Research

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Predator-mediated interactions through changes in predator home range size can lead to local prey exclusion

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The strength of indirect biotic interactions is difficult to quantify in the wild and can alter community composition. To investigate whether the presence of a prey species affects the population growth rate of another prey species, we quantified predator-mediated interaction strength using a multi-prey mechanistic model of predation and a population matrix model. Models were parametrized using behavioural, demographic and experimental data from a vertebrate community that includes the arctic fox (*Vulpes lagopus*), a predator feeding on lemmings and eggs of various species such as sandpipers and geese. We show that the positive effects of the goose colony on sandpiper nesting success (due to reduction of search time for sandpiper nests) were outweighed by the negative effect of an increase in fox density. The fox numerical response was driven by changes in home range size. As a result, the net interaction from the presence of geese was negative and could lead to local exclusion of sandpipers. Our study provides a rare empirically based model that integrates mechanistic multi-species functional responses and behavioural processes underlying the predator numerical response. This is an important step forward in our ability to quantify the consequences of predation for community structure and dynamics.

1. Introduction

Understanding how and to what extent biotic interactions influence species occurrence is a major challenge because of the myriad ways species interact in natural communities [1]. Indirect biotic interactions are especially hard to tackle because they arise through chains of direct interactions [2]. In theory, negative indirect interactions between species that share a common predator (hereafter predator-mediated interactions) may alter community composition by excluding species that are more vulnerable to predation. Although such indirect interactions are likely widespread [3], they are difficult to quantify in complex natural communities (e.g. [4–7]).

Predator-mediated interactions can be quantified according to the change in the number of prey acquired per predator per unit of time (the functional response) and to the change in the number of predators (the numerical response) as a function of prey density. The net effect of the indirect interaction on a given prey species can be either null, negative (e.g. apparent competition) or positive (e.g. apparent mutualism) depending on the relative strength of the predator functional and numerical response [3]. For instance, increasing the abundance of a prey *i* could theoretically release predation on prey *k* due to reduced time spent searching for that prey [8,9]. Alternatively or additionally, increasing the density of a prey *i* could increase the density of predators, and consequently
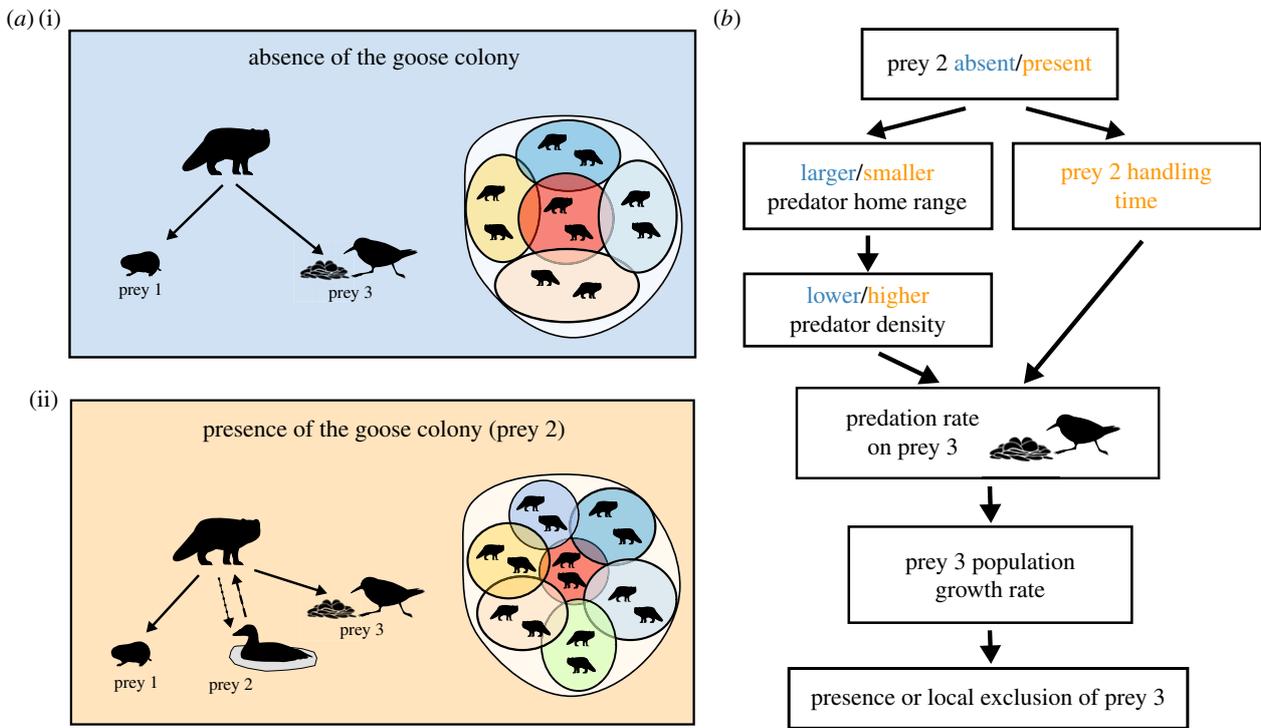
Figure 1. (*a*) Diagrams of simplified arctic food webs and of fox home range size showing direct links between a predator (arctic fox), prey 1 (lemmings), prey 2 (goose eggs) and prey 3 (sandpiper eggs) in the absence *a*(i) and presence *a*(ii) of the goose colony. (*b*) Schematic of hypothesized mechanisms underlying the indirect interaction of prey 2 (goose eggs) on prey 3 (sandpiper eggs) through a shared predator (arctic fox). Although the time required to handle goose eggs can reduce the time available to search for sandpiper nests (dotted arrow in *a*(ii)), we predicted that this positive effect can be outweighed by an increase in predator density in the goose colony associated with a reduction in fox home range size (dashed arrow in *a*(ii)).

