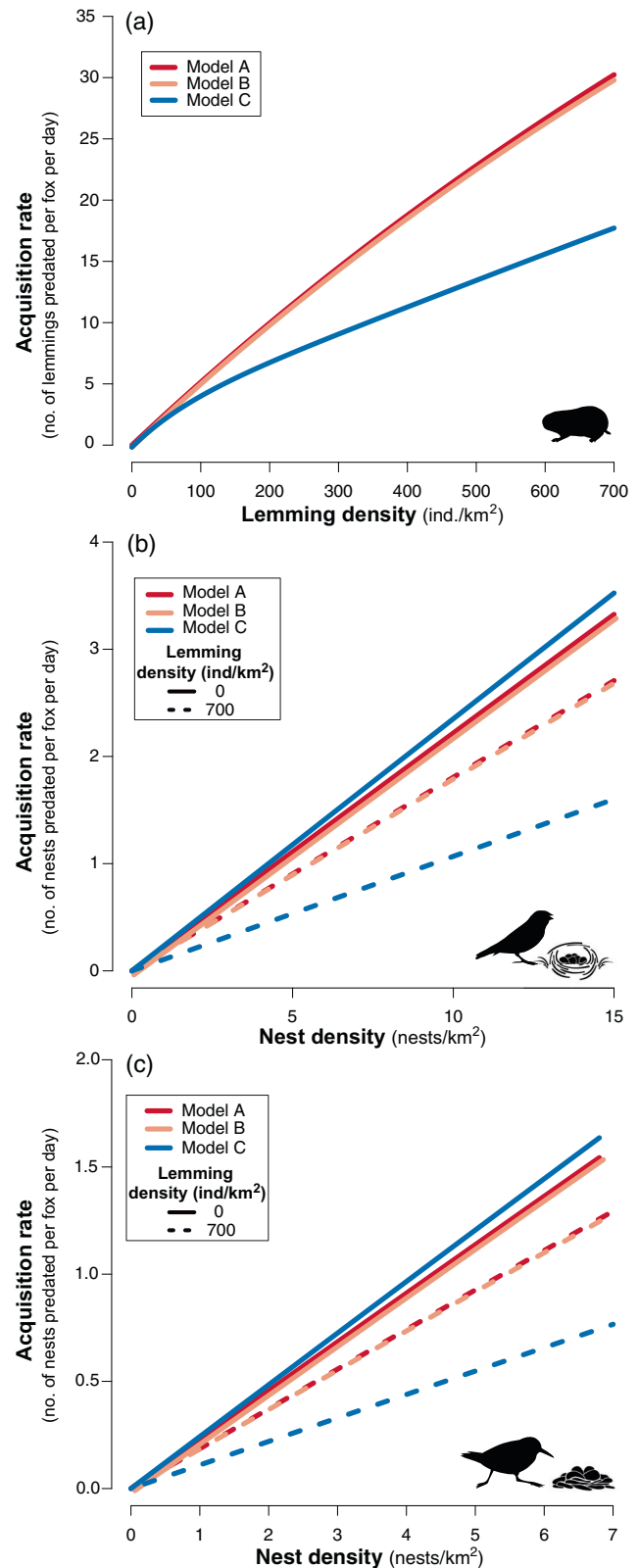


FIGURE 4 Legend on next page.

the most pronounced effect as it reduced the slope of passerine and sandpiper nest acquisition rate by 54% between a low and high lemming year.

Field evaluation of the multi-prey models

Summer lemming density varied from 2 to 648 individuals/km² from 2005 to 2019. A total of 625 passerine nests were monitored during this period and annual nesting success of passerines averaged 48% (range: 8%–88%; Figure 5a). From 2005 to 2019, 292 sandpiper nests were monitored and annual nesting success of sandpipers averaged 50% (range: 4%–100%; Figure 5b).

