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RESEARCH ARTICLE

Predator home range size mediates indirect interactions between prey species in an arctic vertebrate community

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Abstract

1. Indirect interactions are widespread among prey species that share a common predator, but the underlying mechanisms driving these interactions are often unclear, and our ability to predict their outcome is limited.
2. Changes in behavioural traits that impact predator space use could be a key proximal mechanism mediating indirect interactions, but there is little empirical evidence of the causes and consequences of such behavioural-numerical response in multispecies systems.
3. Here, we investigate the complex ecological relationships between seven prey species sharing a common predator. We used a path analysis approach on a comprehensive 9-year data set simultaneously tracking predator space use, prey densities and prey mortality rate on key species of a simplified Arctic food web.
4. We show that high availability of a clumped and spatially predictable prey (goose eggs) leads to a twofold reduction in predator (arctic fox) home range size, which increases local predator density and strongly decreases nest survival of an incidental prey (American golden plover). On the contrary, a scattered cyclic prey with potentially lower spatial predictability (lemming) had a weaker effect on fox space use and an overall positive impact on the survival of incidental prey.
5. These contrasting effects underline the importance of studying behavioural responses of predators in multiprey systems and to explicitly integrate behavioural-numerical responses in multispecies predator–prey models.

KEYWORDS
apparent competition, arctic, home range, indirect effects, numerical response, predation, prey, tundra

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Pierre Legagneux, Joël Bêty and Dominique Berteaux share equal authorship.

1 | INTRODUCTION

Interspecific interactions are central to the functioning of ecological communities and can be a critical driver of species distributions (Case et al., 2005; García-Girón et al., 2020). In their simplest form, co-occurring species have direct impacts on each other through mechanisms such as competition, facilitation and predation, the strength and outcome of which shape species ability to coexist. However, predicting the effect that a species has on another species becomes increasingly complex as the size of the ecological network increases (Godsoe et al., 2017), and co-occurrence alone is a poor proxy of ecological interactions (Blanchet et al., 2020). This is largely due to indirect interactions that connect species together through chains of direct interactions with one or multiple mediating species. Untangling the mechanisms that link species across systems is key to understanding what structures ecological communities.

Indirect interactions are widespread among prey species that share a common predator (Holt & Bonsall, 2017). They occur when the availability of one prey species increases (apparent competition) or reduces (apparent mutualism) predation pressure on an alternate prey through the response of the shared predator (Holt, 1977; Holt & Bonsall, 2017). The resulting effect on the receiving species depends on two main mechanisms: how fluctuating prey availability changes predator per capita acquisition rate (the functional response) and how it impacts predator number (the numerical response) typically through changes in demographic rates (Solomon, 1949). Fluctuations in prey density can also modulate predator behaviour, causing swift changes in predator local density (behavioural-numerical response or aggregative response) with consequential impacts on alternate prey species (Holt & Kotler, 1987). For example, in subtidal cobble reefs, experimentally increasing bivalve density (a favoured prey) led to the local aggregation of predators, in turn reducing the survival of co-occurring gastropods (an alternate prey) (Schmitt, 1987). In coastal ecosystems, the behavioural response of a fearful mesopredator (racoon) exposed to playbacks of a large carnivore (dog) reduced its local abundance and foraging efforts, thereby strongly benefitting its prey (crabs, fish and worms) (Suraci et al., 2016). Such changes in predator behavioural traits typically respond faster to fluctuating prey density than demographic rates and could be a primary mechanism driving indirect interactions (Werner & Peacor, 2003). Recent empirical-based models also indicate that numerical response mediated by changes in predator space use, especially home range size, can ultimately affect prey species coexistence in the wild (Beardsell et al., 2023).

Home range formation is a fundamental behavioural trade-off that acts as the primary link between environmental fluctuations and local predator density, especially in territorial animals (Grant & Kramer, 1990; López-Sepulcre & Kokko, 2005). Home ranges are usually smaller as resource quality and abundance increase (Loveridge et al., 2009; Sells et al., 2022) and are shaped by resource characteristics such as their spatial distribution, predictability and accessibility (Dickie et al., 2022; Maher & Lott, 2000). The home range size of a predator should reflect a dynamic compromise between the benefits of prey acquisition and the combined costs of movements and competitive interactions with peers (Hixon, 1980; Schradin et al., 2010). Surprisingly, empirical and theoretical evidence of the ultimate consequences of these variations in home range size for prey species are still scarce.

The relationships between the abundance of multiple distinct prey species and predator home range size, and the consequences of changes in predator home range size on prey demographic parameters, are rarely quantified in natural communities (Beardsell et al., 2023). This strongly reduces our ability to (i) fully integrate behavioural-numerical responses in multispecies predator–prey models and (ii) identify the dominant mechanisms driving predator-mediated interactions in the wild. Here, we use a comprehensive 9-year data set simultaneously tracking predator space use, prey densities and prey mortality rate in a simplified Arctic food web to investigate the role of behavioural-numerical response (predator space use) in mediating indirect interactions among prey species. Specifically, we combine spatial and demographic data from seven prey species and their common predator to (1) assess the interacting effects of the primary prey species (snow goose *Anser caerulescens atlanticus*, brown lemming *Lemmus trimucronatus* and collared lemming *Dicrostonyx groenlandicus*) on the home range size of a shared predator (arctic fox *Vulpes lagopus*), (2) quantify the consequences of changes in predator home range size on nest survival of sympatric incidental prey species (American golden-plovers *Pluvialis dominica*, Lapland longspurs *Calcarius lapponicus*, Baird's sandpiper *Calidris bairdii* and White-rumped sandpiper *Calidris fuscicollis*), and (3) test the hypothesis that adjustment in predator home range size can be a key proximal mechanism mediating apparent competition in terrestrial arctic communities.