increase predation rate on prey *k* [10,11]. The balance between such opposing indirect effects has been well-studied theoretically [12] but theoretical predictions have rarely been tested in natural communities. This is in part due to difficulties in obtaining empirically based multi-species functional response models [13,14] and in measuring the relative effects of the predator functional and numerical responses on the net interaction strength. Process-based mechanistic models (hereafter referred to as mechanistic models) can allow us to disentangle the relative strength of the functional and numerical responses of predators, and ultimately improve our ability to accurately quantify the strength of the net indirect interactions in ecological communities [15,16].

An increase in prey densities may result in higher predator density through behavioural or demographic processes. In most predator–prey models, the numerical response of a predator is incorporated through reproduction and survival parameters [13,17–19]. Although a change in prey density is likely to influence the predator density via reproduction or survival, changes in predator behaviour can also lead to marked changes in predator density. For instance, an increase in prey density modifies the costs and benefits of movements and competitive interactions, with direct effects on both home range size and local density [20,21]. Although this idea is intuitive, the link between predator home range size and predator density is rarely explicitly incorporated in predator–multi-prey models. Yet this is important to understand the mechanistic processes and model the net effect of predator-mediated interactions in natural communities.

Our objectives were twofold. First, we built a multi-prey mechanistic model of predation by breaking down every step of the predation process to assess whether the presence of a prey species *i* affects acquisition rate of a prey species *k*

by a shared predator. We then calculated the resulting predation rates by also considering changes in predator density associated with an adjustment in predator behaviour (reduction in home range size) induced by the presence of prey *i*. Second, we used a population matrix model to evaluate whether changes in predation rates caused by the presence of prey *i* can indirectly generate the local exclusion of prey *k*. This was illustrated in an arctic vertebrate community composed of a generalist predator, the arctic fox (*Vulpes lagopus*), feeding primarily during the summer on small cyclic mammals and eggs of various tundra bird species, including colonial nesting geese (prey *i*) and sandpipers (prey *k*).

