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Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds

Jean-François Lamarre,[1,4,†] Pierre Legagneux,[1] Gilles Gauthier,[2] Eric T. Reed,[3] and Joël Bêty[1]

[1]*Département de Biologie, Chimie et Géographie and Centre d'études Nordiques (CEN), Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Quebec G5L 3A1 Canada*
[2]*Département de Biologie and Centre d'études Nordiques (CEN), Université Laval, 1045 Avenue de la Médecine, Québec, Quebec G1V 0A6 Canada*
[3]*Canadian Wildlife Service, Environment and Climate Change Canada, 5019 52nd Street, Yellowknife, Northwest Territories X1A 2P7 Canada*

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Abstract. Overabundant species can strongly impact ecosystem functioning through trophic cascades. The strong increase in several arctic geese populations, primarily due to changes in agricultural practices in temperate regions, can have severe direct impacts on tundra ecosystems through vegetation degradation. However, predator-mediated negative effects of goose overabundance on other tundra species can also be significant but are poorly understood. We tested the hypothesis that goose abundance negatively affects arctic-nesting shorebirds by increasing nest predation pressure. We used six years of data collected within and near a greater snow goose colony (*Chen caerulescens atlantica*) to evaluate the effect of geese on the spatial variation in (1) the occurrence of shorebird nest predators, (2) the nest predation risk (with artificial shorebird nests), and (3) the occurrence of nesting shorebirds. We found that the goose colony had a strong influence on the spatial distribution of nest predators and nesting shorebirds. Occurrence of predators decreased, while occurrence of nesting shorebirds increased with distance from the centroid of the colony. The strength of these effects was modulated by lemming density, the preferred prey for predators. Shorebird nest predation risk also decreased with distance from the colony. Overall, these results indicate that goose abundance negatively affects arctic-nesting shorebirds through shared predators. Therefore, we show that the current decline of some arctic shorebird populations may be in part mediated by a negative effect of an overabundant species.

Key words: Arctic; bird colony; conservation; global change; indirect interactions; shared enemy; shorebirds; species distribution; waders; waterfowl.

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[4] Present address: Polar Knowledge Canada, Canadian High Arctic Research Station (CHARS), 1 Uvajuq Road, Cambridge Bay, Nunavut X0B 0C0 Canada.
† **E-mail:** jflamarre@gmail.com

INTRODUCTION

Natural ecosystem functioning and species communities are dramatically affected by human activities (Vitousek et al. 1997, Worm and Paine 2016). Exploitation of anthropogenic food subsidies can induce ecological and evolutionary changes at individual, population, community, and ecosystem levels (Newsome et al. 2015). Exploitation of such subsidies is considered responsible for much of the demographic explosion of a wide range of species (Jefferies et al. 2004*a*, Allombert et al. 2005, Castro et al. 2005, Rotem et al. 2011, Oro et al. 2013). The impact of such overabundant species can modify trophic relationships and potentially induce trophic cascades within a given ecosystem

(Latham et al. 2011) and even outside this ecosystem when overabundant species migrate (Jefferies et al. 2006, Bauer and Hoye 2014). For instance, the increase in agricultural food subsidies available during winter caused a demographic explosion of several goose populations both in Europe and in North America (Batt 1998, Jefferies et al. 2004*b*, Fox et al. 2010) inducing not only crop damages (Fox et al. 2005, Simonsen et al. 2016), but also intense overgrazing on their breeding grounds. In addition to strong cascading effects on arctic tundra through overgrazing (Jefferies et al. 2004*b*, 2006, Fox et al. 2005), large goose colonies also represent a predictable pulse resource that can induce indirect trophic interactions by affecting the behavior and abundance of predators (Madsen et al. 1999, McKinnon et al. 2013).

Shared predation is a widespread phenomenon that can affect prey species abundance and coexistence in natural communities (Holt 1977, Holt and Kotler 1987). Symmetrical or asymmetrical apparent competition can arise when two species negatively affect each other by enhancing the density or by changing the behavior of shared predators. Shared predators can also generate non-reciprocal negative effects if either of the two prey species has small per capita effects on the population size or behavior of shared predators (Chaneton and Bonsall 2000). Iles et al. (2013) reported negative effect of goose abundance on arctic-nesting common eiders (*Somateria mollissima*) and concluded that apparent competition could partly explain the long-term decline in eider nest survival.

While most goose populations have been increasing across the Arctic, many shorebird populations have been decreasing throughout the same range (Morrison et al. 2006, Deinet et al. 2015). There are some indications in the literature that large goose colonies can negatively affect shorebird density (Jehl 2007, Sammler et al. 2008, Hines et al. 2010). Such findings suggest potential local exclusion of shorebirds by geese due to habitat degradation or increased predation risk. Predator-mediated effects of geese on shorebirds are poorly understood and are still neglected (McKinnon et al. 2013). Predation avoidance was recently highlighted as one of the key drivers explaining long-distance migrations and species distribution of arctic-nesting shorebirds (Gilg and Yoccoz 2010, McKinnon et al. 2010*b*). Hence, changes in enemy-free space in the Arctic could have profound effects on shorebirds.

