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Variable strength of predator-mediated effects on species occurrence in an arctic terrestrial vertebrate community

Éliane Duchesne, Jean-François Lamarre, Gilles Gauthier, Dominique Berteaux, Dominique Gravel and Joël Bêty

É. Duchesne (https://orcid.org/0000-0003-2597-3442) ✉ (eliane_duchesne@uqar.ca), J.-F. Lamarre (https://orcid.org/0000-0003-2640-1817), D. Berteaux (https://orcid.org/0000-0003-2728-5985) and J. Bêty (https://orcid.org/0000-0002-8775-6411), Dépt de Biologie, Chimie et Géographie, Univ. du Québec à Rimouski, Rimouski, Canada; Center for Northern Studies, Laval Univ., Quebec, Canada. – J.-F. Lamarre also at: Science and Technology Program, Polar Knowledge Canada, Cambridge Bay, Nunavut, Canada. – G. Gauthier, Center for Northern Studies, Laval Univ., Quebec, Canada; Dépt de Biologie, Univ. Laval, Quebec, Canada. – D. Berteaux and J. Bêty also at: Chaire de Recherche du Canada en Biodiversité Nordique, Univ. du Québec à Rimouski, Rimouski, Canada; Quebec Centre for Biodiversity Science, McGill Univ., Montreal, Canada. – D. Gravel, Center for Northern Studies, Laval Univ., Quebec, Canada; Quebec Centre for Biodiversity Science, McGill Univ., Montreal, Canada; Dépt de Biologie, Univ. de Sherbrooke, Sherbrooke, Canada and also at: Chaire de Recherche du Canada en Écologie Intégrative, Univ. de Sherbrooke, Sherbrooke, Canada.

Indirect effects resulting from species sharing the same enemy can shape spatio-temporal variations in species occurrence. The strength of such effects remains poorly known in natural communities composed of species from different trophic levels interacting in heterogeneous landscapes. Benefiting from a well-known arctic vertebrate community and marked spatio-temporal variations in the density of key prey species, we examined the effects of direct predator-prey and indirect predator-mediated effects on species occurrence in the landscape. We found both positive effects of one prey (lemmings), as well as negative indirect effects of another prey (colonial nesting snow geese) on the occurrence of species (ground-nesting birds) belonging to different guilds and trophic levels but sharing a common predator (arctic fox). However, species using prey refuges available in the landscape were not or less affected by predator-mediated effects. Similarly, the smallest (a passerine) and the largest and most dangerous species (an owl) for the shared predator were not affected by these effects. Our study provides one of the rare empirical evidence of predator-mediated effects ascending the food web (i.e. negative indirect effect of an herbivore on avian predators) and underlines how habitat structure and species traits can modulate the strength of indirect effects in natural communities.

Keywords: indirect interactions, landscape, prey community, prey refuges, shared predator, species coexistence, species distribution

Introduction

Assessing how and to what extent biotic interactions affect species occurrence and coexistence is a major challenge in ecological systems due to the multiplicity of direct and indirect interspecific interactions that are involved (Godsoe et al. 2017). Indirect

biotic interactions are especially difficult to study because they arise from interweaving chains of direct interactions. Trying to understand the role of these interactions using large scale occurrence and co-occurrence data alone is not possible, because this type of data does not inform about the nature and strength of biotic interactions (Cazelles et al. 2016, Blanchet et al. 2020). Investigating the mechanisms by which direct and indirect interactions affect species occurrence at the landscape scale and examining how these effects interact with other environmental factors, is one way to circumvent these constraints (Morales-Castilla et al. 2015, Godsoe et al. 2017).

Predation is a ubiquitous interaction that can shape prey distribution and abundance through consumptive (i.e. prey removal by predators) and non-consumptive effects (i.e. prey response driven by predation threat) (Menge and Sutherland 1976, Lima 1998, Wisz et al. 2013). Non-consumptive effects can lead to avoidance by prey of risky areas and can ultimately influence species occurrence and reduce density, as consumptive effects (Fortin et al. 2005, Gervasi et al. 2013). When multiple prey share a common predator, changes in the abundance of one prey can spread through the food web and change community structure through both consumptive and non-consumptive effects of predation on other prey (Angelstam et al. 1984, Werner et al. 2016, Lamarre et al. 2017). These predator-mediated effects can lead to positive or negative indirect interactions among prey, such as apparent competition or apparent mutualism (Strauss 1991, Holt and Lawton 1994, Wootton 1994). Predator-mediated effects on one or two focal species have been demonstrated (Bêty et al. 2002, Roemer et al. 2002, Werner et al. 2016). However, it is challenging to study how these effects impact the occurrence of species with various traits, especially when these species are interacting in heterogeneous landscapes. Hence, the strength of predator-mediated effects remains poorly known in natural communities (Boutin et al. 1995, Schmidt and Whelan 1998, Suraci et al. 2014).

Avoidance is a one of the common prey strategies to escape predation. Predator movements can be hindered by physical characteristics of the environment and create habitat patches with reduced predation risk that can be used by prey species (i.e. prey refuges: Mallory and Forbes 2011, Anderson et al. 2015, Gauthier et al. 2015). The presence of such refuges in the landscape could affect the strength of predator-mediated effects generated by changes in the abundance and distribution of other prey. Although habitat structure has been identified as a key factor in resource-consumer models (Ellner et al. 2001, Janssen et al. 2007, Kalinkat et al. 2013), its effect on indirect species interactions in ecological communities remains virtually unexplored, except in simple systems of two prey sharing a common predator (Holt 1984, 1987, Oliver et al. 2009). Studying multiple species varying in their habitat use but sharing a common predator is a key step to improve our understanding of the effect of habitat structure on the strength of predator-mediated interactions in natural communities.

To better understand how species traits and habitat structure modulate the strength of predator-mediated effects in natural communities, we took advantage of a long-term monitoring program and past field experiments that provided rare empirical data on biotic interactions at work in an arctic terrestrial vertebrate community. We specifically investigated indirect effects of predation on the occurrence of multiple species sharing a common predator in a landscape in which suitable habitat and refuges are available for prey. We used natural spatio-temporal variations in the abundance of key prey species to examine how predator-mediated interactions modulate the occurrence of other species in their suitable nesting habitat.