The focal High Arctic community is characterized by high-amplitude fluctuations of lemming populations (with peaks occurring every 3–4 years) and by the presence of a large breeding colony of greater snow geese (*Anser caerulescens atlanticus*; [22]). In this community, the occurrence probability of nesting shorebirds decreases when colonial nesting geese are present, and shorebird nest predation risk (measured with artificial nests) is higher at high goose nest densities [23,24]. Although the time required to handle goose eggs can reduce the time available to search for other prey (e.g. sandpiper nests), we predicted that this positive effect can be outweighed by an increase in predator density in the goose colony associated with a reduction in fox home range size (figure 1). We expected that the resulting predation rates in the presence of the goose colony can be high enough to induce sandpiper local exclusion (without sandpiper immigration). The originality of this study lies in our ability to identify dominant mechanisms affecting prey coexistence (or the lack of) in a natural vertebrate community using models parametrized from a combination of behavioural, demographic and experimental data acquired over 25 years [22,25,26].
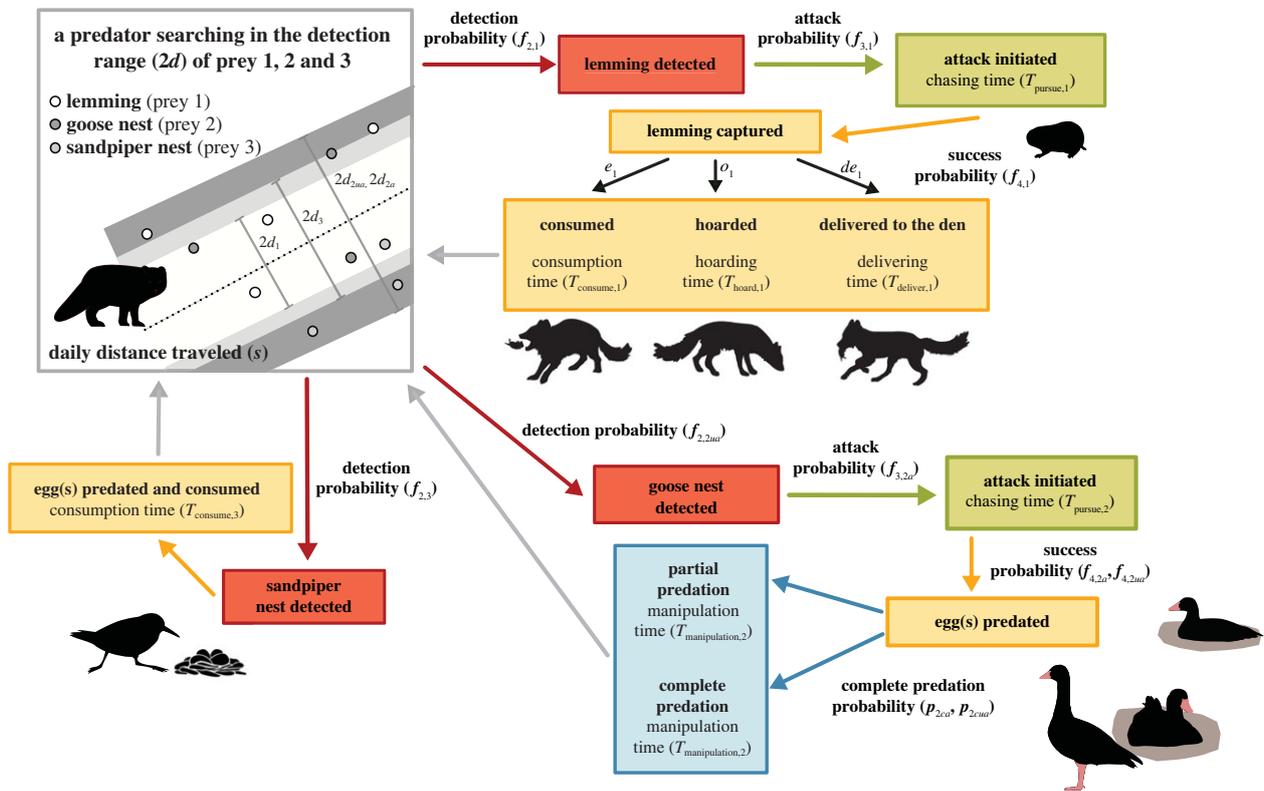
Figure 2. Conceptual multi-prey mechanistic model of arctic fox functional response to density of lemmings (prey 1), goose eggs (prey 2) and sandpiper eggs (prey 3). Each box represents one or more components of predation (search, prey detection, attack decision, pursuit, capture and manipulation). Arrows represent the probability that the predator reaches the next component. When there is no parameter near an arrow, the probability of reaching the next component is 1. As incubating geese can actively protect their nests from arctic foxes, their presence at the nest strongly influences fox foraging behaviour. Thus, most parameter values were estimated separately for goose nests that were attended and unattended (indicated by two symbols near the arrows). Unlike geese, sandpipers cannot protect their nests once they are detected by a fox. We therefore assumed that once a nest is detected, it is consumed.

2. Methods

(a) Study area and species

The mechanical model of predation was built using detailed empirical data from a long-term ecological study on Bylot Island, Nunavut, Canada (73° N; 80° W). The study area (approx. 500 km^2) encompasses a greater snow geese colony of approximately 20 000 pairs, which is concentrated in an area of 50–70 km^2 [27]. The location of the goose colony centroid is relatively stable across years [28]. Two cyclic species of small mammals are present: the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings [22]. The most common ground-nesting sandpipers found in the study area are the Baird's (*Calidris bairdii*) and white-rumped (*Calidris fuscicollis*) sandpipers. Both species nest on the ground at relatively low densities (less than 6 nests km^{-2}; [25]). The arctic fox is an active-searching predator [29] and the main predator of goose and sandpiper eggs [30,31]. In the study area, the same home range is used throughout the summer, and the degree of overlap between home ranges is generally low in the population studied [32]. Arctic foxes are also generally faithful to their home range year after year [33,34]. In the study area, the majority of juveniles disperse at the end of the summer [35], and hence the density of adult foxes does not appear to be influenced by the local reproduction of the previous year. Adult survival of arctic foxes is not driven by resource variation (goose eggs and lemmings) in the study area [36].

(b) Multi-prey model of predation

We built on a previous mechanistic model of arctic fox functional response to lemming and sandpiper nests developed at the same study area [15]. We incorporated goose nests into this model

based on a mechanistic model previously developed for the fox–goose dyad [25]. This model used the Holling disk equation as a starting point and follows the theoretical framework of [16]. The model was derived by breaking down fox predation into a maximum of six steps: (1) search, (2) prey detection, (3) attack decision, (4) pursuit, (5) capture and (6) manipulation. Each step was adapted to each prey species according to their anti-predator behaviour and the fox hunting behaviour [15,25]. Figure 2 provides an overview of the multi-prey mechanistic model (prey 1 is lemmings, prey 2 is goose nests and prey 3 is sandpiper nests).

For the three prey species ($i = 1, 2, 3$), the area searched ($A_{\text{search},i}$, km^2) by the predator is expressed as the product of the daily distance travelled by the predator (s; km day^{-1}), the reaction distance to a prey item (d_i, km), and the time spent searching (T_{search}, day)

$$A_{\text{search},i} = s \cdot (2d_i) \cdot T_{\text{search}}. \tag{2.1}$$

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 two dimensions, detection region = $2d_i$; [37]). As not all prey within the searched area may be detected, attacked and subdued by the predator, we introduced the detection probability ($f_{2,i}$), the attack probability ($f_{3,i}$) and the success probability of an attack ($f_{4,i}$).