Our long-term study was conducted in the arctic tundra where large numbers of migratory birds, and small rodent species, share a common territorial and generalist predator, the arctic fox. The study system includes multiple contrasted prey species, with lemmings showing strong interannual variations in abundance, and goose eggs that are spatially clumped and predictable in both space and time. For many birds, fox predation is the primary cause of nest failure (Bety et al., 2002; McKinnon & Bêty, 2009; Smith et al., 2007). This shared predation generates numerous predator-mediated interactions among the prey (Bety et al., 2002; Mckinnon et al., 2013; Nolet et al., 2013; Summers et al., 1998), which can impact their population dynamics (Beardsell et al., 2023; Nolet et al., 2013) and distribution (Duchesne et al., 2021; Lamarre et al., 2017; Léandri-Breton & Bêty, 2020). The proximal mechanisms driving these indirect interactions are uncertain. Interestingly, the different prey types (cyclic lemmings and goose eggs) induce opposing indirect effects (Duchesne et al., 2021), leading to either short-term apparent mutualism (Bêty et al., 2001; McKinnon et al., 2014; Pedersen et al., 2018) or apparent competition (Flemming, Nol, et al., 2019; Lamarre et al., 2017; Mckinnon et al., 2013) with other incidental prey. Indeed, predation risk for nesting birds is generally released at high lemming abundance (Bêty et al., 2001; McKinnon et al., 2014) partly due to predators spending less time foraging and travelling smaller distances within their home range (Beardsell et al., 2022), whereas high availability of goose eggs increases nest predation risk for prey species located in the goose colony (Lamarre et al., 2017; Mckinnon et al., 2013), likely through predator numerical response (Beardsell et al., 2023; Giroux et al., 2012; Lamarre et al., 2017). Arctic fox presents strong territoriality (Grenier-Potvin et al., 2021), and home range size is expected to vary according to prey availability (Eide et al., 2004; Pletenev et al., 2021). Variations in home range size of resident adults can affect fox density and could act as a key mechanism mediating indirect interactions among tundra nesting birds.

As a result of the economical trade-off between the benefit of prey acquisition and the combined costs of movements and competitive interactions, we expected fox home ranges to be smaller when their primary prey, lemmings and goose eggs, are more abundant (P1). Second, we expected that nests of incidental prey (shorebirds and passerines) located in smaller fox home ranges would have lower survival rates (P2) given their exposure to a higher local predator density. Finally, we expected that the direct effects linking goose egg availability to home range size and home range size to nest survival of incidental prey would explain the previously reported apparent competition between geese and incidental prey in this system (Duchesne et al., 2021; Lamarre et al., 2017; Mckinnon et al., 2013), with no remaining relationship between goose nest availability and incidental prey nest survival after controlling for fox home range size (P3).

2 | MATERIALS AND METHODS

2.1 | Study system

Field work was conducted from 2008 to 2016 in the southwest plain of Bylot Island (72°530N, 79°540W), in Sirmilik National Park, Nunavut, Canada. The landscape is mostly composed of mesic tundra, with complex polygon networks and wet meadows in the valley bottoms. The study area is ~500 km^2 and includes a large snow goose colony where ~20,000 pairs nest annually over ~70 km^2 (Reed et al., 2002). Goose nesting density and the extent and location of the colony are relatively stable across years (Duchesne et al., 2021; Gauthier et al., 2013).

The arctic fox is the main terrestrial predator on Bylot. It primarily preys on brown and collared lemmings and on the eggs of greater snow geese. Lemmings are resident, distributed over the entire study area and follow marked cycles of abundance with a period of 3–4 years (Fauteux et al., 2015; Gruyer et al., 2008). They are virtually absent during years of low density, with a combined wet biomass of less than 0.8 kg/km^2, and may reach up to 35 kg/km^2 during peak years (Figure 1). On the contrary, goose eggs are consistently available during summer, are massively stored by foxes for consumption in later seasons when prey are scarce (Careau et al., 2008; Samelius et al., 2007) and are clumped in a colony with high spatial predictability. Over the 9 years of the study, goose eggs represented an average wet biomass of 74 kg/km^2 (range 29–112 kg/km^2; Figure 1) in the colony. In addition to these primary prey, foxes opportunistically consume the eggs of all other tundra nesting birds, referred to as incidental prey. Among these are passerines such as Lapland longspur, as well as shorebirds including Baird's sandpiper, White-rumped sandpiper and American golden plover, which are mainly found in mesic habitat and distributed over the entire study area. While these incidental prey are consumed by foxes upon encounter, they occur at low densities and represent negligible biomass (Beardsell et al., 2021; Duchesne et al., 2021). Their own influence on fox movement and home range size is thus likely minimal.

2.2 | Fox capture

Foxes were captured in May–August 2008–2016 using methods described in Lai et al. (2015). They were sexed, marked with ear tags and equipped with Argos transmitters mounted on collars (KiwiSat 202 and 303, Lotek, Newmarket, Ontario, Canada; 95–115 g; <5% of body mass). Transmitters provided a location every 1 or 2 days depending on settings. Dens were monitored from May to July using automated cameras, and the reproductive status of marked individuals was determined based on the presence or absence of pups on their dens (Chevallier et al., 2020).

2.3 | Home range estimation

We quantified fox's annual home range (95% isopleth) using autocorrelated kernel density estimation (Fleming et al., 2015) implemented in the ctmm R package (Calabrese et al., 2016). This approach accounts for location accuracy and provides a reliable measure of the estimation error associated with each home range contour. We estimated fox annual home ranges using locations collected between 01 May and 30 October, to maximize data between the onset of goose laying and the end of the ice-free season (Lai et al., 2017). We used filtered Argos locations as available in the Movebank data repository (Berteaux, 2020), and only kept the most precise positions with location classes LC3 and LC2, which correspond to positioning errors having a 68% probability of being <250 and <500 m (CLS, 2016). As advised in Fleming et al. (2015), we then made scatter plots of the relocation data and calculated empirical variograms to identify and remove obvious extraterritorial trips and to ensure that all foxes included in the analyses showed range residency. An appropriate home range model was selected for each individual using Akaike information criterion (AICc) to compare different movement processes (independent identically distributed, Ornstein–Uhlenbeck, integrated Ornstein–Uhlenbeck, Ornstein–Uhlenbeck Foraging; see Calabrese et al. (2016) for information on movement processes). We estimated the area of the 95% home range contour for each individual-year based on the selected models and extracted the variance of each home range area to account for estimate uncertainty in subsequent analyses. All estimated home range contours are shown in Appendix S1.