Our study system is located in the High Arctic where the arctic fox *Vulpes lagopus* is the main predator of bird eggs. The risk of nest predation varies annually with changing lemming density and spatially with the distance from a snow goose colony (Fig. 1; McKinnon et al. 2013, Lamarre et al. 2017). The numerical and behavioral responses of foxes to cyclic fluctuations in lemming density result in annual variation in nest predation risk (lower risk at high lemming density; Bêty et al. 2002, Royer-Boutin 2015, Lamarre et al. 2017). The presence of a goose colony causes a predator aggregative response, resulting in increasing nest predation risk towards the center of the colony (Lamarre et al. 2017). We thus examined how the spatio-temporal variation in main fox prey abundance (lemmings and geese), and hence predation risk, affects the probability of occurrence of various ground nesting avian species. We tested the hypothesis that the abundance of the main fox prey induced a corresponding variation in the occurrence of avian species in the landscape (Fig. 1). We predicted that bird occurrence probability in their suitable nesting habitat should vary in time and space, because of risk avoidance, early predation, or resource availability in the case of avian lemming consumers. Occurrence should be highest during years of high lemming density and away from the goose colony. However, species nesting in prey refuges should be less affected by predator-mediated effects than species nesting in riskier habitat patches.

Material and methods

Study site and species

Bylot Island (72°54′N, 79°54′W; Fig. 2) is located north of Baffin Island in the Canadian Arctic. Most of the study area is covered with mesic tundra in the uplands and an assemblage of mesic tundra and wetlands in the lowlands (Gauthier et al. 2013). More than 35 bird species, including waterfowl, shorebirds, seabirds, raptors, and passerines nest on the island (Lepage et al. 1998, see Table 1 for the list of the most common species nesting in the study area).

Approximately 20 000 pairs of greater snow geese *Chen caerulescens atlantica* nest mostly in a large colony of ca 70 km² (Fig. 2; Reed et al. 2002). Colony size at Bylot island
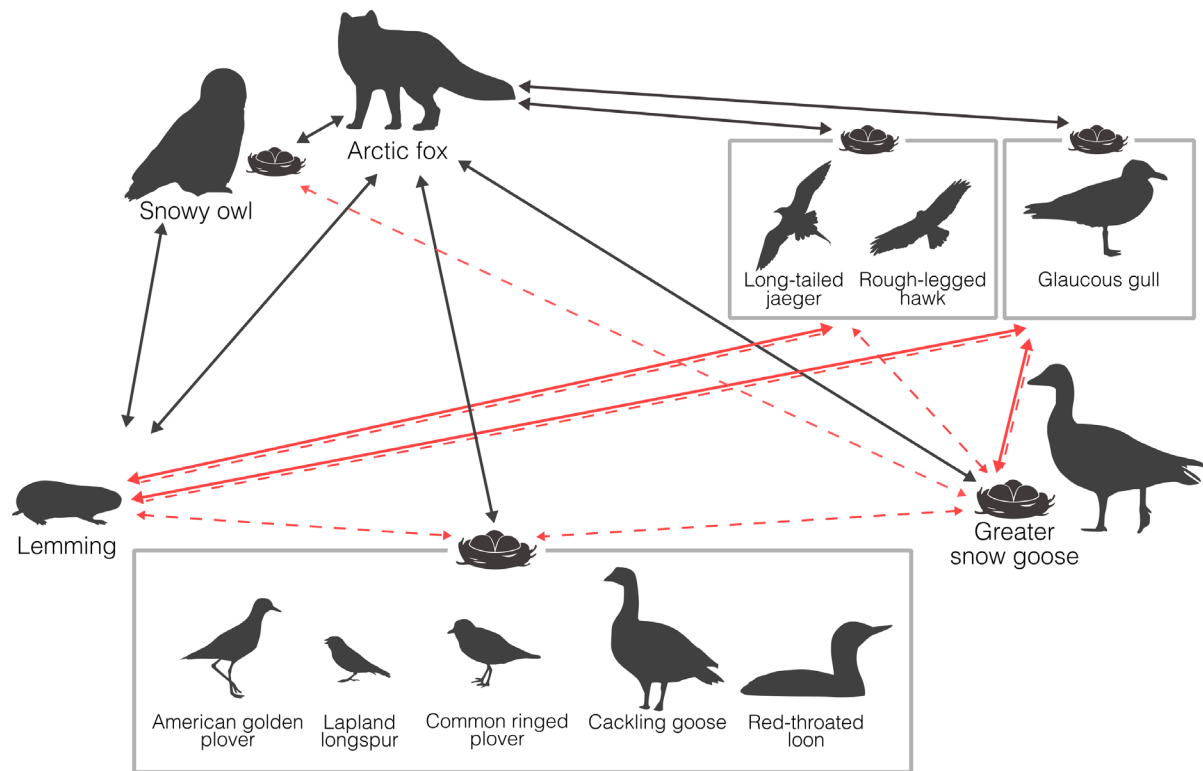
Figure 1. Network of vertebrate species at Bylot Island (Nunavut, Canada) showing direct trophic interactions between species (plain lines) and potential predator-mediated interactions targeted by this study (dashed lines). Interactions investigated by this study are in red. Arctic fox is a predator of lemmings, goose eggs and nests of all focal bird species. Snowy owl is the only species that can effectively exclude foxes from its nest vicinity. Like the arctic fox, three bird species (snowy owl, long-tailed jaeger and rough-legged hawk) consume lemmings, and one (glaucous gull) consumes both lemmings and goose eggs.

have remained relatively stable in the past 20 years and the colony represents an abundant and predictable food source for predators (Giroux et al. 2012, Gauthier et al. 2013, Lefebvre et al. 2017). Other herbivores include brown lemming *Lemmus trimucronatus* and collared lemming *Dicrostonyx groenlandicus*, both showing 3–4 years cycles of abundance (Gauthier et al. 2013)

The arctic fox, the main predator in this system, relies primarily on lemmings to breed successfully (Fig. 1), but also shows an aggregative response to the goose colony (increased overlap between adjacent territories, reduced distance between neighboring reproductive dens, and high occurrence and activity: Giroux et al. 2012, Lai 2017, Lamarre et al. 2017, Bédard et al. unpubl.). Foxes also prey upon eggs of various bird species during the summer, mostly waterfowl, shorebirds and passerines (Bêty et al. 2002, McKinnon and Bêty 2009, Giroux et al. 2012). Although foxes are the dominant nest predators of all ground-nesting birds in our study area, some avian predators, such as gulls *Larus hyperboreus*, ravens *Corvus corax* and parasitic jaegers *Stercorarius parasiticus*, can occasionally prey upon bird nests (Bêty et al. 2002, McKinnon and Bêty 2009). Their influence on species occurrence in the landscape is likely low and hence indirect effects mediated by avian predators were not considered in our study.

The most common avian predators breeding in the study area include the rough-legged hawk *Buteo lagopus*, long-tailed jaeger *Stercorarius longicaudus*, snowy owl *Bubo scandiacus*, (which all feed primarily on lemmings, and do not prey upon goose eggs) and the glaucous gull which consumes both lemmings and goose eggs (Fig. 1 and Table 1). Foxes can prey upon avian predator eggs when nests are accessible (Fig. 1; Gauthier et al. 2015, Beardsell et al. 2016). The large and aggressive snowy owl is the only avian predator that can effectively exclude foxes from its nest vicinity (Bêty et al. 2001).