The number of sandpiper nests predated per fox per day (the predator acquisition rate) is expressed as

$$FR_3(N_1, N_2, N_3)$$

$$= \frac{\phi_{\text{active}}(N_1) \cdot \alpha_3(N_1) \cdot N_3}{1 + \alpha_1(N_1) \cdot h_1 \cdot N_1 + \alpha_2(N_1) \cdot h_2 \cdot N_2 + \alpha_3(N_1) \cdot h_3 \cdot N_3}, \tag{2.2}$$

where ϕ_{active} is the proportion of time the predator spent active in a day, N the density of each prey (ind km^{-2}), α the capture efficiency (km^2 day^{-1}) and h the handling time per prey item (days per prey item). Capture efficiency of a lemming (α_1) is expressed as the product of the daily distance travelled by the predator (s; km day^{-1}), the reaction distance (d_1; km), the detection probability ($f_{2,1}$), the attack probability ($f_{3,1}$) and the success probability of an attack ($f_{4,1}$)

$$\alpha_1(N_1) = s(N_1) \cdot (2 \cdot d_1) \cdot f_{2,1} \cdot f_{3,1} \cdot f_{4,1}. \tag{2.3}$$

Because sandpipers cannot protect their nests once they are detected by a fox, we assumed that once a nest is detected, it is consumed. Thus, the capture efficiency of sandpiper nests is simply the product of s, the reaction distance (d_3, km) and the detection probability ($f_{2,3}$). Since we have evidence that the values of ϕ_{active} and s depend on lemming density (Model C in [15]), the values of ϕ_{active} and α are expressed as a function of lemming density (electronic supplementary material, appendix S1; Fig. S1). The handling time equations for all prey and capture efficiency equations for geese can be found in the electronic supplementary material, appendix S2 and associated parameter values in table 1.

The predator acquisition rate of sandpiper nests in the absence of a goose colony is obtained by setting the density of geese (N_2) to 0 in equation (2.2). Detailed equations of the functional response model for each prey species can be found in electronic supplementary material, appendix S2 and associated parameter values in table 1. For more details on the construction of the model, see [15,25].

We estimated predator density (NR_j; number of predators per km^2) as follows:

$$NR_j = \frac{Np}{H_{0,j}}, \tag{2.4}$$

where Np is the number of predators sharing the same home range and H_{0j} is the size of the home range exclusively shared by Np (km^2). As fox pair members share a home range [32], we assumed that two foxes were foraging per home range ($Np = 2$). We calculated H_{0j} as follows:

$$H_{0,j} = H_j \cdot (1 - V), \tag{2.5}$$

where H_j is the home range size (km^2) and V is the proportion of overlap between adjacent home ranges. The value of H_j simply depends on whether a goose colony is absent ($j = 0$) or present ($j = 1$). We calculated fox density for the whole range of home range sizes observed in the presence or the absence of a goose colony (figure 3a). We assumed that a part of the home range is always used exclusively by Np (V cannot be equal to 1). We did not consider the presence of floaters (non-resident foxes) in the number of predators.

The number of sandpiper nests predated per day per km^2 ($P_{3,j}(N_1, N_2, N_3)$, hereafter the predation rate) is given by the product of the predator acquisition rate ($FR_3(N_1, N_2, N_3)$; nests predated per fox per day; equation (2.2)) and predator density (NR_j; fox per km^2; equation (2.4)):

$$P_{3,j}(N_1, N_2, N_3) = FR_3(N_1, N_2, N_3) \cdot NR_j. \tag{2.6}$$

(c) Parameter values

We estimated summer home range size of arctic foxes using telemetry data (Argos) of 113 foxes from 2008 to 2016 on Bylot Island. Foxes were captured and equipped with Argos radio collars as described in [38], providing a location every 1–2 days. We estimated the area of the 95% home range contour for each individual-year between May–October using the autocorrelation-informed home range estimation workflow described in [39], and implemented in ctmm R package ([40], Dulude et al. [41]). Home range size averages 10.8 km^2 ($n = 56$ home ranges) and

18.2 km^2 ($n = 57$) in the presence and absence of the goose colony, respectively (figure 3a). Based on high-frequency gps data (13 foxes in summer 2019), the average proportion of overlap between adjacent home ranges is 0.18 on Bylot Island [32].

We set the average density of goose nests within fox home ranges at 255 nests per km^2. We derived this estimate from an exhaustive count of all goose nests present within the colony (an area of 56 km^2 in 2019; see methods in [42]). The year 2019 falls within the long-term average of goose nest density measured in an intensive monitoring area (0.5 km^2) in the core of the colony from 1989 to 2019 [43].

Values for the remaining parameters of the functional response of foxes to lemmings, sandpipers and geese were extracted from [15,25], and are summarized in table 1. In short, parameter values were estimated from a combination of high-frequency GPS and accelerometry data (23 summer foxes, 2018–2019), behavioural observations in the field ($n = 124$ h, 1996–2019), field experiments and camera traps deployed at nests (2006–2016).