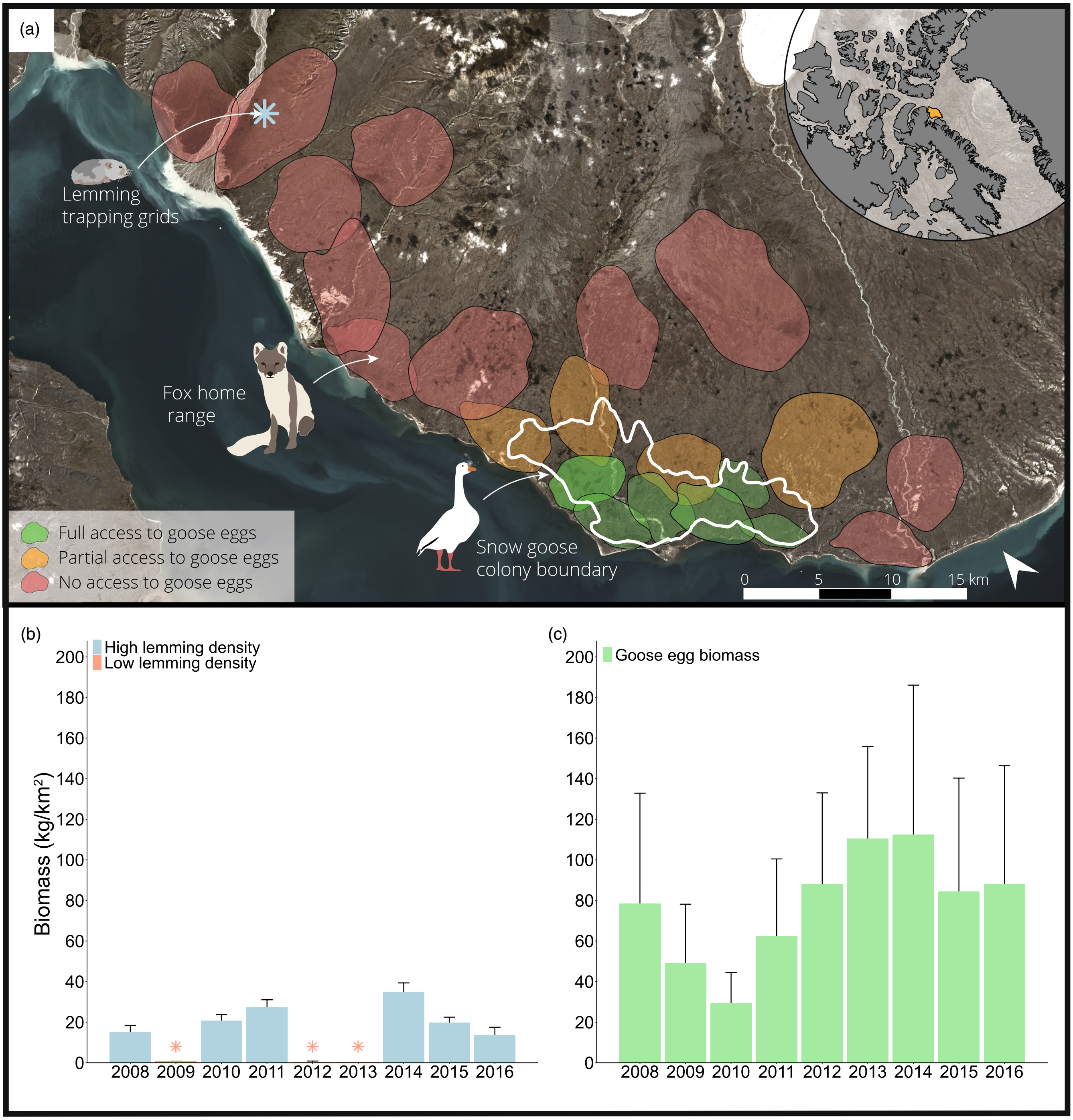

FIGURE 1 (a) Bylot island study area with the location of lemming trapping grids, the goose colony boundary and a subset of fox home ranges. All estimated home ranges and annual colony boundaries are shown in Appendix S1. Incidental prey nest survival was monitored within each home range. Panels (b, c) show the biomass of fox main prey, lemmings and greater snow goose eggs, within the study area (2008–2016). Lemming biomass was estimated using the combined density of brown and collared lemmings, multiplied by the average mass of adults on Bylot Island (respectively 51 and 57 g). Goose egg biomass was estimated annually by multiplying (1) nest density calculated as the proportional average nest density in mesic and humid habitats based on systematic surveys, (2) average clutch size and (3) average goose egg mass upon laying on Bylot Island. Years of low lemming biomass are annotated with a star. Note that lemmings are available all year, while only cached eggs are available outside the 1-month nesting period.