Lemming density and distance to the goose colony
Lemming density was estimated from 2010 to 2019 with live-trapping sessions in two 11-ha trapping grids (one in mesic and one in wetland habitats). We estimated lemming density with a capture-recapture method in July and pooled densities of brown and collared lemmings (details in Fauteux et al. 2015). Lemming density obtained using this approach has been shown to affect goose, shorebird and artificial nest survival in our study area (Bêty et al. 2001, Royer-Boutin 2015, Lamarre et al. 2017). We used two categories for the analyses: low density, ≤ 0.3 lemmings/ha, and high density, ≥ 1.3 lemmings/ha (Supporting information). This threshold closely matches an increase in the proportion of fox dens with
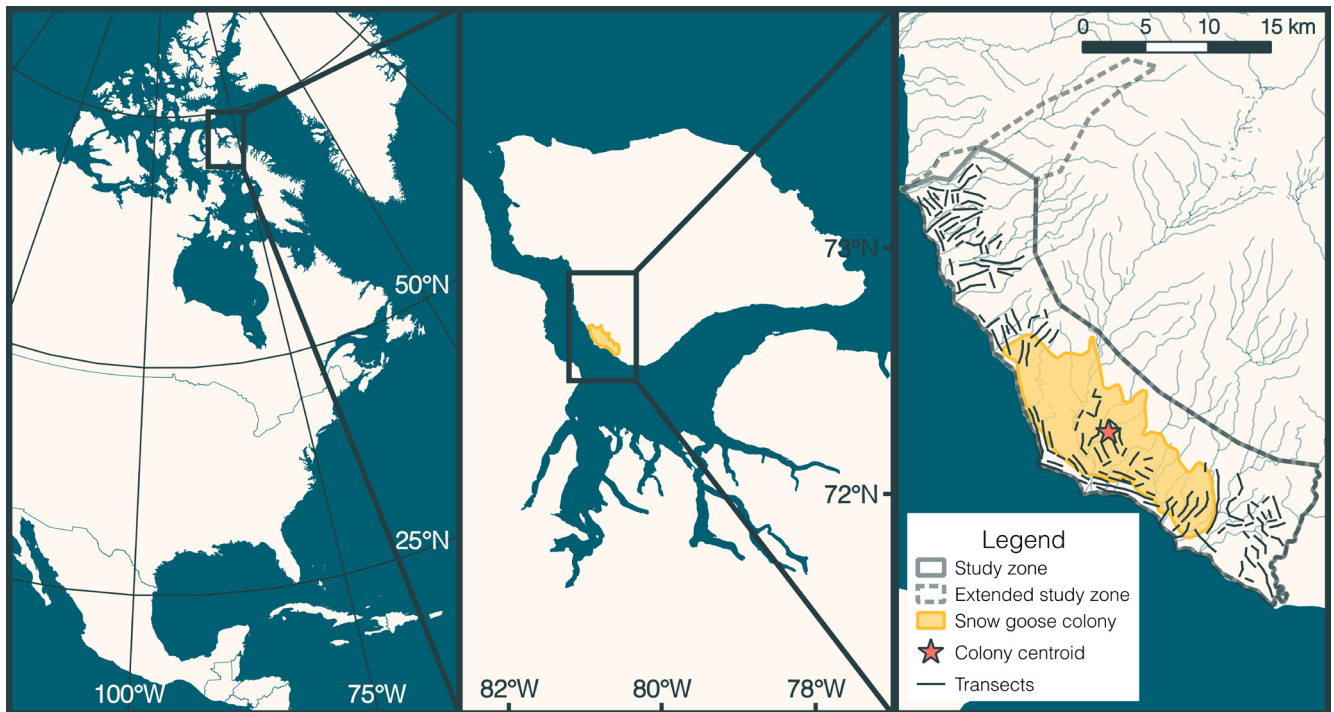
Figure 2. Location of the Bylot Island study area (left and center panels). Right panel shows the study zone for all species (gray line), the extended study zone for the rough-legged hawk (dotted gray line), the nesting goose colony and its centroid (yellow polygon and red star), and spatial distribution of the 500 m transects used to survey species nesting mostly in mesic tundra (black lines).

breeding foxes in our study area (Juhasz et al. 2019). During the study period, we observed six years of high lemming density and four years of low density (Supporting information).

Each year, we traced the goose colony boundary using a GPS receiver aboard a helicopter flying along the colony border. Maximum distance between centroid and boundary (Mean = 9.8 km, min = 9.0 km, max = 10.7 km) and centroid location were relatively stable across years (distance between annual and mean centroid: mean = 0.52 km, max = 1.3 km, min = 0.13 km) (Supporting information). Euclidean distance between the goose colony centroid and each sampling unit (i.e. transect/nesting zone, see below)

was calculated with the sf package in R ver. 4.0.3 (Pebesma 2018, <https://www.R-project.org/>). We used this metric and the lemming density categories because they had been previously linked to predation risk in our study area using artificial nest experiments (risk decreased by 0.5% and 0.9% per km away from the colony centroid at high and low annual lemming density, respectively: see Lamarre et al. 2017).

Prey refuges in the landscape

Habitat characteristics can affect predator movements and activity, and thus generate patches with different levels of

Table 1. Average adult body mass, main nesting habitat, diet and sampling years of bird species, lemmings and the arctic fox (main predator) studied at Bylot Island.

Species	Mass (g)	Nesting habitat	Diet	Sampling years
Arctic fox	2500	-	Generalist predator	-
Lemmings	50	-	Herbivore	2010–2019
Greater snow goose	3000	Mesic	Herbivore	2010–2019
Snowy owl	1830	Mesic	Lemming specialist	2010–2019
Long-tailed jaeger	300	Mesic	Lemming specialist	2010–2018
Rough-legged hawk	990	Cliffs[*]	Lemming specialist	2012–2019
Glaucous gull	1400	Islets/Wetlands[*]	Generalist predator	2014–2019
American golden-plover	145	Mesic	Insectivore	2010–2018
Lapland longspur	27	Mesic	Insectivore	2010–2018
Common-ringed plover	60	Gravel beds along rivers[*]	Insectivore	2015–2019
Cackling goose	1600	Islets/wetlands[*]	Herbivore	2014, 2016–2019
Red-throated loon	1400	Islets/wetlands[*]	Piscivore	2014, 2016–2019

Nesting habitat that can offer prey refuges (reduced predation risk) at small spatial scale are indicated with an asterisk ([*]). Generalist predators feed on both lemmings and goose eggs.