When considering only prey handling processes, model A and B generated very limited temporal variations in bird nesting success (Figure 5). This indicates that lemming handling time alone cannot generate fluctuations in annual bird nesting success consistent with our time series. Model C including a dependence in predator foraging behavior with lemming density generated temporal variations in bird nesting success that were relatively consistent with those observed in our study system, including a marked release in predation pressure at high lemming densities (Figure 5). However, annual variations in bird nesting success generated by model C were of smaller amplitudes than empirical observations. Our main results were robust to variation in density-dependent functions of the predator daily proportion of time spent active and distance traveled (see Appendix S2).

DISCUSSION

In this study, we first derived a mechanistic multi-prey functional response model by breaking down key components of predation (i.e., search, attack, pursuit, and handling). We also incorporated prey density dependence in predator foraging behavior in the model. We then applied this model to an intensively studied arctic vertebrate community to evaluate the relevance of various proximate mechanisms that could explain the short-term positive

indirect effects observed between tundra prey species. We showed that handling processes cannot explain the predation release on nesting birds observed during lemming peaks. However, we found evidence that changes in predator daily activity budget and distance traveled with respect to prey density can at least partly explain the positive indirect effects observed in a vertebrate community. These mechanisms have been little studied to date and may play a significant role in modulating species interaction strength. By disentangling the various components of predation, our approach allows for comparison of the different mechanisms modulating predator acquisition rates in order to unravel the biological underpinnings of species interactions. Although the model was inspired by an active hunting predator, modular approach could conceivably be applied to a broad range of food webs by incorporating ecological processes and constraints relevant to the study system (e.g., predator hunting strategy, predator interference; see Wootton et al., 2021).

Multi-prey quantitative models are commonly used and they traditionally assume a saturation of predator acquisition rates with increasing prey availability due to rate-limiting handling processes (Matthiopoulos et al., 2007; McLellan et al., 2010; Serrouya et al., 2015; Turchin & Hanski, 1997). However, predator saturation by prey handling processes does not appear to be frequently observed in the wild (Chan et al., 2017; Novak, 2010; Preston et al., 2018), and our results showed that fundamentally different mechanisms may limit predator acquisition rate. Handling time is often estimated by fitting a statistical functional response model to empirical data (Paterson et al., 2015; Smout et al., 2010) but as pointed out by Griffen (2021), this method does not ensure that handling time is an ecologically meaningful parameter. Thus, when traditional statistical models (Holling's type II and III) are fitted, care must be taken in interpreting predator foraging behavior.

We included density dependence in handling processes of the main prey through prey delivery to offspring in our model. While this mechanism plays a minor role in our study system, the sensitivity of predator acquisition rate to this modification of the activity budget is likely to depend on predator home range size, prey load size, predator movement rate, and predator ability to forage while delivering food. For instance, prey delivery could represent a significant proportion of the activity budget for a predator with a large foraging range (e.g., albatrosses; Weimerskirch et al., 1993) or constrained to bring one prey at a time to the breeding site. This type of prey density-dependent mechanism remains to be explored in other natural predator–prey systems.

Numerous studies highlight the relevance of improving functional response models and integrating alternative

FIGURE 4 Functional response of the predator (arctic fox) to prey 1 (lemmings; a), prey 2 (passerine nests; b) and prey 3 densities (sandpiper nests; c) according to models A, B, and C. Model A is based on the multi-prey version of the Holling disk equation, model B modifies model A by adding density dependence in lemmings handling processes through prey delivery, and C modifies model A by adding density dependence in predator activity time and distance traveled. Densities of prey 2 and 3 are set at intermediate densities in (a)