Shorebirds and geese share several natural enemies, including jaegers, gulls, ravens, and especially the Arctic fox (*Vulpes lagopus*; Fig. 1), which is the primary egg predator (Bêty et al. 2002, Liebezeit and Zack 2008, McKinnon and Bêty 2009, Royer-Boutin 2015). In areas where Arctic foxes mainly feed on cyclic small rodents during the summer, geese and shorebirds are typically considered as alternative or incidental prey (Angelstam et al. 1984, Bêty et al. 2001, 2002, McKinnon et al. 2013). Lemming population cycles induce strong numerical and functional response of both avian and mammalian predators, with cascading effects on breeding geese and shorebirds (Bêty et al. 2001, 2002, Gauthier et al. 2004, Morrissette et al. 2010, Nolet et al. 2013). Moreover, breeding Arctic foxes show an aggregative response to the presence of the snow goose colony modulated by lemming density (Giroux et al. 2012). We used data collected over six years within and near a large greater snow goose (*Chen caerulescens atlantica*) colony in the Canadian High Arctic (Bylot Island, Nunavut) to test the hypothesis that geese negatively affect arctic-nesting shorebirds by increasing nest predation pressure. We specifically investigated the effect of a goose colony on the spatial variation in (1) the occurrence of shorebird nest predators, (2) the nest predation risk, and (3) the occurrence of breeding shorebirds. By sampling both within and outside the goose colony, we thus expected that the distance from the goose colony would drive nest predation pressure on shorebirds especially at low lemming density.

METHODS

Study site

The study took place from 2010 to 2015 on Bylot Island, Sirmilik National Park, Nunavut, Canada (73°08′ N, 80°00′ W; Fig. 2). The study area is dominated by mesic tundra on the uplands and a mixture of mesic tundra and wetlands (primarily polygonal tundra) in the lowlands (see Gauthier et al. 2013 for details). Each summer, ~20,000 pairs of greater snow geese nest in one large colony covering approximately 65 km^2 on the southern plain of Bylot Island (Fig. 2; Appendix S1). The greater snow goose population increased exponentially near the end

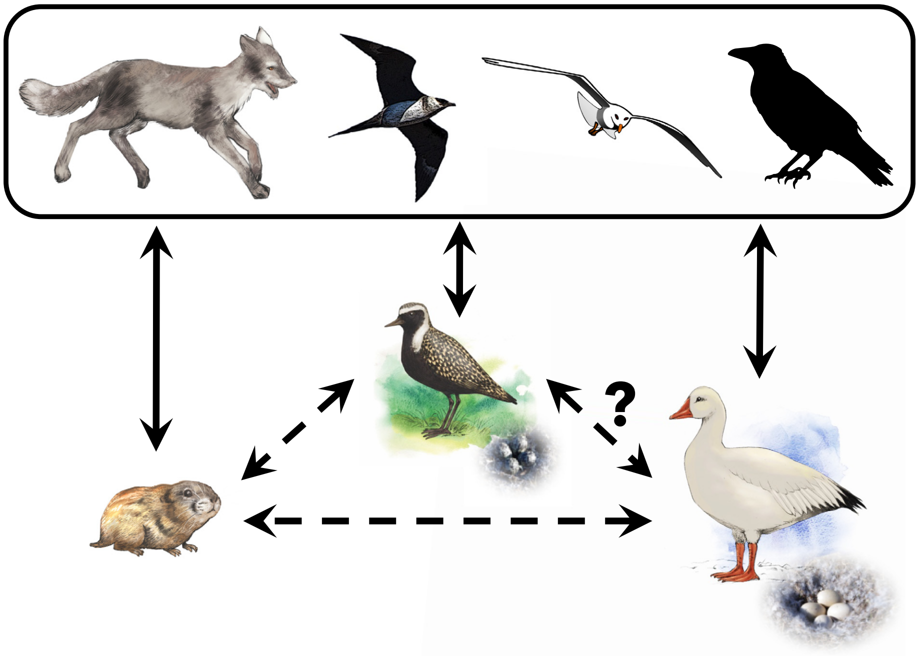

Fig. 1. Food web of the study system indicating the direct (solid lines) and indirect (dashed lines) links. The main trophic link targeted in this study is indicated by the question mark.