(d) Estimating nesting success

We estimated annual nesting success of sandpipers (prey 3) for the whole range of home range sizes observed in the presence ($N_2 = 255$ nests per km^2) and the absence ($N_2 = 0$ nest per km^2) of the goose colony using a set of differential equations. These equations allowed us to calculate the total number of nests predated per km^2 over the sandpiper nesting period (i.e. the average duration between the laying date and hatching date) while considering that the density of nests decreases each day. We assumed that the bird nesting period is synchronized, that fox predation is the only cause of nest failure and that predated nests are not replaced. The rates of change in the total number of goose (prey 2) and sandpiper (prey 3) nests predated per day per km^2 are given by

$$\frac{dPR_2}{dt} = P_{2,j}(N_1, N_2, N_3) \tag{2.7}$$

and

$$\frac{dPR_3}{dt} = P_{3,j}(N_1, N_2, N_3). \tag{2.8}$$

The rates of change in goose and sandpiper nest density (respectively, N_2 and N_3) are expressed as follows:

$$\frac{dN_2}{dt} = -PR_2 \tag{2.9}$$

and

$$\frac{dN_3}{dt} = -PR_3. \tag{2.10}$$

The total number of sandpiper nests predated (nests per km^2) over the nesting period (24 days) was divided by the number of nests present at day 1 of nest initiation (the density of N_3 at day 1), giving us an estimate of the proportion of nests predated annually (1 minus this proportion gives the annual nesting success). The annual nesting success in the absence of the goose colony was obtained by setting the density of geese (N_2) to 0 and by using only equations 2.8 and 2.10.

We also estimated annual nesting success of geese with equations 2.7 and 2.9. The total number of goose nests predated (nests per km^2) over the nesting period (28 days) was divided by the number of nests present at day 1 of nest initiation (the density of N_2 at day 1), giving us an estimate of the proportion of nests predated annually (1 minus this proportion gives the annual nesting success).

Since lemming densities fluctuate with high amplitude between years, we computed the average sandpiper nesting success over the 13-year time series of lemming densities on Bylot Island (electronic supplementary material, appendix 1; Fig. S2). Inclusion of interannual variability in lemming density (from 2 to 648 ind. km^{-2}) results

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), goose nests (prey 2) and sandpiper nests (prey 3). Parameter values were estimated from a combination of high-frequency GPS and accelerometry data (23 summer foxes, 2018–2019), ARGOS telemetry data (113 summer-foxes), behavioural observations in the field ($n = 124$ h, 1996–2019), the literature and camera traps (2006–2016). Most details regarding the estimation of parameter values can be found in [25]. Parameters related to lemming manipulation times and the fox activity budget can be found in [15].

parameter name	symbol	value(s)	unit
arctic fox			
home range size	H	3.7–48.4	km^2
average proportion of overlap between adjacent home ranges	V	0.18	—
daily proportion of time the predator spent active (function of N_1)	ϕ_{active}	figure S1	—
daily distance travelled (function of N_1)	s	figure S1	km day^{-1}
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	$f_{2,1} \cdot f_{3,1}$	0.15	—
success probability	$f_{4,1}$	0.51	—
chasing time	$T_{pursue,1}$	1.0×10^{-3}	day ind.$^{-1}$
consumption time	$T_{consume,1}$	3.8×10^{-4}	day ind.$^{-1}$
consumption probability	e_1	0.48	—
hoarding time	$T_{hoard,1}$	4.9×10^{-4}	day ind.$^{-1}$
hoarding probability	o_1	0.32	—
delivering time	$T_{deliver,1}$	3.9×10^{-3}	day ind.$^{-1}$
delivering probability	de_1	0.20	—
goose nests			
goose nest density	N_2	255	nests km^{-2}
nest unattendance probability	w	0.021	—
chasing time	$T_{pursue,2}$	8.3×10^{-4}	day nest^{-1}
manipulation time (includes consumption and hoarding time)	$T_{manipulation,2}$	5.8×10^{-3}	day nest^{-1}
goose attended nests			
maximum reaction distance	d_{2a}	0.033	km
average attack probability within the reaction distance	$f_{3,2a}$	0.05	—
success probability	$f_{4,2a}$	0.098	—
complete predation probability	p_{2ca}	0.47	—
goose unattended nests			
maximum reaction distance	d_{2ua}	0.11	km
average detection probability within the reaction distance	$f_{2,2ua}$	0.37	—
success probability	$f_{4,2ua}$	0.93	—
complete predation probability	p_{2cua}	0.69	—
sandpiper nests			
sandpiper nest density	N_3	3.1	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	$T_{consume,3}$	2.8×10^{-3}	day nest^{-1}

in a 7% decrease in average nesting success of sandpipers relative to a constant average lemming density (i.e. 204 ind. km^{-2}). This is consistent with the results of a different system [44].