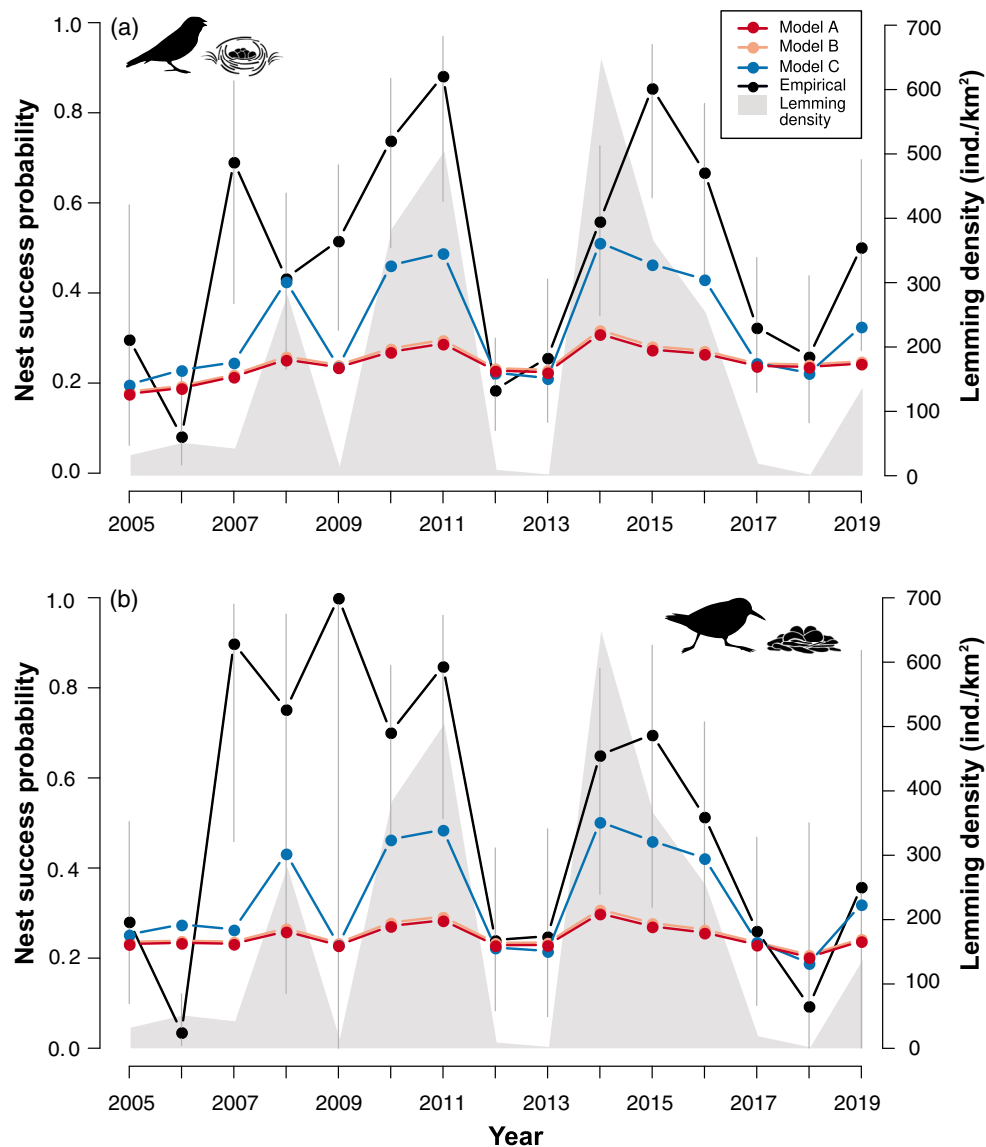


FIGURE 5 Temporal fluctuations in lemming densities (cyclic prey 1), and nesting success of passerines (a; prey 2) and sandpipers (b; prey 3). Model A is based on the multi-prey version of the Holling disk equation, model B modifies model A by adding density dependence in lemmings handling processes through prey delivery, and C modifies model a by adding density dependence in predator activity time and distance traveled. Model results for A and B overlap. Empirical data (lemming density and birds nest success) were acquired through long-term monitoring in the Canadian high Arctic. Error bars are the 95% confidence intervals of nesting success estimates

mechanisms that can modulate animal acquisition rates, such as predator activity level (Toscano & Griffen, 2014), prey digestion time (Jeschke, 2007; Papanikolaou et al., 2020), or time spent in vigilance (Sirot et al., 2021). Although many empirical studies have demonstrated links between prey availability and predator foraging behavior (Bertrand et al., 2014; Busdieker et al., 2019; Harding et al., 2007), empirically based relationships of the dependence of predator foraging behavior on prey density are rarely included in predator-prey models (Stouffer & Novak, 2021). We recognize that the density-dependent functions used in our study were derived from limited empirical data. Further field investigations, such as long-

term GPS and accelerometer tracking of predators over a wide range of prey densities, are needed to refine functions and fully integrate changes in predator foraging behavior in response to varying prey density. Overall, our results highlight the need to reinforce the links between multi-species functional response models and the dynamics of vertebrate communities.