To investigate and rule out potential biases in home range size due to the low accuracy and low frequency of Argos locations, we simulated Argos location error and frequency on high-resolution GPS data obtained in the same population in 2018 and 2019 (Clermont, Grenier-Potvin et al., 2021). This allowed us to compare home range sizes obtained from GPS data degraded to reflect the lower quality of Argos data (see Appendix S2), to home range sizes obtained from nondegraded GPS data. Home range estimates from both data sets were highly correlated ($r^2 = 0.7$; Appendix S2), although home ranges from degraded data were consistently 30% larger. To ensure that home range sizes reported in our study are comparable to those calculated from GPS data, and thus informative of fox true local density, we used the relationship between home range sizes obtained from degraded and nondegraded GPS data to scale all home ranges included in the manuscript (See Appendix S2 for details on validation and scaling of home ranges). This facilitated biological interpretation with no impact on the results as all home ranges were adjusted using the same scaling factor.

2.4 | Primary prey availability

Foxes whose home range overlaps the goose colony have access to goose eggs, while others do not. In contrast, all foxes in the study area benefit from the additional food generated by years of high lemming density. This produces highly contrasted prey availability across space and time. We thus classified each annual fox home range based on its spatial location relative to the goose colony (to reflect goose egg availability) and on the annual density of lemmings (to reflect lemming availability).

We traced the contour of the goose colony every year from 2010 to 2016 during the incubation period using a GPS receiver aboard a helicopter. The contour of the colony was not mapped in 2008 and 2009. The centroid location and spatial extent of the colony are stable across years (Duchesne et al., 2021). We therefore used the contour of the earliest recorded year, 2010, to classify home ranges of foxes tracked in 2008 and 2009. Using the colony contour, we classified each fox home range into one of three classes of goose availability: (1) centroid of home range inside the goose colony—*full access*, (2) centroid outside of the colony but home range overlaps the colony—*partial access* and (3) centroid outside the goose colony and no overlap—*no access*.

Lemmings were live-trapped in two 11-ha permanent grids, one in wet and one in mesic habitat, to obtain mark–recapture estimates of density as described in Fauteux et al. (2015). The trapping grids are located within the study area about 30 km north of the goose colony centroid. Trapping sessions were conducted in June, July and August with 144 Longworth traps deployed in each grid and checked twice a day during three consecutive days. Captured lemmings were identified to species, marked with unique ear-tags and a Passive Integrated Transponder tag (Avid Identification Systems, Norco, CA, USA), and all subsequent recaptures were noted. We used the average density for all three sessions and both lemming species to obtain annual lemming density. We then classified each annual fox home range into one of two classes of lemming density, that is low (<14.2 lemming/km^2) or high (>235.2 lemmings/km^2). No intermediate lemming density was observed during the study period. Given the work-intensive protocol used to estimate lemming densities, we could not survey lemmings in each fox home range. However, systematic records of incidental field observations suggest that fluctuations in lemming density within the goose colony and the lemming trapping grids are synchronized (Appendix S3). Moreover, the two lemming density categories we used are closely reflected by fox breeding propensity throughout the study area (Giroux et al., 2012; Juhasz et al., 2020), which further suggests overall synchrony. The home range of a given fox in a given year could thus fit one of six prey availability categories (3 goose × 2 lemming availabilities).

2.5 | Nest predation risk for incidental prey

To assess how changes in fox home range size impact nest survival of incidental prey, we monitored shorebird and passerine nests each year from mid-June to mid-July (Lamarre et al., 2017). Nests were found opportunistically or through line transect surveys conducted within fox home ranges across the study area, both inside and outside the goose colony. Lay date and expected hatch date were calculated for nests found during laying, or estimated using the flotation method for nests found during incubation (Liebezeit et al., 2007). Nest status was assessed every 2–6 days, increasing monitoring efforts when nearing the expected hatch date. A nest was considered successful if at least one egg hatched, or if one of the following criteria was met: (1) small fragments of residual egg shells were found in the nest material close to the expected hatch date, (2) the nest was hatching (starred or pipped) on the last visit and was empty on the following visit and (3) the nest was empty on the last visit and the banded adult was resighted with chicks (McKinnon et al., 2014).

2.6 | Data analyses

To evaluate the relationship between the availability of fox primary prey and fox home range size (P1), we used a linear mixed model fitted with log-home range size as the response variable, and goose egg availability (three-level factor), lemming density (two-level factor) and their interaction as fixed effects. Sex and reproductive status of foxes could impact home range size and were thus included as fixed covariates. Fox identity and year were included as random intercepts to account for repeated measurements. Foxes live in pairs sharing a common home range, so pair mates were given the same fox identity to reflect this strong dependency. We included the variance of each home range size as weight in the linear model to reflect the fact that our response variable was estimated (see home range estimation above). Home range sizes were log-transformed to respect the assumption of normality in model residuals.

2.7 | Path analysis

To evaluate the hypothesized causal relationships linking primary prey availability, fox home range size and nest survival of incidental prey (P2, P3), we used a restricted data set of complete cases within a path analysis framework (Shipley, 2009). A path analysis evaluates the plausibility of a causal model that links a set of variables together through direct and indirect relationships (Shipley, 2009). This is done by performing a simultaneous test of all conditional independence claims, known as a directional-separation test, implied by the hypothesized causal model (Shipley, 2000). The causal model is considered consistent with the data if the sum of all its conditional independence claims is no different from a chi-squared distribution (that is, if the test statistic, Fisher's *C*, is above the significance threshold, set here at 0.05). The path analysis routine was fitted separately for American golden plovers, Sandpipers (including nests of Baird's and White-rumped sandpipers), and Lapland longspurs. We thus kept for each path analysis only those home ranges in which nest survival was monitored for a given incidental prey species.

The models linking prey availability to home range size were the same as those used to test P1, with log-home range size as the response variable, lemming and goose egg availability as fixed effect, as well as fox identity and year as random intercepts. Given the small sample size and the weak and nonsignificant effects of reproductive status and sex on home range size in the previous analysis (see results), we did not include these variables in the path analysis. In addition, goose egg availability was fitted as a two-level categorical variable (*full access* and *no access*) instead of a three-level variable because the restricted data sets contained ≤5 *partial access* home ranges, causing convergence issues when included. Home ranges with *partial access* were therefore excluded from this analysis.