(e) Sensitivity analysis

We quantified the relative influence of model parameter values on the estimation of sandpiper annual nesting success by using the Latin hypercube sampling technique (an efficient implementation of the Monte Carlo methods; [45]). This analysis allowed us to investigate the uncertainty in the model output generated by the uncertainty and variability in parameter values. Each parameter was represented by a probability distribution (uniform or normal truncated) based on the distribution of empirical data. For some parameters, the biological information was limited, so we assigned a uniform distribution allowing for a large

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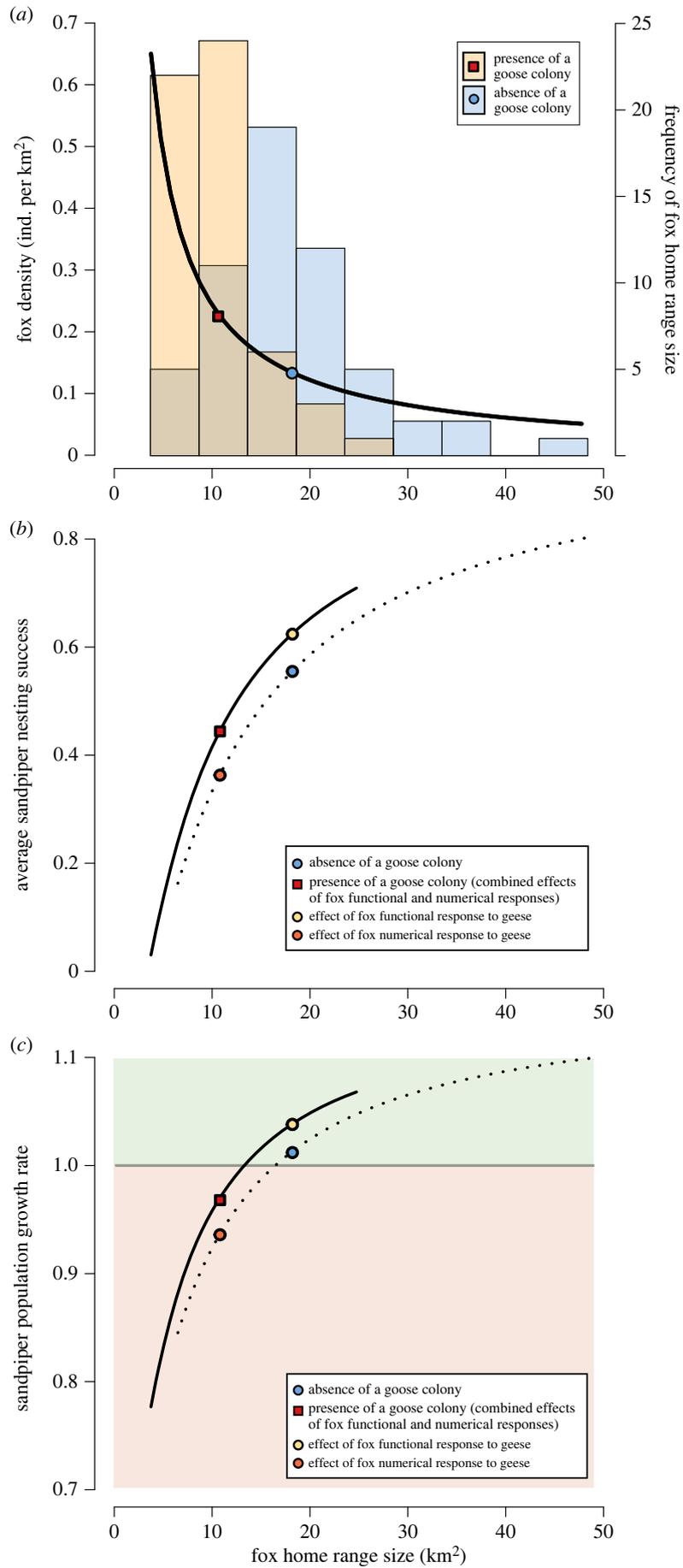
Figure 3. (*Caption overleaf.*)

Figure 3. (*Overleaf.*) (*a*) Relationship between fox density and summer home range size of arctic foxes derived from equation (2.4), and histograms of home range size (estimated from telemetry data; $n = 113$) in the presence and absence of the goose colony. Points indicate average home range size in the presence and absence of the goose colony. (*b*) Relationship between average nesting success of sandpipers and summer home range size of arctic foxes for goose nest densities within (plain line, $N_2 = 255$ nests per km^2) and outside (dashed line, $N_2 = 0$ nests per km^2) the goose colony. (*c*) Relationship between local growth rate (λ) of sandpipers and summer home range size of foxes for goose nest densities within (plain line, $N_2 = 255$ nests per km^2) and outside (dashed line, $N_2 = 0$ nest per km^2) the goose colony. Points show the average nesting success (*b*) or the local growth rate (*c*) of sandpipers for an average fox home range size in the absence of geese and in presence of geese when considering the functional response of foxes to geese, the numerical response of foxes to geese, or the combined effects (functional and numerical response of foxes to geese). Areas where λ is >1 are in green and <1 in red.

range bounded by minimum and maximum values. Latin hypercube sampling was then applied to each distribution ($N = 1000$ iterations). For simplicity, the sensitivity analysis was conducted on the predation model (equation (2.6)) including the presence of the goose colony ($j = 1$), without density-dependence in parameters s and ϕ_{active} and with fixed prey densities ($N_1 = 204$ individuals km^{-2}, $N_2 = 255$ nests km^{-2}, $N_3 = 3.1$ nests km^{-2}).