The short-term, positive indirect effect of lemmings on tundra nesting birds due to shared predators was reported several decades ago and was studied over the circumpolar arctic since then (Summers et al., 1998; Underhill et al., 1993). Various mechanisms have been proposed to explain the observed pattern, including

predator satiation, but none has been demonstrated (Blomqvist et al., 2002; Bowler et al., 2020; McKinnon et al., 2014; Summers et al., 1998; Underhill et al., 1993). Our results indicate that predation release on tundra birds at high lemming densities is primarily due to a reduction in arctic fox daily activity time and distance traveled. A change in prey preference is another potential mechanism that could contribute to predation release on birds (Bêty et al., 2002; Bowler et al., 2020). It refers to a situation where the preference for a prey i by the predator is greater when prey i is abundant relative to another prey, and inversely smaller when prey i is less abundant than other prey (Murdoch, 1969). An increase in preference for an abundant prey i may translate into an increase in the probability of its detection, attack, and/or success as prey i density increases because of changes in predator behavior or foraging strategy.

Changes in prey preference remain to be fully explored and demonstrated in our study system and more empirical data are needed to investigate the effect of lemming density on the probability of lemming and bird nest detection by foxes, as well as their attack and success probability. However, changes in prey preference are expected to play a relatively minor role. Indeed, even if foxes capture more lemmings when they are abundant, the handling time per lemming captured is still likely to be too low to have a significant effect on bird nest predation rates. Moreover, highly vulnerable prey like passerines and sandpipers are unable to protect their clutches against arctic foxes (Hussell & Montgomerie, 2020; Smith & Edwards, 2018). Consequently, once the nest is detected, the probability of nest attack by foxes is likely to remain high in all years because attacking these vulnerable prey systematically provides benefits to the predators and engenders very low costs (i.e., low handling time and no risk of injury). Inter-annual changes in the probability of nest attack by foxes may nonetheless occur in large-bodied nesting species able to fight back and defeat arctic foxes, as reported in Snow Geese (Bêty et al., 2002). Our multi-prey model could be adapted to explore the effects of such changes on annual nest predation rate.

Some variability in shorebird and passerine nesting success remains unexplained in our study system and this can be the result of a combination of factors. First, we assumed that lemming density and parameter values were homogeneous across the landscape. Better knowledge of potential spatial variation, especially within fox territories, would likely contribute to explaining variation in bird nesting success. Second, the empirical measurement of nesting success may be overestimated since nests predated very early in the nesting period were not necessarily found by observers. This may partly explain the

relatively high nest success observed in some years of low lemming density (Figure 5). Moreover, potential mechanisms that are not included in our model could also contribute to such discrepancy. For instance, we assumed that two foxes were foraging in the monitoring area of passerine and sandpiper nests in all years. Although this is most likely the predominant situation (Clermont, Grenier-Potvin, et al., 2021; Lai, 2017), slight changes in number of foxes could generate substantial variation in annual bird nesting success.

A growing number of studies aim to predict trophic links based on species traits, especially body size (Gravel et al., 2013; Ho et al., 2019; Portalier et al., 2019), but multi-species mechanistic models quantifying interaction strength in natural communities are still lacking. With recent advances in biologging technology, high-frequency GPS, acoustic and accelerometer data are increasingly used to study free-ranging organisms (Pagano et al., 2018; Studd et al., 2021; Williams et al., 2014). As illustrated in our study system, the parametrization of mechanistic models with such data is a promising method to accurately quantify interaction strength in natural systems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.


DATA AVAILABILITY STATEMENT

Data (Beardsell et al., 2022) on bird nesting success and prey densities, along with data related to fox foraging behavior, are available in Dryad at <https://doi.org/10.5061/dryad.8w9ghx3pf>.

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