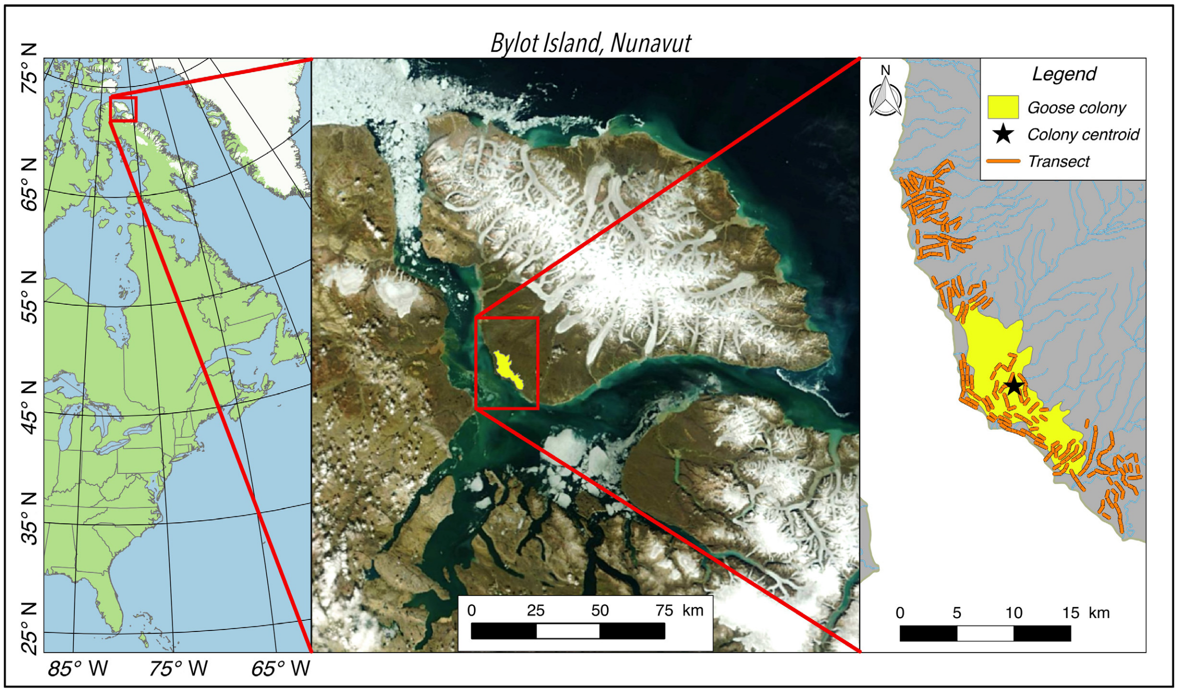

Fig. 2. Location of the study area and survey transects performed within and in the surroundings of the greater snow goose colony on Bylot Island in the Canadian High Arctic (satellite image from NASA MODIS Rapid Response).

of the 20th century (Menu et al. 2002, Gauthier et al. 2005) and was declared overabundant due to the potential impacts of the growing population on wetland habitats and on other species (Batt 1998). The approximate boundary of the goose colony was mapped each year during the nesting period with a helicopter and was relatively stable across years (maximum distance between centroid and boundary from 9.0 km to 10.7 km; mean = 9.7 km; Appendix S1).

Lemming density

Lemmings were live-trapped every summer with Longworth traps to obtain mark–recapture estimates of abundance as described in Fauteux et al. (2015). The trapping session lasted three days and traps were checked twice a day. We had two 11-ha trapping grids, one in mesic and the other in wetland habitats, each containing 144 traps. The July trapping session took place while transects and artificial nests were performed. Therefore, we pooled data from this session only to have a total of all lemmings of the species present on Bylot Island (collared lemmings [*Dicrostonyx groenlandicus*] and brown lemmings [*Lemmus sibiricus*]). We used the average between grids, as a measure of overall lemming density. Considering the distribution of the annual lemming density observed during the study period, we used two categories in our analyses (low density, <2.5 lemmings/ha; and high density, >6 lemmings/ha; Appendix S2).

Spatial variation in the occurrence of nesting shorebirds and nest predators

We focused our study on one of the most common shorebird species nesting on Bylot Island (Lepage et al. 1998), the American golden-plover (*Pluvialis dominica*, which will be referred to as plover hereafter). In our study area, the presence of plover is a good indicator of shorebird diversity and abundance in mesic tundra habitat (Appendix S3) and plovers react strongly to a human intruder when nesting (Byrkjedal 1989), increasing detectability by observers. The reaction distance of incubating plovers to the observer is 61 m SE = 8 m in our study area (n = 23 nests; J.-F. Lamarre and J. Bêty, *unpublished data*). Data collection took place during the plover's incubation period (between 21 June and 14 July). Median estimated initiation date of plover nests during those years was 18 June (n = 374), and median observed hatch date was 16 July (n = 55). To quantify the effect of the goose colony on the occurrence of predators and nesting shorebirds, we conducted surveys through 500 m long transects located within (from 34 to 63 transects annually) and outside (from 96 to 191 transects annually) the snow goose colony (Fig. 2; Appendix S1). The visibility on each side of transects was >150 m (estimated by observers trained with range finder at three points on each transect), and all vertebrates seen within 150 m from the transect were recorded. All the transects were located in mesic tundra with low vegetation, which is the preferred nesting habitat for plovers (Connors et al. 1993, Byrkjedal and Thompson 1998).

Plovers producing distraction displays such as rodent run, broken wing, and/or insistent calls were considered as breeders (Byrkjedal 1989). Birds that did not react to the presence of the observer and/or were foraging, flying by, or resting were considered non-breeders. Status was confirmed by moving towards the individuals. Plover original location upon detection was obtained with a handheld GPS to later calculate the nearest distance to the transect.

When predators were sighted (nest predators shared by shorebirds and geese: parasitic jaeger (*Stercorarius parasiticus*); glaucous gull (*Larus hyperboreus*); common raven (*Corvus corax*); and Arctic fox), a single individual was spotted on most occasions: 51% (n = 394) and 93% (n = 81) for avian predator and Arctic fox, respectively. Therefore, occurrence (probability to observe at least one individual on transect) was used in the analyses.