The paths linking home range size to nest survival 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 variations in the length of nest monitoring period. The model was fitted with survival as a binary response variable (1: success, 0: failed), log-home range size as a fixed effect and fox identity nested within year as random variables to control for variation in the number of nests monitored within each annual home range. Exposure time was calculated as the number of days elapsed between the date a nest was found and one of the following dates: (1) for successful nests, observed or estimated hatch date, (2) for failed nests, observed predation date or mid-point between the date when fate was determined and the last date when the nest contained eggs and (3) for nests with undetermined fate, date of the last visit for which a status was recorded. For all models described above, there was no multicollinearity (all VIF <2) among variables included in the same model. Statistical analyses were done in R version 4.2.3 (R Core Team, 2021).

3 | RESULTS

3.1 | Effects of main prey on fox home range size

We estimated 170 annual home ranges from 109 foxes over 9 years and belonging to 91 pairs of known reproductive status. Home range size varied from 4.7 to 65.3 km^2 with a median of 14.9 km^2. Lemming densities varied from 1.6 to 647.9 lemmings/km^2 with 3 years (2009, 2012, 2013) classified as low lemming density and 6 years as high lemming density (Figure 1a shows annual biomass). Goose nest density was generally stable across years, averaging 178 nests/km^2 (SD = 62, range = 66–257) (Figure 1b shows annual biomass).

The availability of goose eggs had a strong effect on fox home range size (Figure 2; Table 1). In years of low lemming abundance, foxes with full access to the goose colony had home ranges on average 2 and 2.5 times smaller, respectively (estimate [95% CI] = 11.3 [8.24, 15.4] km^2) than those with partial (22.1 [16, 30.5] km^2) or no access (28.1 [19.6, 40.2] km^2) to goose eggs. The same pattern was observed when lemmings were abundant (Figure 2), with home range size being 1.4 times smaller for foxes that had full access to the colony (12.9 [10.4, 16.1] km^2) compared to those with partial (17.2 [13.5, 22.0] km^2) or no access (18.3 [14.7, 22.8] km^2). Similarly, increasing lemming density reduced fox home range size, but the effect was weaker and only present for foxes with limited or no access to goose eggs (Table 1). Indeed, home range size was 1.2 and 1.3 times smaller at high compared with low lemming densities for foxes with partial or no access to goose eggs, respectively, while home range size did not vary with lemming density for foxes with full access to the colony (Figure 2). Reproductive foxes had slightly larger home ranges than nonreproductive ones, but this effect was not conclusive, with confidence interval marginally overlapping 0. Fox sex had no detectable effect on home range size. Among foxes with partial and no access to the goose colony during years of high lemming density, three individuals had particularly large home ranges (Figure 2). When these three individuals were excluded, all effect sizes and confidence intervals remained virtually unchanged (Appendix S4); therefore, results are presented with these individuals included.

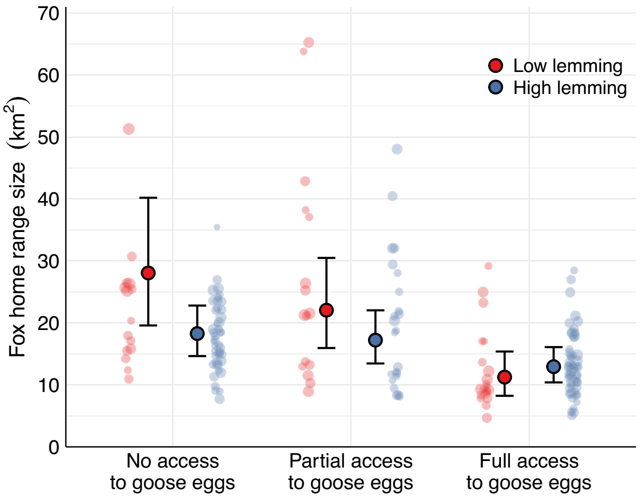

FIGURE 2 Influence of prey availability on home range size of foxes on Bylot Island, Nunavut (2008–2016). Dots and error bars represent the mean and 95% confidence intervals of home range size predicted after accounting for sex, reproductive status, year and individual pair identity. The jittered dots show raw home range estimates, and dot sizes reflect precision of the estimate (1/variance), with smaller dots indicating less precise estimates.

3.2 | Indirect effect of primary prey on incidental prey through fox home range size

To test the effect of home range size on nest survival of incidental prey and perform the path analyses, each incidental prey species was analysed separately. Our data sets contained 116 nests monitored in 37 fox home ranges over 9 years (American golden plover), 110 nests monitored in 17 fox home ranges over 9 years (sandpipers) and 200 nests monitored in 16 fox home ranges over 7 years (Lapland longspur). We verified that the relationships linking prey availability to fox home range size were still present with these reduced data sets. We confirmed a strong negative effect of goose egg availability on fox home range size for the American golden plover (Table S3; Appendix S5) and Lapland longspur (Table S4; Appendix S5) data sets. Coefficient estimates were also consistent with a weak negative effect of lemming density dampened inside the goose colony, but the effect was no longer significant in these two data sets. There were no significant relationships in the sandpiper data set (Table S5; Appendix S5).

TABLE 1 Generalized linear mixed model testing the effect of prey availability on arctic fox home range size at Bylot Island, Canada (2008–2016). Conclusive fixed effects are in bold.

	Fox home range size
Predictors	**Estimates [95% CI]**
(Intercept)	3.23 [2.91, 3.55]
Partial access to colony	−0.24 [−0.52, 0.03]
Full access to colony	**−0.91 [−1.19, −0.64]**
High lemming	**−0.43 [−0.84, −0.02]**
Sex [M]	−0.01 [−0.11, 0.08]
Breeder	0.11 [−0.07, 0.28]
Partial access × High lemming	0.18 [−0.14, 0.5]
Full access × High lemming	**0.57 [0.27, 0.87]**
Random effects	
$\tau_{00\text{ fox pair}}$	0.08
$\tau_{00\text{ year}}$	0.04

Note: $n_{\text{total}}=170/n_{\text{year}}=9/n_{\text{fox pair}}=91$.