(f) Sandpiper population model

We evaluated whether changes in nest predation rates caused by the presence of the goose colony can indirectly generate local exclusion of sandpipers. We used a population matrix model to link estimated nesting success to sandpiper population growth rate. Since most demographic parameters for white-rumped sandpiper and/or Baird's sandpiper are poorly documented on Bylot Island, we built upon a projection matrix model developed in [26] for the semipalmated sandpiper (*Calidris pusilla*; hereafter sandpiper), a tundra nesting species for which the demographic parameters are relatively well documented across the North American Arctic (electronic supplementary material, appendix S3; Fig. S8). We calculated growth rate (λ) using the mean values of each vital rate while varying average nesting success values (NS_{ini} and NS_{renest}; see electronic supplementary material, table S1 in appendix S3). Given the strong influence of annual adult survival on λ [26], we calculated λ values for different values of adult survival. We used the *popbio* package v. 2.7 [46] in *R* [47] to calculate λ. Details regarding the matrix model are available in electronic supplementary material, appendix S3. We conducted all models and simulations in *R* v. 4.2.2 [47].

3. Results

Summer home range size of arctic foxes varied from 3.7 to 48.4 km^2 in the study area (figure 3*a*). The average home range size was smaller within the colony (10.8 km^2) than outside (18.2 km^2), hence the estimated fox density was on average 1.7 times higher in the goose colony (figure 3*a*). The estimated goose nesting success was 77%, which is consistent with the average success estimated from intensive annual goose nest monitoring in the colony (68% between 1991 and 2015 [48]). In the absence of nesting geese, the estimated nesting success of sandpiper was 56% (figure 3*b*). This is also consistent with the average nesting success observed in a monitoring area located approximately 30 km away from the goose colony on Bylot Island (50% $\pm$ 0.08 (s.e.) between 2005 and 2019; [15]). There is no estimate of annual sandpiper nesting success in the goose colony because sandpiper nest density is too low [23]. Functional and total responses of the predator (arctic fox) to sandpiper nests as a function of each prey density are shown in electronic supplementary material, appendix S1; Fig. S3.

Sensitivity analysis indicated that four parameters had a significant effect on annual sandpiper nesting success (electronic supplementary material, appendix S1; Fig. S4). A change in

the value of these four parameters by 50% generated changes in sandpiper annual nesting success by 24%, 15%, 12% and 11%, respectively, for predator home range size, daily distance travelled by the predator, proportion of time spent active by the predator and detection probability of sandpiper nests (electronic supplementary material, appendix S1; Fig. S5). Neither daily distance travelled nor activity level was correlated to fox home range sizes based on high-frequency GPS and accelerometry data (electronic supplementary material, appendix S1; Fig. S6). Although some parameters directly related to goose nest predation had a statistically significant influence on sandpiper nesting success (electronic supplementary material, appendix S1; Fig. S4), their biological effects were limited as indicated by the low correlation coefficient of the relationship (less than 0.21; electronic supplementary material, appendix S1; Fig. S5). Predator home range size was thus the most influential parameter in the model.

We evaluated the net effect of colonial geese on the average sandpiper nesting success. We first computed nesting success of sandpipers from the multi-prey mechanistic models over the range of fox densities (home range sizes) observed in the study area (figure 3*b*). For a given arctic fox density, the presence of nesting geese increased the estimated sandpiper nesting success by 7% (functional response effect only: figure 3*b*). This release of predation pressure was the result of time constraints related to goose egg handling (including chasing, hoarding, consumption), which reduced the time available to search for other prey like sandpiper nests. On the other hand, when considering only the increase in fox density caused by the presence of colonial geese (from 0.13 ind. km^{-2} to 0.22 ind. km^{-2}; figure 3*a*), the estimated sandpiper nesting success decreased by 18% (numerical response effect only: figure 3*b*). The negative effect mediated by arctic fox home range size adjustment thus outweighed the predation release due to goose egg handling time, resulting in an 11% decrease in average sandpiper success in the goose colony overall (see combined effects in figure 3*b*).

We investigated the net effect of the goose colony on sandpipers demography. Population growth rate (λ) derived from the sandpiper matrix population model indicated that changes in sandpiper nesting success caused by the presence of colonial geese can affect local sandpiper population dynamics (figure 3*c*). While the predation release on sandpiper nests generated by the goose egg handling time could increase λ by 3% (functional response effect only), the reduction in sandpiper nesting success caused by higher density of foxes in the goose colony resulted in a 7% decrease in λ (numerical response effect only: figure 3*c*). The negative effect mediated by the increased predator density thus outweighed the positive effect generated by the functional response. When fox home range size is smaller than 13.5 km^2, which includes 80% of empirically estimated home range sizes in the presence of the goose colony ($n = 56$), the local growth rate of sandpipers is less

than 1, in the absence of immigration (figure 3c). In the absence of the goose colony, the local growth rate of sandpipers is greater than 1 when fox home range is larger than 16 km² (which includes 54% of empirically estimated home range sizes in the absence of the goose colony; $n = 57$: figure 3c). For the average fox home range size observed in the goose colony on Bylot Island, model outputs indicated that sandpiper adult survival has to reach a minimum of 0.78 for a $\lambda > 1$ without immigration (electronic supplementary material, appendix S1; Fig. S7).