Predation risk

Predation risk was assessed with artificial nests (93–185 nests annually) made with four Japanese quail (*Coturnix japonica*) eggs placed in a small man-made depression comparable to nest scrapes made by shorebirds. Experiments took place in late June to early July, during the plover and goose incubation period. Quail and shorebirds eggs are similar in coloration and size. Prior to deployment, eggs were inspected, washed, and air-dried to minimize smell related to transport and storage. We marked nests with a tongue depressor at 5 m and a feather at 7 m while wearing clean nitrile gloves. Nests were installed at each end of transects located within and outside the snow goose colony and were revisited after 48 h. Nest failure was defined as the predation of one or more eggs from the artificial nest. Shorebird nests and artificial nests have the same dominant predator in our study area (Arctic foxes; McKinnon and Bêty 2009, Royer-Boutin 2015). Although artificial nests cannot be used to infer predation rate on real nests, our technique provides a reliable measure of spatial variation in relative nest predation risk (see McKinnon et al. 2010*a*, *b*).

Statistical analyses

General linear mixed models (GLMM) were used to model predator and nesting plover occurrence and nest predation risk with lme4 (Bates et al. 2015) in R version 3.2.4 (R Core Team 2016). We used a binomial error structure and a logit-link function, with predator or nesting plover occurrence (one individual seen on transect = 1, no individual seen = 0) as the response variable. GLMM were also used to model nest predation risk with nest fate (one or more eggs depredated = 1, no eggs depredated = 0) as the response variable.

In all the analyses, all continuous variables were standardized by subtracting the mean and dividing by the standard deviation. The fixed effects were distance from the centroid of the goose colony (DIST, continuous variable), lemming density (LEM, factor: years classified as high or low lemming density, Appendix S2), and interaction between LEM and DIST. To account for a non-linear effect of DIST, a quadratic term was added (DIST2). To better interpret non-linear relationships, we used the *lavielle* function of the R package *adehabitatLT* (Calenge 2006) to identify segments (thresholds) on the fitted logistic relationships. This function performs a non-parametric segmentation with the penalized contrast method of Lavielle (1999, 2005) to find the distance from the centroid of the colony at which the occurrence (or nest predation risk) starts changing. This analysis is usually applied to time series but because transects were well spread around the colony, we calculated the mean occurrence of predators or nesting plovers for each 0.5 km away from the colony and applied the *lavielle* function on this dataset. All values are presented with ±95% CI unless specified otherwise. The centroid of the goose colony and distances between the centroid and transects were calculated for each year with the rgeos R package (Bivand et al. 2014). Transects were performed only once each year and almost all (91%, $n = 267$) were repeated at least four years. To account for potential pseudo-replication, transect or nest number was used as a random factor in all the analyses (Bolker et al. 2009). Because transects were performed over a 23-d period and because the detection of predator or nesting plovers, as well as predation of artificial nests, could change over time, standardized day of year was also included as a random factor in all our analyses. Models were selected according to their corrected Akaike information criterion (AICc). Parameter estimates were derived from averaging all models (model.avg in MuMIn R package; Bartoń 2015).

RESULTS

Lemming density and nest predator occurrence

Over the years of the study, 1242 surveys were performed on 267 unique transects (from 130 to 249 transects per year). Annual lemming density varied during the study period (from 0.05 to 6.93 lemming/ha), resulting in three years of relatively high density (>6.0/ha: 2010, 2011, 2014) and three years of lower density (<2.5/ha; 2012, 2013, 2015; Appendix S2). Occurrence of predators also varied, with Arctic foxes sighted more during years of low lemming density (Fig. 3). In contrast, avian predators were more abundant during years of high lemming density except for the common raven (Fig. 3). Because common raven occurrence was very low compared to the other two avian predator species and because glaucous gulls and parasitic jaegers showed similar patterns (Fig. 3), we combined all avian predators in subsequent analyses.

The distance to the centroid of the goose colony influenced the occurrence of predators but in interaction with lemming density (Table 1, Fig. 4a, b). Fewer Arctic foxes were sighted far from the colony centroid, but the relationship was not significant at high lemming abundance ($\beta = -1.32$; 95% CI [−1.88, −0.76] and $\beta = -0.37$; 95% CI [−0.94, 0.20] for low and high lemming year, respectively; Table 1a, Fig. 4a). The non-linear relationship detected in the model selection better described the relationship between Arctic fox occurrence and distance to