predation risk. Mesic tundra is the dominant habitat and is easily accessible to foxes, rich in prey (such as lemmings) and is thus riskier for nesting birds (Lecomte et al. 2008, Léandri-Breton and Bêty 2020). It is the dominant nesting habitat for nesting snow geese, American golden-plovers *Pluvialis dominica*, Lapland longspurs *Calcarius lapponicus*, long-tailed jaegers and snowy owls. Some prey also nest in habitat patches that constraint fox movements or patches that are less used by foraging foxes (Grenier-Potvin et al. 2021). The use of such patches by nesting birds can offer protection and are thus considered as prey refuges (Clermont et al. 2020). Wetlands composed of ponds with islets and peninsulas as well as complex water channels can limit arctic fox movements compared to surrounding mesic patches and act as refuges (Lecomte et al. 2008, Gauthier et al. 2015). These wetlands are predominantly used by nesting glaucous gulls, cackling geese *Branta hutchinsii* and red-throated loons *Gavia stellata*. Within the boundary of the colony, some snow geese also nest in wetland patches occurring in polygon-patterned ground (Lecomte et al. 2007). In addition, cliffs and gravel beds along rivers can act as refuges for nesting rough-legged hawk and common ringed plover *Charadrius hiaticula*, respectively. Artificial and real nest monitoring showed that nest predation risk is lower in gravel beds compared to the surrounding mesic tundra (Léandri-Breton and Bêty 2020) and for some cliff edges or steep hillsides used by hawks and inaccessible to foxes (Beardsell et al. 2016). Moreover, GPS tracking of arctic foxes conducted in our study area during the goose incubation period showed that foxes tend to avoid wetlands and gravel beds along rivers compared to mesic habitats (Grenier-Potvin et al. 2021).

Spatio-temporal variation in probability of occurrence of nesting birds

Occurrence of nesting birds in the study area was determined annually during the bird incubation period (Table 1). For three species dispersed in the landscape and nesting primarily in mesic tundra (i.e. American golden-plover, long-tailed jaeger, Lapland longspur), probability of occurrence was derived from observations of nesting individuals along transects. Transects were positioned in relatively homogeneous habitat (mesic tundra with low vegetation) suitable for nesting American golden-plovers, long-tailed jaegers and Lapland longspurs (Drury 1961, Andersson 1971, Connors et al. 1993, Lamarre et al. 2017) and dispersed in the study area to cover a gradient of distance to the goose colony. We surveyed each year from 145 to 295 transects spread within the study area (total of 2171 surveys between 2010 and 2018) and conducted between 21 June and 14 July (Fig. 2, Lamarre et al. 2017). All birds detected within 150 m each side of the 500 m long transects were recorded and their reproductive status was determined (distance was estimated by observers trained with a range finder). For plovers, distraction displays (broken wing, rodent run) and insistent calls indicated a nesting individual (Byrkjedal 1989, Lamarre et al. 2017). Status was confirmed by moving towards the individuals. Birds that did not react to the presence of the observer or were foraging, flying

by, or resting, were considered non-breeders. For jaegers, we considered that any detection of one or two individuals along a transect indicated a nesting pair, as jaegers typically leave their nesting territory when they fail or skip breeding. Non-incubating jaegers typically feed in groups, and often in coastal habitats (Andersson 1976, De Korte 1984). Non-breeders were therefore defined as individuals observed in groups of three or more. We considered that all detected Lapland longspurs were nesting because they were usually singing and performing display flights, or responded to our approach with alarm calls (Drury 1961, Hunt et al. 1995).

We conducted annual intensive snowy owl nest searches between 21 June and 14 July. We followed ridges and scanned the surrounding landscape from vantage points. Owls nest on conspicuous, elevated mounds and can be seen from a relatively long distance sitting on the nest or flushing from the nest. They also reveal their presence with alarm calls or nest defense displays. We are confident that nest detection probability was very high given the open landscape (Therrien et al. 2014).

Five bird species (rough-legged hawk, glaucous gull, common ringed plover, cackling goose and red-throated loon) use specific nesting habitats that have a patchy distribution in the study area. We visited annually and searched for nests of these species in their specific nesting habitat patches throughout the study area during the incubation period (Table 1 for sampling years). Rough-legged hawk nests were searched in an extended study area to cover an important stream valley where exposed bedrock provides suitable nesting sites (Fig. 2; Beardsell et al. 2016). All these species can reuse the approximate nest location from year to year (Dickson 1993, Gauthier et al. 2015, Beardsell et al. 2016). For each species, we used a cluster analysis to define a number of nesting zones that had a species-specific diameter and that can be used repeatedly (annually) for nesting (Supporting information for the detailed calculation of nesting zones). We obtained a total of 205 unique nesting zones (all five species combined) in which presence or absence of a nesting bird in a given year was determined 881 times (20–193 nesting zones surveyed per year). For rough-legged hawk, we determined the potential accessibility by arctic foxes of each nesting zone based on a characterization of all known nest cups used by this species in the study area realized by Beardsell et al. 2016. To control for a non-random distribution of inaccessible nests in the study area, we generated a second dataset excluding zones containing at least one inaccessible nest cup.

The sampling of transects and nesting habitat patches located near and far from the goose colony was alternated during the field season to control for the effect of decreasing detection probability over the season due to nest failure (Lamarre et al. 2017). We only used nesting zones and transects located in suitable nesting habitat in our subsequent, species-specific analyses (i.e. for each species, we only used sites that provided characteristics suitable to lay and incubate eggs). Transects used at least once by a nesting bird during the study period were considered located in suitable nesting habitat and were kept for the analyses.

This allowed us to exclude the potential effect of spatial variation in availability of nesting habitat per se on the occurrence of avian species in the landscape. Hence, we assumed that any association between the probability of occurrence of a given species in a suitable nesting habitat with lemming density or distance to the snow goose colony was caused by three main mechanisms: 1) birds avoiding nesting in suitable habitat due to high predation risk; 2) early nest failure (i.e failure that happened before our sampling period) caused by direct predation and; 3) for species consuming lemmings, inability to initiate breeding or early failure due to lack of food resources. Our approach could, however, underestimate the effect of the goose colony if birds never nest in areas of high goose nest density or are never detected in such areas due to strong apparent competition (McKinnon et al. 2013, Lamarre et al. 2017 for the specific case of the American golden-plover).

Statistical analyses

We modeled the probability of occurrence of nesting bird species along a transect or in a suitable nesting zone (see above) as a function of lemming density and distance to the snow goose colony. We modeled separately the occurrence of each nesting bird species (except snowy owl, see below) using generalized linear mixed models (GLMMs, package lme4; Bates et al. 2015). We used a logit-link function and a binomial distribution for the occurrence response variable (a nesting bird on transect or in nesting zone = 1, no nesting bird = 0). Fixed effects included in full models were lemming density level (lem), distance to goose colony centroid in km (dist, scaled by its standard deviation) and their interaction (lem X dist). We added transect or nesting zone ID and year as random effects in all models. For rough-legged hawks, we ran a second set of models, removing the nesting zones containing inaccessible nests to foxes (see details above). The GLMMs were fitted using the Laplace approximation and the "bobyqa" optimiser (lme4 package; Bates et al. 2015) and were checked for presence of outliers, homogeneity and approximate normality of residuals. We compared models with the corrected Akaike information criterion (AICc) and considered models with ΔAICc < 2 as competitive. Effects are presented with the slope and 95% confidence interval.