For American golden plover, the path analysis confirmed that the structure of the data was consistent with the hypothesis (P3) that fox home range size is the proximal mechanism mediating apparent competition between geese and plover nest survival (Fisher's $C_2=0.03$, p-value$=0.98$). Nest survival of American golden plovers increased steeply with fox home range size, with most variation occurring in the lower end of the home range distribution and an inflection point at 11.5 km^2 (Figure 3a). As fox home range size ranged from 5 to 12 km^2, nest survival over the average 10-day monitoring period went from 0 [0, 23]% to 55 [11, 86]%. It then reached 80 [49, 95]% at 15 km^2 and plateaued afterward. Thus, the availability of goose eggs directly reduced fox home range size, which in turn reduced plover nest survival (Figure 4). After accounting for fox home range size, there was no remaining effect of the goose colony on plover nest survival. On the contrary, despite the weak negative effect of lemming availability on fox home range size detected when testing our first prediction, lemmings had a positive overall effect on plover nest survival (Figure 4; Appendix S6).

For sandpipers (Figure 3b) and Lapland longspurs (Figure 3c), there was no detectable relationship between fox home range size and nest survival. In both groups, only lemming availability had a

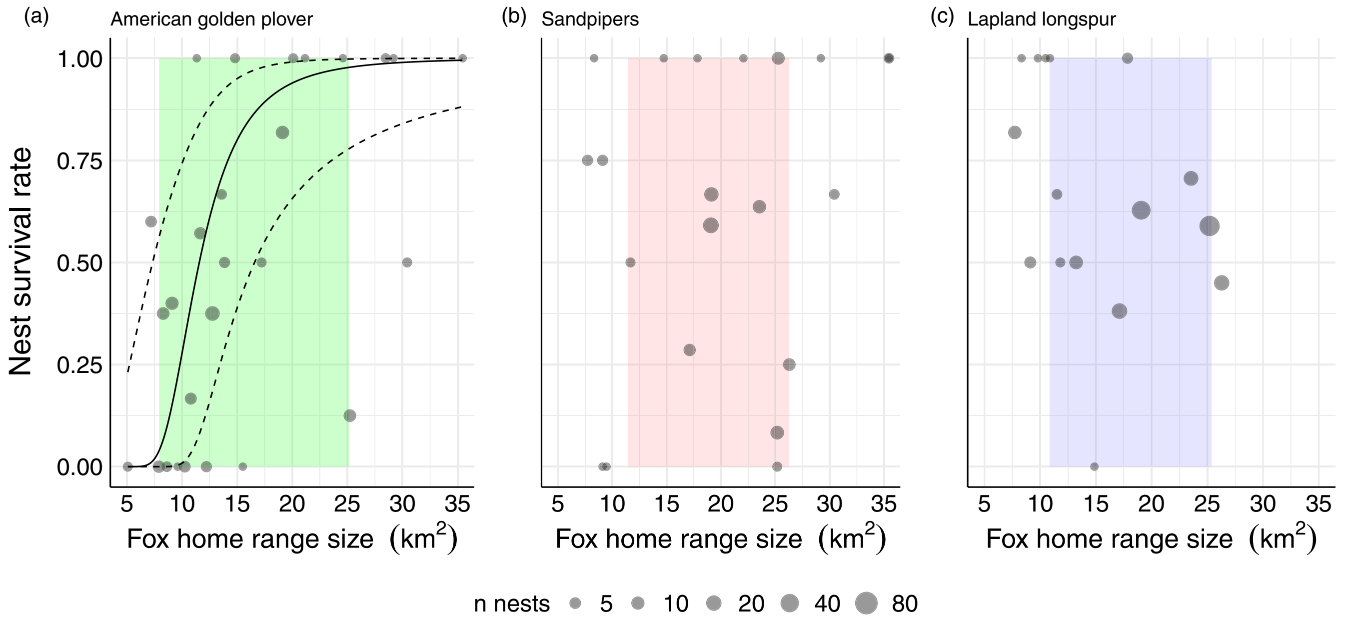

FIGURE 3 Influence of fox home range size on 10-day nest survival rates of (a) American golden plovers, (b) sandpipers, and (c) Lapland longspur on Bylot Island, Nunavut (2008–2016). The full line is the mean model prediction over the average nest monitoring period (10-days) and is presented with its 95% CI. The dots are raw nesting success averaged over equally sized intervals. Shaded areas represent the distribution of home ranges that include 90% of monitored nests for each species.