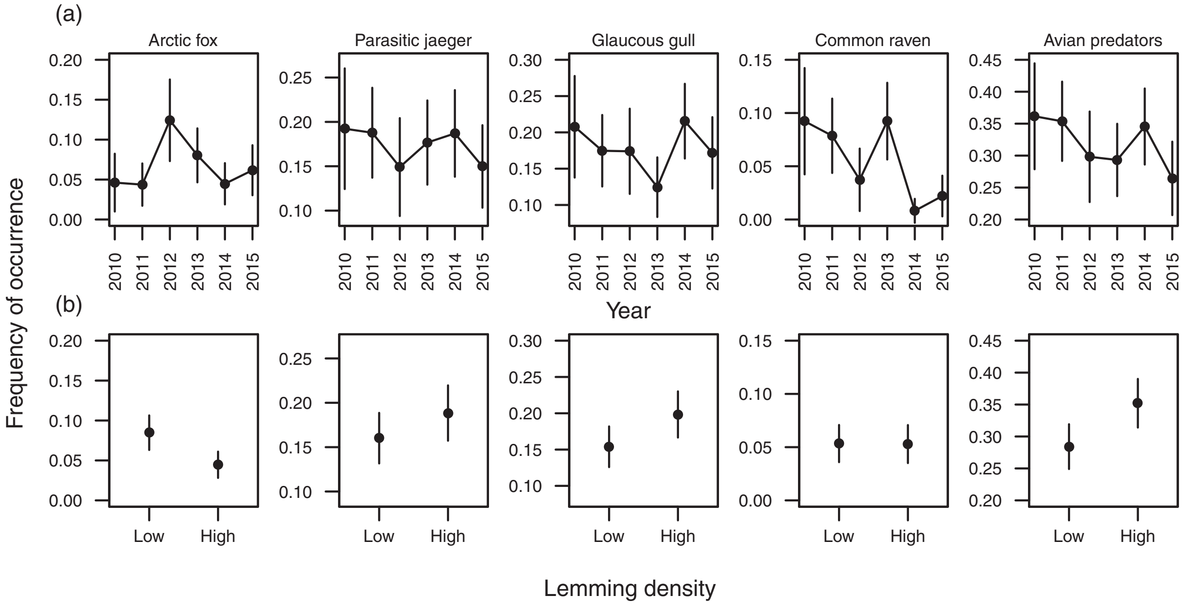

Fig. 3. Frequency of occurrence (probability to observe at least one individual) on transects (a) by year (2010–2015) and (b) split by level of lemming density with error bars representing 95% confidence intervals of the four nest predators shared between shorebirds and snow geese. Occurrence of all three avian predator species combined is also presented.

the colony at low lemming density (Table 1a, Fig. 4a). We found an inflection point at 8.5 km from the centroid of the colony at low lemming density. On average, the occurrence of foxes was seven times higher at low lemming density and two times higher at high lemming density below the inflection point, which was fairly close to the mean maximal extent of the goose colony (Fig. 4a). At low lemming density, Arctic fox occurrence decreased by 2.0% per km away from the centroid of the goose colony for the first 8.5 km and this value decreased to 0.29% per km for the 8.5–20 km away from the centroid of the colony.

Occurrence of avian predators was strongly related to distance to the centroid of the goose colony, and this was modulated by lemming density (β = −1.14; 95% CI [−1.44, −0.83] and β = −0.74; 95% CI [−1.01, −0.47] for low and high lemming density, respectively; Table 1b, Fig. 4b). Breakpoints were found at 10.5 km and 8.5 km at high and low lemming density, respectively (Fig. 4b). For the first 8.5 km away from the centroid of the goose colony, occurrence of avian predators decreased by 6.8% per km at low lemming density, a value decreasing to 1.1% for the 8.5–20 km away from the centroid of the colony. This effect weakened slightly at high lemming density (6.1% per km for the first 10.5 km, decreasing to 0.7% per km for the 10.5–20 km away from the centroid). On average, the occurrence of avian predators was three times higher below the breakpoint than above it (Fig. 4b).

Nest predation risk

Overall, about 19% of all the artificial shorebird nests (n = 911) were depredated after 48 h of all exposure. Lemming density and distance to the centroid of the goose colony influenced predation risk (Table 2a). Nest predation risk was lower at high lemming density (β = −0.62; 95% CI [−1.14, −0.12]; Fig. 4c) and decreased with the distance to the goose colony centroid (β = −0.36; 95% CI [−0.65, −0.07], β = −0.30; 95% CI [−0.61, 0.01] for low and high lemming year, respectively; Table 2a, Fig. 4c). Nest predation decreased by 0.9% and 0.5% per km away from the centroid of the goose colony at low and high lemming density, respectively. No breakpoint was detected.

Table 1. Model selection of the effects of lemming (LEM; years categorized as high or low lemming density), distance from the centroid of the goose (DIST), and two-way interactions on (a) Arctic fox and (b) avian predator occurrence along transects (*n* observations = 1242 from 267 different transects used as a random factor)†,‡,§.

Model name	K	ΔAICc	ωi	LL
(a)				
DIST*LEM	6	0.00	0.61	−266.10
DIST*LEM+DIST2	7	1.93	0.23	−266.05
DIST*LEM+DIST2*LEM	8	3.26	0.12	−265.71
DIST+DIST2*LEM	7	7.21	0.02	−268.70
DIST+LEM	5	7.43	0.01	−270.83
DIST+DIST2 + LEM	6	8.86	0.01	−270.53
DIST	4	15.32	0.00	−275.78
DIST+DIST2	5	16.75	0.00	−275.49
LEM	4	31.88	0.00	−284.06
null	3	39.18	0.00	−288.71
(b)				
DIST*LEM+DIST2	7	0.00	0.65	−660.47
DIST*LEM+DIST2*LEM	8	1.91	0.25	−660.41
DIST+DIST2 + LEM	6	4.86	0.06	−663.91
DIST+DIST2*LEM	7	6.46	0.03	−663.70
DIST+DIST2	5	8.25	0.01	−666.61
DIST*LEM	6	16.13	0.00	−669.55
DIST+LEM	5	22.04	0.00	−673.51
DIST	4	25.82	0.00	−676.41
LEM	4	88.88	0.00	−707.94
null	3	92.39	0.00	−710.70

† A non-linear relationship between Arctic fox occurrence and the distance to the centroid was tested by including a quadratic term (DIST2).