Snowy owls almost never nest at Bylot when lemming densities are low (Therrien et al. 2014), so we only examined if the goose colony affected the spatial distribution of their nests. To do so we tested whether nest distribution was random relative to the distance to the goose colony centroid. Years with fewer than three nests in the study area were excluded. We computed distance between each nest of a given year and the goose colony centroid of that year. Then, we sampled the same number of random points in the study area (Fig. 2), after removing unsuitable habitats (wetlands and lakes). We constrained the distance between random points to a minimum of 438 m, the smallest distance observed between owl nests. We compared the mean distance of nests and random points to the colony centroid with a t-test. We repeated this process 500 times and extracted the mean distance for random points, its 95% confidence interval and the p-values.

Results

The simultaneous effect of lemming density and the proximity of a snow goose colony on the probability of occurrence of nesting birds in suitable habitat was tested on nine species, including four lemming consumers and five species not consuming lemmings. Five species nest primarily in habitats offering some refuge against fox predation (Table 1). The average annual number of transects with a nesting bird ranged from 35 for long-tailed jaegers to 219 for Lapland longspurs. The average number of nesting zones with a nesting pair ranged from 9 per year for rough-legged hawk to 22 for common ringed plover (Supporting information for mapped data). Average probability of occurrence of nesting birds in a suitable nesting habitat varied from 0.92 in high lemming years for Lapland longspurs to 0.11 in low lemming years for long-tailed jaegers (Fig. 3).

Lemming consumers

Snowy owl nests were abundant in 2010 (19 nests) and 2014 (47 nests), two years of high lemming density (4.0 and 6.3 lem/ha), but rare in 2016 and 2019 (≤ 2 nests) when lemmings densities were moderate (2.3 and 1.4 lem/ha), and absent in other years (Supporting information). However, high lemming density at Bylot island does not seem to be a sufficient condition in itself to explain the presence of the owl locally, because no nest was found in the high lemming year of 2011 (6.9 lem/ha). We found no effect of the snow goose colony on owl distribution as their nests were randomly distributed relative to the colony centroid. The mean distance between owl nests and goose colony centroid (9.2 in 2010 and 10.3 km in 2014) was similar for random points (9.4 km 95% CI [9.3–9.5] and 9.7 km 95% CI [9.6–9.8], all p-values > 0.46).

The probability of occurrence of two other lemming specialists (long-tailed jaegers and rough-legged hawks) generally increased with lemming density (Table 2A, B). For the long-tailed jaeger, there was a significant interaction between distance to goose colony centroid and lemming density, as the probability of occurrence decreased with distance to the colony during low lemming years ($\beta = -0.53$ 95% CI [−0.80 − −0.27]), but it tended to increase during high lemming years ($\beta = 0.15$ [−0.003 − 0.31], Fig. 4A). Close to the colony centroid, the probability of occurrence was similar for high and low lemming years (0.24 [0.14–0.40] and 0.18 [0.08–0.34] respectively) whereas 20 km away from the colony, it was 10 times higher in high compared to low lemming years (0.35 [0.22–0.52] and 0.03[0.01–0.08] respectively). The probability of occurrence of rough-legged hawks also increased with distance to goose colony centroid (Fig. 4B). Excluding a nesting zone offering inaccessible sites to foxes led to a similar result ($\beta = 0.77$ [−0.08 − 1.63]). Finally, the
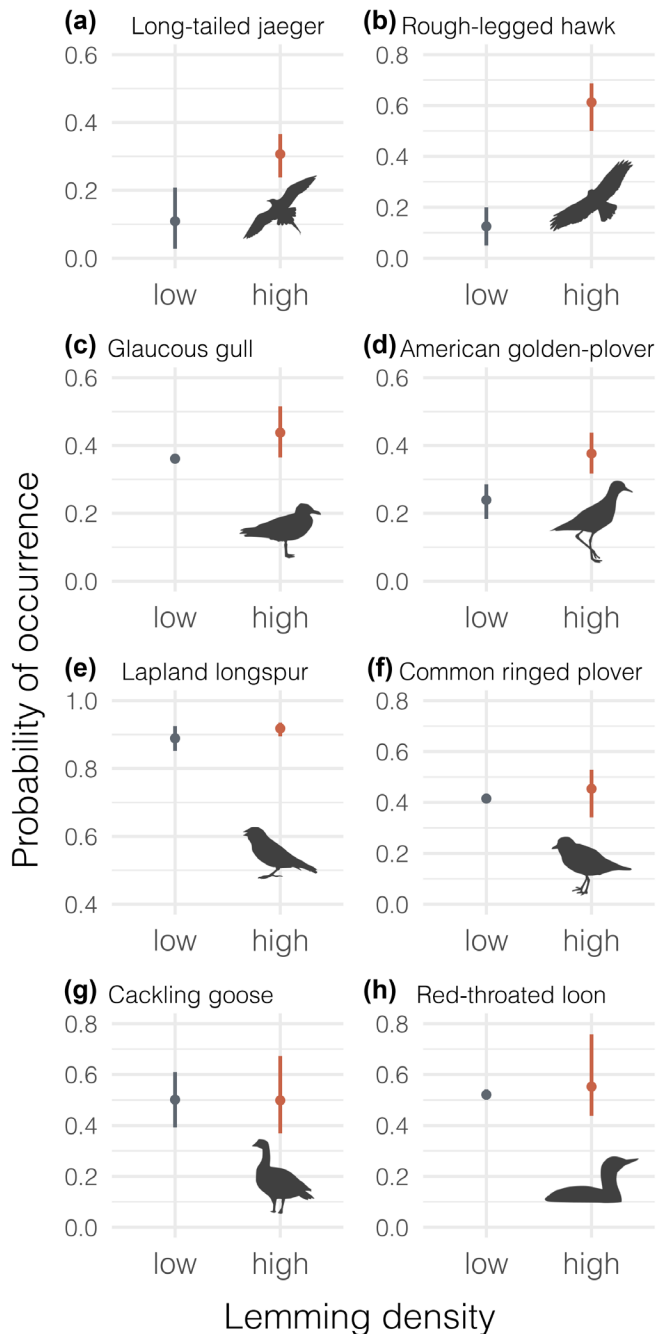
Figure 3. Mean probability of occurrence of nesting birds consuming lemmings (A–C) and not consuming lemmings (D–H) during years of low and high lemming abundance at Bylot Island. Probabilities of occurrence are averaged for 2–4 low lemming years and 3–5 high lemming years according to the species. Error bars show 95% confidence interval. Probabilities of occurrence were averaged for transects or nesting zones used by a given species at least once during the study period (i.e. suitable nesting habitat, see methods). The number of suitable transects or nesting zones sampled annually for each species varied between 90–295 and 11–55, respectively.

occurrence of the glaucous gull, a generalist predator, was not affected by lemming density nor distance to the goose colony centroid (constant probability of occurrence of 0.32 95% CI [0.21–0.46]; Fig. 4C, Table 2C).