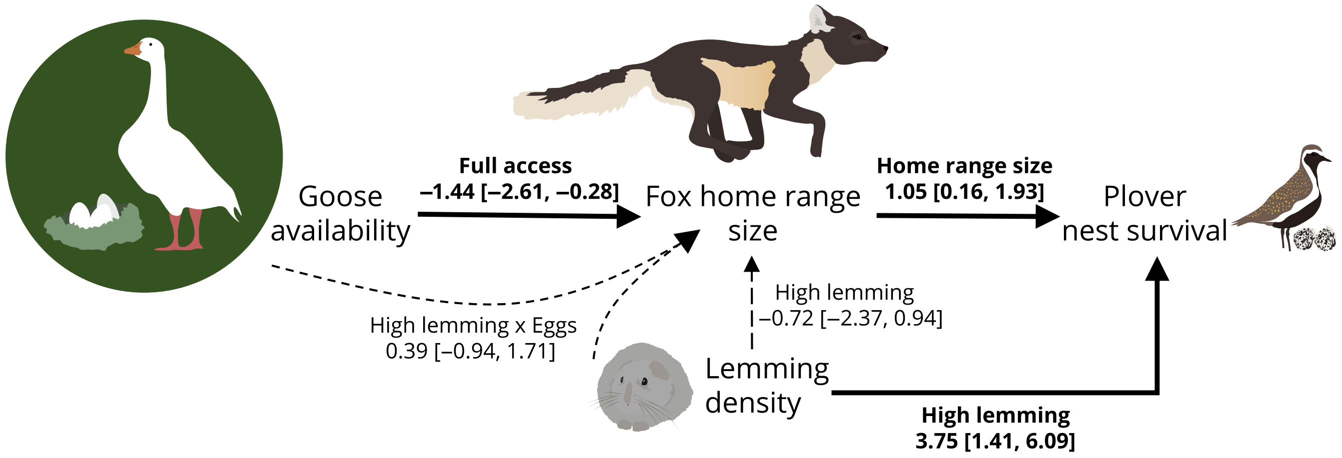

FIGURE 4 Direct and indirect relationships between primary prey availability, fox home range size and American golden plover nest survival at Bylot Island, Nunavut (2008–2016). Standardized path coefficients (95% CI) are presented above each path. Solid and dashed lines, respectively, represent conclusive and inconclusive relationships. The model was consistent with the structure of the data (Fisher's $C_2 = 0.03$, $p = 0.98$).

conclusive and positive effect on nest survival (Appendix S6). The distribution of home range sizes in the sandpipers and Lapland longspurs analyses was narrower and included fewer small home ranges than for American golden plovers (Figure 3), with 22 individual home ranges under 12 km^2 for plovers compared to only five for sandpipers and nine for Lapland longspurs. To assess the impact of this discrepancy in the distribution of home range sizes, we again ran the analysis on plover keeping only home ranges over 12 km^2 and found no conclusive relationship. This indicates that apparent differences observed between prey species could be due to sample sizes.

4 | DISCUSSION

Our study provides empirical evidence of the role of behavioural-numerical responses, through changes in predator space use, as a driver of indirect interactions in an arctic vertebrate community. Benefitting from a 9-year data set based on the simultaneous monitoring of multiple prey species and their common predator, we show that high availability of primary prey (lemmings and geese) contracts predator (arctic fox) home range, which increases effective predator density and reduces nest survival of an incidental prey (American golden plover). This behavioural-numerical response was strongest in the dense and spatially predictable goose colony, and fully accounted for the apparent competition associated with this prey species. Lemming abundance had a weaker effect on fox home range size and an overall positive impact on incidental prey. These contrasting effects underline the importance of studying behavioural changes of predators in multiprey systems and to explicitly integrate behavioural-numerical responses in multispecies predator–prey models.

As expected, high availability of goose eggs and lemmings both reduced the size of fox home ranges. This is consistent with previous studies (Loveridge et al., 2009; Sells et al., 2022), including in arctic fox (Angerbjörn et al., 1997; Eide et al., 2004; Pletenev et al., 2021), suggesting that high resource availability should tip the economical trade-offs of home range formation towards smaller home ranges. However, the effect of the goose colony was stronger than that of lemming, and variations in lemming density had no detectable effect on home range size when foxes were inside the goose colony. Having access to an abundant alternative prey, here goose eggs, might have allowed foxes to maintain small home ranges in years of low lemming density. Nonetheless, home ranges in the colony were not further reduced in years of high lemming density, when the combined abundance of both prey type was likely higher than when only goose eggs were available. There are multiple differences between these two prey types that can help understand their respective effects on fox home range size. Goose nests are highly concentrated within the colony, offering higher food density compared with lemmings even during years of high lemming abundance. Spatial clumping of food resources can facilitate the formation of small home ranges (Maher & Lott, 2000; Pletenev et al., 2021) as individuals may reduce the costs of movements and competitive interactions, while still fulfilling their energetic needs. In addition, the goose colony provides a consistent and spatially predictable food resource, whereas there are marked annual variations in lemming abundance and their spatial distribution is potentially more heterogenous (Gruyer et al., 2008). In high lemming years, foxes throughout the study area benefit from abundant lemming prey, which consistently translates into higher proportion of breeding dens (Giroux et al., 2012; Juhasz et al., 2020). Nonetheless, small-scale spatial variations in lemming density within each home range could have been missed by our annual estimates. Such spatial heterogeneity could have reduced our ability to detect stronger effects for this prey as well as decrease its overall predictability for foxes. On the contrary, given the high spatiotemporal predictability of the goose colony, the benefits of adjusting their home range to prey abundance might be higher for foxes established in the colony compared to those relying on the less predictable prey. In addition, goose eggs are heavily cached by foxes for future consumption (Careau et al., 2008; Samelius et al., 2007). Stored eggs increase the long-term value of home ranges located in the colony, benefiting foxes who maintain small stable home ranges and potentially providing information on habitat quality to newcomers. Lastly, although we could not delineate the defended part of the home range, previous studies have shown strong territoriality among foxes in the colony (Clermont, Grenier-Potvin et al., 2021; Grenier-Potvin et al., 2021). The higher abundance, spatial clumping, predictability and storage potential of goose eggs could attract a higher number of foxes towards the colony and increase competition compared to elsewhere on the island, thus promoting smaller home ranges.