‡ When there was an interaction (*) between two factors, each individual factor was also retained in the model.

§ K = number of parameters; ΔAICc = difference in AICc between the current and top-ranked model; ω_i = AICc weight in favor of the model; and LL = log likelihood.

Nesting plover occurrence

The occurrence of nesting plovers varied strongly over the study period (Fig. 4d). Both lemming density and the distance to the centroid of the goose colony influenced the probability to find nesting plovers on transects (Table 2b). Nearest distance to the transect of breeding plovers (average = 49 m, SE = 1.9, *n* = 363) was not affected by the distance to the centroid of the colony (β = 0.02, SE = 1.88, *P* = 0.99), indicating that detection probability of plovers was similar over the entire study area. Over 85% of plovers were detected within 90 m from transect. There was also evidence for an interaction between lemming density and distance to the colony with a quadratic effect (β = −0.69; 95% CI [−1.04, −0.34]). More nesting plovers were detected away from the colony (β = 0.86; 95% CI [0.52, 1.21], β = 0.80; 95% CI [0.54, 1.06]; at low and high lemming density, respectively; Table 2b, Fig. 4d). A breakpoint was detected at 9 km from the centroid of the colony, which was close to the maximum extent of the colony boundary (Fig. 4d). For the first 9 km away from the centroid of the colony, the probability of finding a nesting plover increased by 3.0% and 1.3% per km on average at high and low lemming density, respectively. Nesting plover occurrence remained low below the breakpoint, that is, within the goose colony (Fig. 4d). Nesting plover occurrence was, respectively, 4.4 and 2.5 times higher above the threshold at low and high lemming density. The interacting effect of lemming and distance from the colony with a quadratic effect was mostly driven by a stronger increase in plover occurrence above the breakpoint at high lemming density than at low density (Fig. 4d).

DISCUSSION

The rapid growth of arctic-nesting goose populations has caused cascading effects on coastal arctic marshes through overgrazing (Jefferies and Rockwell 2002, Fox et al. 2005). Large goose colonies can also induce indirect trophic interactions by affecting enemy-free space in the Arctic. Such predator-mediated effects are poorly documented (Iles et al. 2013, McKinnon et al. 2013, 2014). In the present study, we found strong evidence that a large greater snow goose colony in the Canadian Arctic influences the spatial variation in (1) the occurrence of nest predators shared by geese and shorebirds, (2) the risk of shorebird nest predation, and (3) the occurrence of nesting shorebirds. The size of our snow goose colony has remained relatively stable in recent years (Appendix S1) and represents a predictable resource for predators (Dickey et al. 2008). The goose colony clearly attracted a high density of both mammalian (Arctic fox) and avian nest predators. As predicted, such predator aggregative responses negatively affected artificial shorebird nest survival and apparently reduced the occurrence of shorebirds within the goose colony. Our results are consistent with recent studies highlighting the importance of predation in shaping trophic relationships within the arctic