4. Discussion

In this study, we used a mechanistic multi-prey predation model to quantify predator-mediated interaction strength in a natural system. We analysed the model to quantify the indirect interaction between two prey species (colonial nesting geese and sandpipers) sharing a common predator (the arctic fox). We incorporated predation rates into a population matrix model to evaluate the consequences of predator-mediated interactions on local prey growth rates. Our results showed that the positive effects of the presence of the goose colony on sandpiper nesting success (due to a reduction of search time for sandpiper nests by the predator) were outweighed by the negative effect of an increase in fox density, associated with a reduction in fox home range size in the presence of the goose colony. Thus, the net interaction resulting from the presence of the goose colony on sandpiper nesting success was negative. The strength of the negative net interaction obtained could be sufficient to cause local exclusion of sandpipers for various values of adult sandpiper survival rate observed in the wild. Overall, our results indicate that predator-mediated effects could explain the low occurrence of Arctic-nesting shorebirds in areas of high goose nesting density [23,28,49].

The strength of the negative indirect interaction of geese on sandpipers was potentially underestimated due to a combination of factors. First, in addition to reducing home range size, the presence of abundant resources could also increase overlap between fox home ranges [33,50]. This was not taken into account in our models because adjacent fox home ranges were not systematically monitored. Second, in addition to causing lower egg survival, higher fox density is likely to reduce chick survival. However, empirical data on chick survival are limited because sandpiper chicks leave the nest shortly after hatching. Finally, a higher density of avian predators within the goose colony [23] may also decrease survival rate of sandpiper chicks. These three factors would have amplified the strength of the negative effect of the presence of geese on sandpipers.

Along with changes in the predator home range size, additional components of predator behaviour are likely to change in the presence of geese and more data is needed to fully explore the possible links between those parameters. Our sensitivity analysis indicated that three parameters have a notable influence on sandpiper nesting success, namely (i) daily distance travelled by the predator, (ii) proportion of time spent active by the predator and (iii) sandpiper nest detection probability by the predator. We recognize that further field investigations, such as long-term GPS and accelerometer tracking of predators over a wide range of prey densities, are needed to investigate the effect of prey densities on the value of predator movement parameters. This would be especially important in our study system since changes in these movement parameters are known to be related to lemming density [15]. Regarding the detection probability of sandpiper nests, there is no evidence that this parameter is affected by the presence of geese. This absence of effect probably reflects that attacking sandpiper nests provides systematic benefits to foxes and entails very low costs (e.g. risk of injury, handling time; [15]).

Predator-mediated interactions in natural systems have been investigated using various approaches, including statistical analyses linking prey occurrence probability with density of other prey [28,51], and field experiments involving the addition or removal of prey or predator species [52,53]. Although these approaches can help identify the presence of indirect effects, they provide a limited ability to tease apart and infer proximate mechanisms underlying biotic indirect interactions. Moreover, field experiments in natural food webs can be impossible to implement when predator home range size is large (but see [7]). Although extensive empirical data and detailed knowledge of the study system are needed to use a mechanistic approach, the growing number of technologies allowing remote monitoring of wildlife behaviour (e.g. high-frequency GPS, acoustic and heart rate monitoring devices) should facilitate the application of this approach to more complex systems [54–56].

Variations in the shape of the functional response can have important ecological consequences for the structure and dynamics of communities by altering the coexistence among prey, and the strength and signs of the interactions among them [57–61]. However, very few empirically based, multispecies functional responses have been developed [13,14]. The evaluation of functional response using phenomenological models often fails to discriminate between different response shapes (e.g. between a type 2 and 3) [62], which limits our ability to quantify the strength of predator-mediated interactions in the wild. Although strong empirical foundation of multispecies functional response in natural communities is lacking, they are widely used in predator–prey models [17,19,63–65]. To our knowledge, our study provides a rare empirically based model that integrates mechanistic multi-species functional responses while also taking into account behavioural processes underlying the numerical response of a generalist predator. Our study is a step towards mechanistic approaches and should increase our ability to accurately quantify the consequences of predation on wild animal community structure and dynamics.

Our results show that finer-scale behavioural processes may actually be the main drivers of predator density and prey persistence in the wild. Along with the link between predator home range size and prey availability [20,21,66], other processes could be explored such as the presence of predator social or aggressive interactions and predator group hunting. For instance, we might expect overlap between predator home ranges to vary with the abundance of food resources (e.g. higher overlap when prey density is very high or very low; [67]). In arctic foxes, this could occur during years of low lemming density, in absence of a goose colony or when foxes mainly feed on unpredictable prey (e.g. carcasses). Such effects remain to be explored. As pointed out by [13], our understanding of numerical responses is much more limited than functional responses. To date, the numerical response is typically modelled through demographic processes in classical models (see MacArthur–Rosenzweig equations; [18]). Our approach takes into account diverse proximate mechanisms

underpinning interaction strengths in a multi-prey system and generates novel insights on some of the predator behavioural responses that may influence prey coexistence (or the lack thereof) in vertebrate communities. Overall, this study underlines the need to explicitly investigate the consequences of various behavioural processes underlying predator numerical response.

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