Species not consuming lemmings

The effect of lemming density on the probability of occurrence of American golden-plovers interacted with distance to the goose colony (Table 2D). This probability increased with distance to the colony centroid during high lemming years ($\beta = 0.28$ 95% CI [0.10 – 0.46]), but not during low lemming years ($\beta = -0.036$ [−0.24 – 0.17]). Close to the goose colony, the probability of occurrence was relatively low and not affected by lemming density (probability of occurrence of 0.25 [0.16–0.36] and 0.25 [0.17–0.34] for low and high years, respectively) (Fig. 4D), whereas 20 km away from the colony, the occurrence was almost twice higher in high lemming years compared to low years (probability of occurrence of 0.23[0.16–0.31] and 0.46 [0.37–0.55], respectively). The probability of occurrence of nesting Lapland longspurs was high over the entire study area (0.92, 95% CI [0.89–0.94]) and was not affected by distance to goose colony nor lemming density (Table 2E, Fig 4E).

No evidence was found that lemming density affected probability of occurrence of bird species that do not consume lemmings and that nest in habitats offering prey refuges (i.e. common ringed plovers, cackling geese and red-throated loons) (Table 2F–H). However, probability of occurrence increased with distance to goose colony centroid for the common ringed plover and a similar, non-significant trend, was observed for the cackling goose (Fig. 4F, G). We did not detect any spatio-temporal variation in the probability of occurrence of the red-throated loon (constant probability of occurrence of 0.56[0.38–0.73] (Table 2H and Fig. 4H).

Discussion

Investigating the role of indirect predator-mediated effects in shaping spatio-temporal variations in species occurrence at the landscape scale is challenging in natural vertebrate communities. We took advantage of annual and spatial variation in predation risk caused by large changes in density of two key prey species to evaluate the strength of such effects in a bird community sharing a common predator. As predicted, we found that a large snow goose colony affected the probability of occurrence of several nesting birds in the landscape, with negative effects detected in five out of nine species in years of high lemming density (i.e. high food abundance for lemming consumers). These results indicate that predator-mediated effects can have important consequences on the occurrence of species of different trophic levels and guilds. However, as predicted, the occurrence of species nesting predominantly in

Table 2. Generalized linear mixed model selection of the effects of lemmings (lem), distance from the goose colony (dist) and two-way interactions on species consuming lemmings (A–C) and species not consuming lemmings (D–H) occurrence on transects/in nesting zones at Bylot Island (individual transects/nesting zones and years were used as random factors). Left panel presents null and competitive models (ΔAICc < 2) and right panel presents best model parameter estimates and their 95% confidence interval. Full model selection and summary of all models are presented in Supporting information. †, ‡

Model selection					Best model summary			
Species	Model	K	ΔAICc	W$_i$	Parameter	Estimate	SE	95% CI
A) Long-tailed jaeger	lem × dist	6	0.00	1.00	Intercept	−1.54	0.45	[-2.41 − −0.66]
	null	3	21.20	0.00	dist	−0.53	0.13	**[−0.80 − −0.27]**
					lem high	0.41	0.58	[−0.72 − 1.54]
					lem × dist	0.68	0.16	**[0.38 − 0.99]**
B) Rough legged hawk	lem + dist	5	0.00	0.55	Intercept	−4.91	1.29	[−7.44 − −2.39]
	lem × dist	6	1.49	0.26	dist	0.92	0.44	**[0.06 − 1.78]**
	null	3	14.21	0.00	lem high	3.77	0.81	**[2.19 − 5.36]**
C) Glaucous gull	null	3	0.00	0.45	Intercept	−0.74	0.29	[−1.31 − −0.17]
	dist	4	1.47	0.22				
	lem	4	1.84	0.18				
D) American golden-plover	lem × dist	6	0.00	0.77	Intercept	−1.11	0.27	[−1.65 − −0.57]
	null	3	10.72	0.00	dist	−0.04	0.11	[−0.24 − 0.17]
					lem high	−0.01	0.36	[−0.71 − 0.70]
					lem × dist	0.31	0.14	**[0.042 − 0.58]**
E) Lapland longspur	null	3	0.00	0.35	Intercept	2.41	0.15	[2.12 − 2.70]
	lem	4	0.67	0.25				
	dist	4	1.51	0.17				
F) Common ringed plover	dist	4	0.00	0.48	Intercept	−0.90	0.25	[−1.39 − −0.40]
	lem × dist	6	1.16	0.27	dist	0.40	0.13	**[0.15 − 0.65]**
	lem + dist	5	1.50	0.23				
	null	3	7.75	0.01				
G) Cackling goose	dist	4	0.00	0.42	Intercept	−0.54	0.53	[−1.58 − 0.50]
	null	3	0.85	0.28	dist	0.51	0.30	[−0.08 − 1.10]*
H) Red-throated loon	null	3	0.00	0.47	Intercept	0.24	0.38	[−0.51 − 0.99]
	dist	4	1.75	0.20				
	lem	4	1.97	0.18				