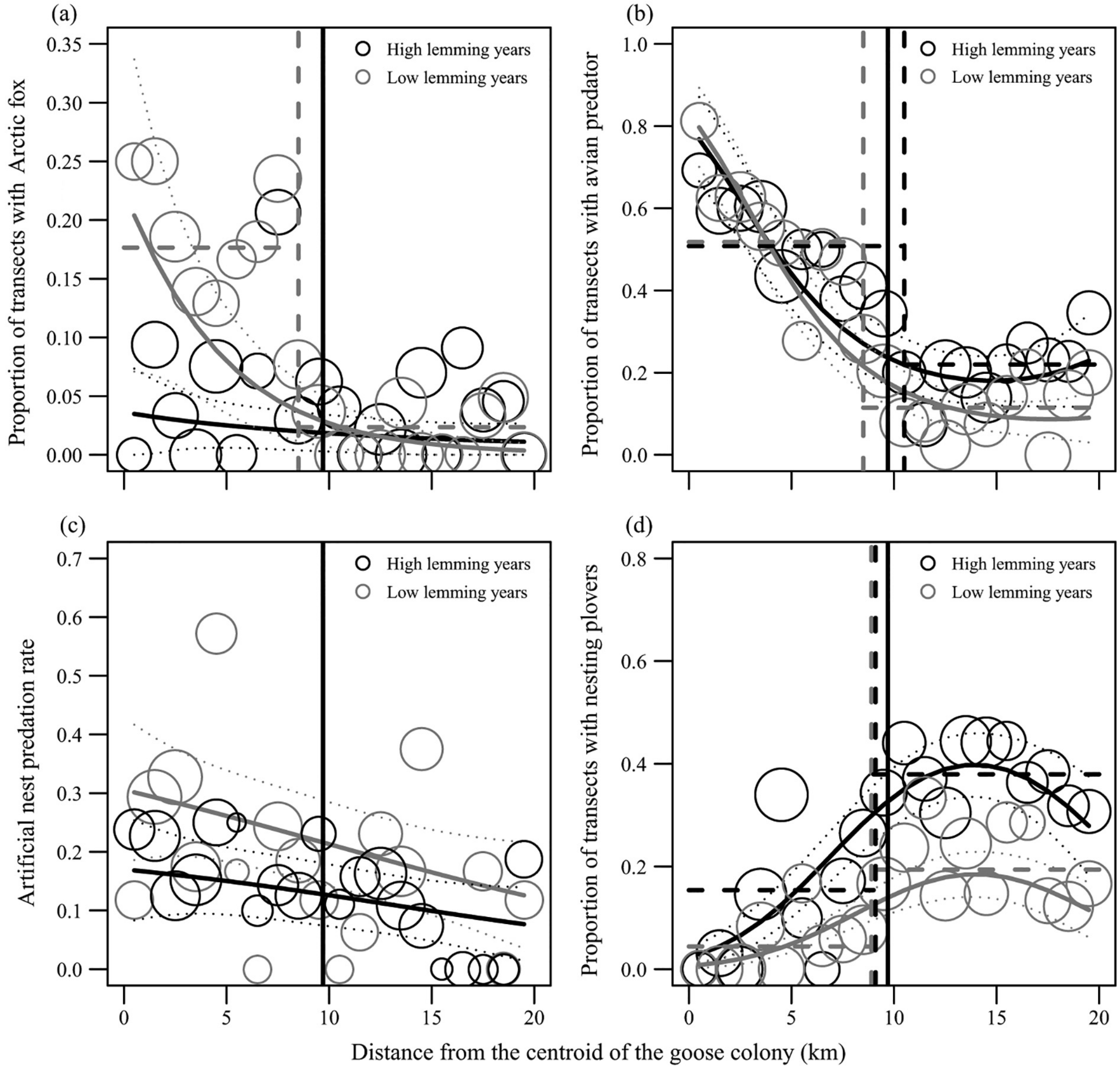

Fig. 4. Occurrence of Arctic fox (a) and of avian predators (b), artificial nest predation rate (c), and occurrence of nesting American golden-plovers (d) on transects according to the distance from the centroid of the goose colony and lemming density. The black and gray lines represent the fit of models, based on model averaging for high and low lemming density, respectively, and dotted lines are 95% CI. Black and gray bubbles represent mean proportions for high and low lemming density, respectively, and the size of the bubble is proportional to log (N). The mean across years of the maximum extent of the goose colony boundary is indicated by the solid vertical line. The vertical dashed lines were obtained from a segmentation analysis (Lavielle 1999, 2005, see *Methods*). The horizontal dashed lines represent the mean occurrence above and below the breakpoint.

tundra and in affecting shorebird species distribution (Gilg and Yoccoz 2010, McKinnon et al. 2013, Legagneux et al. 2014).

Overall, there were more sightings of foxes when lemming abundance was low and the opposite was true for avian predators. Observing fewer avian predators during years of low lemming abundance may be due to predation of avian predators' nests by foxes as has been shown for glaucous gulls at our study site

Table 2. Model selection of the effects of lemming density (LEM; years categorized as high or low lemming density), distance from the centroid of the goose colony (DIST), and two-way interactions on (a) the risk of predation on artificial nests (*n* = 911, deployed on 245 different transects used as a random factor) and (b) probability of observing nesting American golden-plovers along transects (*n* observations = 1242 from 267 transects used as a random factor)†, ‡, §.

Model name	K	ΔAICc	ωi	LL
(a)				
DIST+LEM	5	0.00	0.37	−421.05
DIST*LEM	6	1.39	0.18	−420.73
DIST+DIST2 + LEM	6	1.48	0.17	−420.77
DIST+DIST2*LEM	7	2.62	0.10	−420.33
DIST*LEM+DIST2	7	2.87	0.09	−420.45
DIST*LEM+DIST2*LEM	8	4.07	0.05	−420.03
LEM	4	5.06	0.03	−424.58
DIST	4	7.57	0.01	−425.84
DIST+DIST2	5	9.09	0.00	−425.59
null	3	12.61	0.00	−429.37
(b)				
DIST+DIST2 + LEM	6	0.00	0.44	−553.21
DIST+DIST2*LEM	7	1.44	0.22	−552.92
DIST*LEM+DIST2	7	1.61	0.20	−553.00
DIST*LEM+DIST2*LEM	8	2.23	0.14	−552.30
DIST+LEM	5	23.37	0.00	−565.90
DIST*LEM	6	25.39	0.00	−565.90
DIST+DIST2	5	45.18	0.00	−576.81
LEM	4	58.86	0.00	−584.66
DIST	4	65.94	0.00	−588.20
null	3	95.74	0.00	−604.10

† A non-linear relationship between Arctic fox occurrence and the distance to the centroid was tested by including a quadratic term (DIST2).

‡ When there was an interaction (*) between two factors, each individual factor was also retained in the model.

§ K = number of parameters; ΔAICc = difference in AICc between the current and top-ranked model; ω_i = AICc weight in favor of the model; and LL = log likelihood.

(Gauthier et al. 2015). We found a higher predation rate on artificial nests during years of low lemming abundance, and since we observed more foxes and less avian predators, this confirms that the main predator affecting shorebirds in our system is the Arctic fox (Bêty et al. 2002, McKinnon and Bêty 2009, Royer-Boutin 2015).