Nest survival of plovers declined drastically as fox home ranges became smaller. This behavioural change in predator space use largely explained the known negative predator-mediated interaction between geese and plovers (Duchesne et al., 2021; Lamarre et al., 2017; Mckinnon et al., 2013) as there was no remaining effect of the goose colony on plover nest survival after accounting for fox home range size. The absence of remaining effect also suggests that other mechanisms, such as prey switch (Murdoch, 1969), are not primary mediators of the variations in predation rates associated with the goose colony. The small reduction in home range size associated with high lemming abundance outside the goose colony might also have reduced plover nest survival, but this effect seemed completely buffered by the previously reported positive indirect interaction between lemmings and fox incidental prey (Duchesne et al., 2021; McKinnon et al., 2014). This suggests that other behavioural changes associated with fox response to lemming density released predation pressure on incidental prey when lemmings were abundant. For instance, foxes reproduce massively when lemmings are abundant (Juhasz et al., 2020) and time-consuming behaviours associated with parental care (e.g. cub thermoregulation, lactation, grooming) might reduce fox distance travelled and activity time, thereby lowering encounter rate with incidental prey (Beardsell et al., 2022). Decreasing foraging efforts when food is abundant (Harding et al., 2007) or adjusting prey preference as a function of prey density (i.e. prey switch; Murdoch, 1969) could also release predation on incidental prey. While these mechanisms have yet to be fully explored in our system (Beardsell et al., 2022), the contrasted effects of the two primary prey highlight the importance of studying the behavioural responses of predators, and integrating these responses in predator–prey models.

There was no detectable effect of fox home range size on nest survival of sandpipers and Lapland longspurs. We had expected these species to be impacted by fox behavioural-numerical response, as observed for the American golden plover. Indeed, all three species nest in similar habitats and cannot actively defend their nest against foxes, which should make them equally vulnerable to an increase in encounter rate caused by fox behavioural-numerical response. Potential interpretations of such lack of effect could involve species traits impacting nest detectability or attack probability, such as released odours (Grieves et al., 2022), visual camouflage (Kilner, 2006) and behaviour (Meyer et al., 2020; Smith et al., 2012). However, differences between species need to be interpreted with caution due to limitations in the available data for these analyses. In particular, the range of home range size available was narrower for sandpipers and Lapland longspurs than for American golden plovers. When subsampling the plover data set to keep only home ranges larger than 12 km^2, the relationship for this species also became inconclusive. This suggests that when home ranges are large, variations in size have little impact on nest survival of incidental prey, potentially because encounter rates remain generally low. On the contrary, the strong effect observed in plovers indicates that further contracting small home ranges quickly increases encounter rate, causing a sharp decline in nest survival. This aligns with the predictions of a recent mechanistic model calibrated for sandpipers in the same system (Beardsell et al., 2023). Based on the full distribution of home ranges observed here, the model shows steep variation in sandpipers' nest survival when home ranges are small, and a fading effect in the upper end of the distribution. Thus, although we only had clear and conclusive results for American golden plover, it seems premature to rule out that with more amenable data sets, a similar effect could be found in the other incidental prey.

Behavioural-numerical responses have been documented in other systems (Anderson, 2001; Castorani & Hovel, 2015; Chaneton & Bonsall, 2000), but rarely in a multispecies context (see Abrams (2022) for a discussion on this topic). Here, we show that the behavioural-numerical response of foxes, through changes in home range size, is the proximal mechanism driving apparent competition between geese and shorebirds in an arctic vertebrate community. Using these results, it becomes possible to calibrate mechanistic models of predation and predict how changes in geese distribution and abundance propagate through the food web to impact other co-existing prey (Beardsell et al., 2023). It could also help explain why multiple ground-nesting bird species, including shorebirds and passerines, are often found in lower abundance within goose colonies (Duchesne et al., 2021; Flemming, Smith, et al., 2019). Such behavioural changes in predators are likely common and could be a major driver structuring ecological communities (Schmitz et al., 2000; Werner & Peacor, 2003).

Monitoring fox home ranges allowed us to identify the mechanism driving apparent competition in our system, yet it did not explain apparent mutualism between lemmings and shorebirds. Accounting for changes in predator home range size is a good first step in building accurate behavioural-numerical response as information is readily available for a wide array of species (Broekman et al., 2023) and provides direct insights into local predator densities. However, home range formation is only one behavioural trait that may respond to variations in prey availability and subsequently impact other co-existing prey. There is a need for multispecies studies focussing on other predator behavioural traits such as activity budget, habitat selection, home range overlap and prey preferences to assess how they may change in relation to prey density, and most importantly what are the resulting consequences of these changes for other co-existing prey. The recent developments in biologging technologies based on high-throughput GPS tracking (Nathan et al., 2022), behavioural classification using accelerometers (Clermont, Woodward-Gagné, et al., 2021) and animal-borne sensors such as video cameras

(Brockman et al., 2017) and audio recorders (Studd et al., 2021) open up promising opportunities to study behavioural changes that shape predators' response in the wild. Ecologists and mathematical modellers should establish productive collaborations and take advantage of abundant data arising from these new technologies to fully integrate behavioural changes in predator–prey models (e.g. Beardsell et al., 2023; Northfield et al., 2017).

AUTHOR CONTRIBUTIONS

Frédéric Dulude-de Broin, Pierre Legagneux, Joël Bêty and Dominique Berteaux conceived the study. Frédéric Dulude-de Broin, Andréanne Beardsell, Pierre Legagneux, Dominique Berteaux and Joël Bêty collected the data. Frédéric Dulude-de Broin analysed the data. Frédéric Dulude-de Broin wrote the manuscript with contribution from all authors. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Fox movement data are available on Movebank (https://doi.org/10.5441/001/1.3gg33bd4; Berteaux, 2020). Estimated home range area, prey densities, nesting success and R code are available through the Dryad Data Repository (https://doi.org/10.5061/dryad.f1vhhmh30; Dulude-de Broin et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Home ranges of foxes included in the study.

Appendix S2. Reliability of Argos home range estimates.

Appendix S3. Comparison of relative lemming densities between the goose colony and the lemming trapping grids.

Appendix S4. Similar results after removing three individuals with large home ranges.

Appendix S5. Result tables for the effect of lemming and goose eggs availability on fox home range size based on the prey-specific data sets used for the path analyses.

Appendix S6. Result tables for the effect of fox home range size on incidental prey survival.

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