†Model variables abbreviations: lem, annual lemming density categorized as low or high; dist, distance to goose colony centroid (km, scaled by its standard deviation); ‡K, number of parameters; ΔAICc, difference in AICc between the current and top-ranked model; W$_i$, AICc weight in favor of the model. Confidence limits with a 95% confidence interval not overlapping 0 are in bold and those slightly overlapping 0 are indicated with an asterix (*).
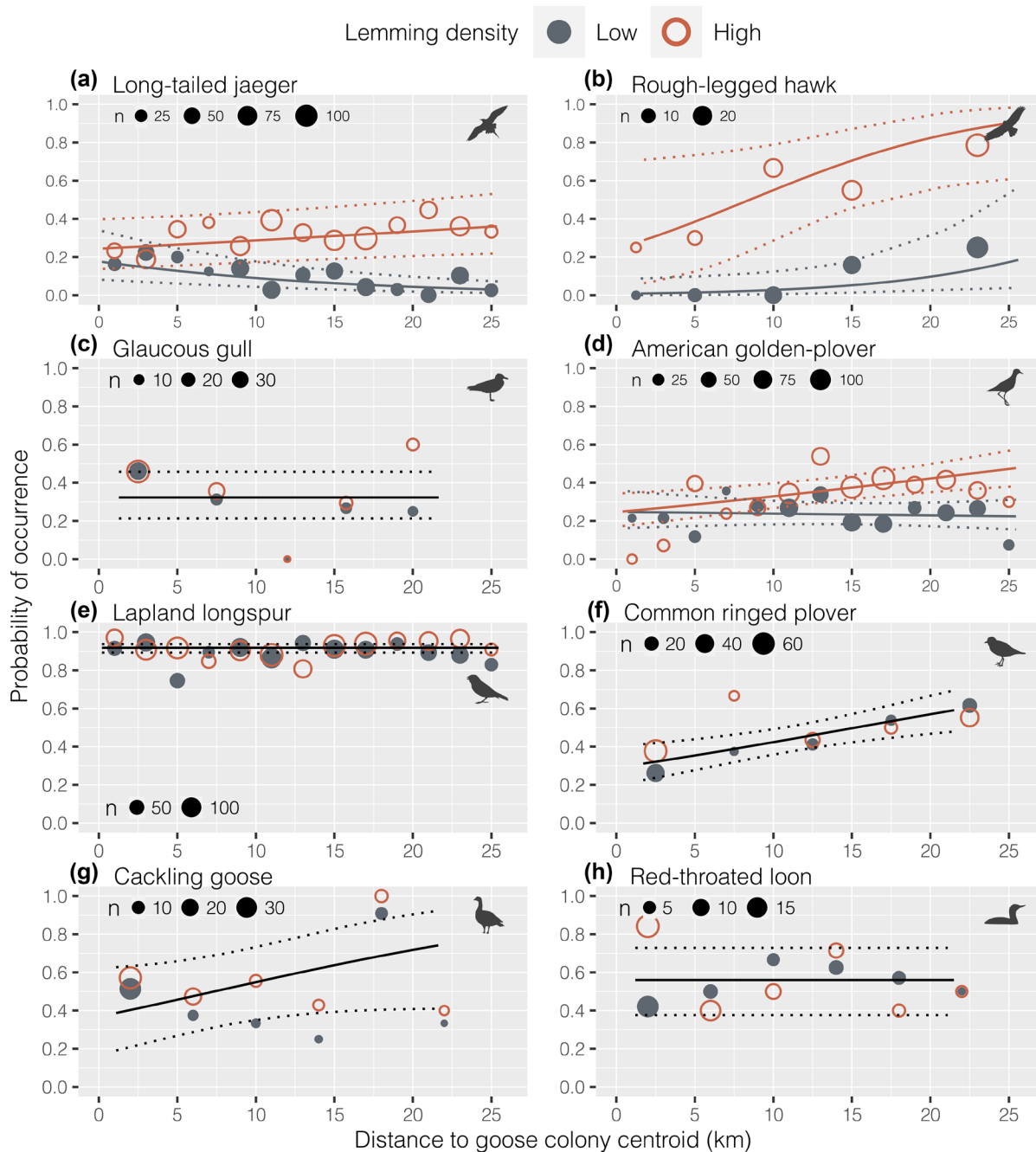
Figure 4. Probability of occurrence of nesting birds consuming lemmings (A–C) and not consuming lemmings (D–H) in suitable nesting habitat (transect or nesting zone used by a given species at least once during the study period) according to the distance from the goose colony centroid and annual lemming density at Bylot Island. Gray and red lines represent the fitted top-ranked models for low and high lemming density, respectively. Black lines represent the fitted top ranked model when no lemming effect was found. Dashed lines show lower and upper 95% confidence intervals. Pooled observed values are shown for low lemming years (gray full circles) and high lemming years (red empty circles). Size of circle is proportional to log(n).

habitats offering refuges was less (or not) affected by predator-mediated effects, as well as the occurrence of the smallest (a passerine) and largest and most dangerous species (owl) for the shared predator (fox). Our results thus suggest that habitat structure and species traits can modulate the strength of predator-mediated effects in natural communities.

Predator-mediated effects

As predicted, the occurrence of several nesting bird species (long-tailed jaeger, rough-legged hawk, American golden-plover, common ringed plover, and cackling goose) was lower near the snow goose colony, which is characterized

by much higher predator activity and nest predation risk (McKinnon et al. 2013, Lamarre et al. 2017). Species that experience large population increase and become overabundant due to the exploitation of anthropogenic food subsidies, like waterfowl, are expected to modify trophic relationships and induce trophic cascades in the ecosystems they inhabit (Latham et al. 2011, Bauer and Hoye 2014). Predator-mediated negative effects of snow geese, a migratory overabundant species, on shorebird occurrence was recently demonstrated within our study area (Lamarre et al. 2017)and at other Arctic sites (Flemming et al. 2019a). Our results show that such negative indirect effects can affect a wide variety of tundra bird species, including avian predators. This is, to our knowledge, one of few empirical evidences of predator-mediated negative effects ascending in the food web (from an herbivorous bird to avian predators sharing a common predator; Roemer et al. 2002).

The lower probability of occurrence near the goose colony could be due to direct nest predation or avoidance of suitable nesting habitat associated with higher predation risk. Our data does not allow us to tease apart consumptive and non-consumptive effects of predation. The influence of lemmings far away from the goose colony on the occurrence of some species that do not eat lemmings nonetheless suggests that consumptive effects contribute to the observed patterns. Indeed, suitable nesting habitats are available in all years far away from the colony and lower occurrence of some species in low lemming years most likely result from direct predation and not from birds skipping reproduction in those years. Similarly, the recurring release in predation pressure at high lemming densities was proposed as a potential mechanism allowing some vulnerable species to persist in the tundra landscape (Gilg and Yoccoz 2010, Léandri-Breton and Bêty 2020). On the other hand, high risk areas generated by the presence of nesting geese could potentially limit the local population growth rate of vulnerable prey and hence reduce their ability to coexist in the goose colony (Lamarre et al. 2017). However, landscapes offering refuges could allow some species to maintain viable breeding populations even within risky areas generated by the presence of overabundant prey species or the absence of lemmings (Léandri-Breton and Bêty 2020).

Spatio-temporal variation in the occurrence of tundra nesting bird species could be affected by factors not considered in our analyses. For instance, lower occurrence of nesting birds in the goose colony could result from severe habitat degradation caused by heavy goose grazing, as reported elsewhere (Sammler et al. 2008, Peterson et al. 2014, Flemming et al. 2019b). This is unlikely at our study site because the intensity of goose grazing, which occur both within and outside the nesting colony during the brood rearing period, is too low to cause habitat degradation (Gauthier et al. 2004). Finally, the lower occurrence of hawks and jaegers close to the goose colony during high lemming years could be due to small spatial scale variation in lemming density. However, this is unlikely as the presence of the goose colony did not affect the distribution of the snowy owl, a lemming specialist that can effectively protect its nest against foxes. Hence, the random distribution of owl nests strongly suggests that lemming density is similar across the study area.