The effect of geese on nest predators and shorebirds was tested with the distance from the centroid of the colony. Our analyses revealed non-linear relationships between the distance and the occurrence of predators or nesting plovers. The segmentation analyses also revealed the existence of breakpoints in these relationships that were always very close to the maximum extent of the goose colony (located ~10 km away from the centroid). Such a close match between the spatial distribution of geese, nest predators, and nesting plovers suggests a clear predator-mediated negative effect of the goose colony on shorebirds.

Although we found evidence that distance from the goose colony affected predation risk, the threshold around 10 km was not found through artificial nest experiments. Deployment of a large number of artificial shorebird nests in the Arctic appears to provide a reliable index of predation risk to compare distant breeding sites, to detect annual variation, and to investigate fine-scale spatial variation of predation risk (McKinnon et al. 2010*b*, 2013, 2014). However, the limited number of artificial nests deployed annually at varying distances and over a short time period (48 h) may have reduced the likelihood of detecting a specific distance threshold of predation risk in our study area. The decreasing predation risk away from the goose colony found in our study is consistent with observations of McKinnon et al. (2013) showing a positive relationship between goose nest density and predation risk within the goose colony. Quantifying the spatial variation in predation rate on real shorebird nests would have strengthened our main conclusions. However, field logistical constraints combined with the low density of nesting shorebirds precluded our ability to monitor an adequate number of real nests both within and outside the goose colony.

The lower occurrence of nesting shorebirds inside the goose colony could result from birds directly avoiding areas with high nesting goose density and elevated predator activity rate. Avoidance of the goose colony could also result from severe habitat degradation caused by heavy goose grazing, as reported for shorebirds and passerines nesting at Cape Churchill (Sammler et al. 2008, Peterson et al. 2014). However, this is unlikely at our study site because goose grazing intensity is high in wetlands (polygon fens) and low in mesic habitat (Duclos 2002, Valéry et al. 2010) where the focal species (plovers) predominantly nest. Although goose grazing in wetlands decreases primary production, it is not high enough to cause habitat degradation (Gauthier et al. 2004, Valéry et al. 2010) probably because the carrying capacity of those habitats is not yet reached on Bylot Island (Duclos 2002). Moreover, the American golden-plover is a site-faithful species with males typically reusing the same territory year after year (Johnson and Connors 2010). Thus, the lower occurrence of nesting shorebirds observed at low lemming density in our study area is possibly due to early failure of nesting activities caused by predation.

Our study provides evidence that, during the breeding season, overabundant geese reduced the amount of enemy-free space in the arctic tundra, leading to a higher predation risk for shorebird nests within a goose colony. Predator-mediated effects appear widespread in the arctic food web (Bêty et al. 2002, Morrissette et al. 2010, McKinnon et al. 2013, Nolet et al. 2013), and predation avoidance was identified as one potential driver of species distribution in arctic-nesting shorebirds (Gilg and Yoccoz 2010, McKinnon et al. 2010*b*). In a recent circumpolar-scale analysis, Legagneux et al. (2014) concluded that small to medium sized vertebrates in arctic terrestrial food webs are under strong top-down control from predation. Tundra-nesting geese migrating annually from temperate agricultural lands can generate a substantial flow of additional food for arctic predators (Giroux et al. 2012), and our results indicate that predation patterns previously reported in the Arctic could be affected at the local scale by the presence of large goose colonies. Further investigations would be needed to determine the resulting indirect interaction between geese and other tundra prey species. Indeed, apparent competition arises when two prey species negatively affect each other but shared predators can also generate non-reciprocal indirect effects, such as indirect amensalism (Chaneton and Bonsall 2000). If shorebirds are being attacked only incidentally (see McKinnon et al. 2013), they could have small per capita effects on the population size or behavior of shared predators, and hence, their indirect effects on geese could be negligible.

Although the present study focused on the occurrence of shorebird species, it is likely that the observed patterns of predation risk could be generalized to other vulnerable tundra-nesting bird species. Results from artificial nests indicate higher predation risk in the goose colony and the main predator of artificial nests is the Arctic fox (Bêty et al. 2002, Liebezeit and Zack 2008, McKinnon and Bêty 2009, Royer-Boutin 2015). Nest monitoring confirmed that predation by Arctic foxes is one of the main causes of nest failure for ground-nesting birds monitored on Bylot Island (including passerines, raptors, geese, and shorebirds; McKinnon and Bêty 2009, Royer-Boutin 2015, Beardsell et al. 2016). Further investigations on the distribution and abundance of avian and mammalian tundra species inside and surrounding the colony would help assess the impacts of geese on local biodiversity.

Our study revealed a significant predator-mediated negative effect at the local colony scale. However, the global impact of increasing goose colonies on population dynamic of shorebirds remains to be quantified but could be significant considering that all three populations of snow geese are designated as overabundant in Canada and that their breeding population across the Canadian Arctic currently exceeds 15 million birds (Alisauskas et al. 2011). Concurrently, several arctic shorebird species have been undergoing important population declines in recent decades (Morrison et al. 2006, Deinet et al. 2015), and it is urgent to evaluate the role of overabundant geese in those declines. An understanding of predator-mediated effects of overabundant geese at larger geographic scales across the North American Arctic would greatly improve our understanding of the impacts of overabundant geese on these ecosystems, to take action and orient conservation measures.

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DATA AVAILABILITY

Data are available online through Dryad: https://doi.org/10.5061/dryad.796t8 (Lamarre et al. 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1788/full