Quality of nesting sites is another factor that could have affected species occurrence. For instance, rough-legged hawk nesting zones used in our analyses could be of lower quality close to the snow goose colony. Beardsell et al. (2017) showed that probability of nest reuse by hawks decreased with the risk of nest destruction (cliff collapsing) and, in our study area, that risk decreases as distance to the goose colony increases (Pearson correlation: $r = -0.55$, 95%CI $[-0.70 - -0.36]$, $n = 67$). Although we cannot fully exclude such alternative explanation, our results suggest that the occurrence of hawks in the landscape is at least partly affected by predator-mediated effects for two reasons: 1) we modeled the probability of occurrence only for nesting zones offering suitable nesting habitat; and 2) we found consistent patterns in two avian predators (rough-legged hawk and long-tailed jaeger), both unable to effectively protect their nest against arctic foxes and using different nesting habitats.

The apparent positive effect of the goose colony on breeding long-tailed jaegers in low lemming years is puzzling. This effect could be due to the presence of additional food sources in the vicinity of the goose colony (either or both terrestrial and marine) allowing jaegers to persist in this area during years of low lemming density. Although we excluded groups of non-breeders, it is possible that individuals that failed or skipped reproduction stayed for a longer period in the goose colony area and hence were detected during our surveys. Indeed, the goose colony centroid is located only ~4 km from the mouth of a glacial river where large groups of jaegers are seen in early summer (presumably non-breeders and failed breeders; De Korte 1984), especially during years of low lemming density. We may have detected individuals from those groups along our survey transects located close to the goose colony centroid.

Our results highlight the strong influence of cyclic small mammals on the occurrence of both avian predators and other birds nesting in the Arctic tundra. The direct effect of lemming density on avian predators is well known and our results showing that probability of occurrence of rough-legged hawks and long-tailed jaegers varied 3-5 fold between low and high lemming years is consistent with previous findings (Gilg et al. 2006, Therrien et al. 2014, Beardsell et al. 2016). Although we cannot tease apart direct food-related and indirect predator-mediated effects of lemmings on the occurrence of these species, the effects of the goose colony on the occurrence of jaegers and hawks suggest that both direct and indirect effects of lemmings are likely to contribute to the observed patterns. Hence, the pronounced annual variation in the probability of occurrence away from the goose colony could be partly due to nest predation occurring early during the breeding cycle of these avian predators, and not only caused by the lack of food resources.

As for the glaucous gull, a generalist avian predator, our results show that lemming density and distance to the goose colony did not affect its probability of occurrence. Virtually

all gull nests were on islets in our study area (>90%) and our results showing a lack of lemming effect on their occurrence are consistent with previous findings indicating that gulls nesting on islets are less affected by annual variation in nest predation risk (Gauthier et al. 2015). The absence of lemming effects on gulls and other species using prey refuges (red-throated loon, common ringed plover and cackling goose), but having highly different food habits supports our hypothesis that the use of refuges can allow species to escape predator-mediated effects generated by changes in the abundance of key prey species. However, the strength of predator-mediated effects could potentially increase if some breeding pairs are forced to nest in risky areas because population size exceeds the availability of refuges in the landscape (Holt 1987, Anderson et al. 2015).

Role of body size and defense ability

Our results also suggest that, in multi-prey systems, predator and prey relative body sizes could affect the strength of predator-mediated interactions, an effect that was investigated in very few natural communities (Frid and Marliave 2010). The absence of predator-mediated effect on the smallest species in our system, the Lapland longspur, is consistent with Brose (2010) models that show lower attack rates on smaller prey and Legagneux et al. (2014), who showed a reduced effect of predation on tundra species of small size. High concealment and lower detectability of nests of small birds probably make them less likely to be preyed upon by foxes (Beardsell et al. 2021). This low detectability, combined with a low profitability for the predator, may explain why longspur nests are less affected by variation in predation risk than bird species that have larger body and egg sizes (e.g. American golden-plover) (Royer-Boutin 2015). On the other hand, attacking the nest of a relatively large and dangerous species like snowy owl is risky for a predator like the arctic fox (Larsen et al. 1996, Smith and Edwards 2018). Snowy owls have sharp and powerful talons and can exclude arctic foxes from their nest vicinity up to 500 m (Bêty et al. 2002, Quinn et al. 2003).

Role of habitat structure and refuge quality

Our empirical results are among the few showing the effect of habitat structure on multiple species interacting through shared enemies (Oliver et al. 2009). Theoretical models suggest that landscape heterogeneity and habitat partitioning can contribute to the coexistence of species indirectly interacting through shared predators (Holt 1984). In addition, the presence of low risk patches could potentially allow the coexistence of more vulnerable species that would be excluded by predator-mediated effects otherwise (Holt 1987). Prey refuges distributed throughout our study area present lower predation risk than the dominant mesic tundra habitat (Lecomte et al. 2008, Gauthier et al. 2015, Beardsell et al. 2016, Léandri-Breton and Bêty 2020) and likely contribute to the persistence of species with higher vulnerability to predation. As some species nesting in refuges appear to escape predator-mediated effects, they should better persist within risky areas such as the snow goose colony. The relative degree of protection offered by the different micro-habitat patches used by various species may also explain why some predator-mediated effects were nonetheless detected among species using refuges.

Conclusion

Overall, our study suggests that the occurrence of vertebrate species in the arctic tundra is partly driven by an interplay between direct and predator-mediated biotic interactions, which are modulated by habitat structure and species traits. Our results suggest that an overabundant prey, colonially nesting species, can negatively affect the occurrence of species belonging to different guilds and trophic levels due to shared predation. Our results are in line with the proposition that cyclic rodent populations can induce recurring releases in predation pressure and allow some vulnerable species to persist in the tundra landscape. Finally, our research suggests that, by shaping trophic interactions, prey refuges in the landscape may promote species occurrence and coexistence in natural communities. We thus stress the need for a better assessment of the quality, quantity and stability of these overlooked habitat features to support tundra species, especially in this era of global changes.

Author contributions

Éliane Duchesne: Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jean-Francois Lamarre**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Gilles Gauthier**: Funding acquisition (supporting); Project administration (equal); Writing – review and editing (equal). **Dominique Berteaux**: Funding acquisition (supporting); Project administration (equal); Writing – review and editing (supporting). **Dominique Gravel**: Conceptualization (supporting); Writing – review and editing (equal). **Joël Bêty**: Conceptualization (lead); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent Peer Review

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Data availability statement

Data are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.pg4f4qrpf>) (Duchesne et al. 2021).

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