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Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra

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Apparent competition between prey is hypothesized to occur more frequently in environments with low densities of preferred prey, where predators are forced to forage for multiple prey items. In the arctic tundra, numerical and functional responses of predators to preferred prey (lemmings) affect the predation pressure on alternative prey (goose eggs) and predators aggregate in areas of high alternative prey density. Therefore, we hypothesized that predation risk on incidental prey (shorebird eggs) would increase in patches of high goose nest density when lemmings were scarce. To test this hypothesis, we measured predation risk on artificial shorebird nests in quadrats varying in goose nest density on Bylot Island (Nunavut, Canada) across three summers with variable lemming abundance. Predation risk on artificial shorebird nests was positively related to goose nest density, and this relationship was strongest at low lemming abundance when predation risk increased by 600% as goose nest density increased from 0 to 12 nests ha^{-1}. Camera monitoring showed that activity of arctic foxes, the most important predator, increased with goose nest density. Our data support our incidental prey hypothesis; when preferred prey decrease in abundance, predator mediated apparent competition via aggregative response occurs between the alternative and incidental prey items.

Apparent competition, whereby one prey item influences the abundance of another prey item via their influence on the population size of a shared predator (Holt 1977), is hypothesized to occur more in poor environments defined by low densities of preferred prey where predators are forced to forage for multiple prey items (Holt and Kotler 1987). In poor environments with patches of variable or low preferred prey density, predators must adopt more opportunistic foraging. Predators should be attracted to foraging areas of high densities of preferred prey, and the time spent in these better quality foraging areas can be extended based on the density of available alternative prey (Holt and Kotler 1987). Therefore, alternative prey are expected to suffer higher predation risk in poor environments where availability of preferred prey is variable or low. In populations where preferred prey exhibit multi-annual cycles in abundance (e.g. arctic voles or lemmings), predators will exert greater predation pressure on alternate prey in years following a peak in preferred prey abundance, resulting in cycles in alternative prey abundance (Summers et al. 1998, Bêty et al. 2001, Blomqvist et al. 2002). This phenomenon is explained by the alternative prey hypothesis, whereby an increase in predator populations (numerical response) due to a peak in preferred prey, and a switch in diet (functional) when the preferred prey population crashes both result in variation in annual predation pressure on alternative prey such as birds eggs (Lack 1954, Angelstam et al. 1984).

Most empirical studies testing predictions of the alternative prey hypothesis to date have studied simple 1 predator: 2 prey systems (1 preferred prey, 1 alternative prey; Roseberry and Klimstra 1970, Vickery et al. 1992, Hoi and Winkler 1994, James et al. 2004, Schmidt 2004). However, even in a relatively simple ecosystem, such as the arctic tundra, there are often several alternative prey items available to predators. When presented with several alternative prey of decreasing profitability, it is likely that a hierarchical chain of interactions between preferred prey and different classes of alternative prey may result (Smout et al. 2010). Evidence of such interactions, however, is difficult to provide in a natural setting which explains why, to our knowledge, few empirical studies have investigated the alternative prey hypothesis in multiple (>2) prey systems (Smout et al. 2010).

In this paper, we propose and test a slightly modified alternative prey hypothesis to describe multispecies interactions between preferred, alternative and incidental prey. As in the alternative prey hypothesis, we suggest that apparent competition via functional and numerical response occurs between preferred (A) and alternative prey (B); the numerical response referring to an increase in predator number due to increases in preferred prey and the functional response referring to a disproportionate increase of alternative prey in the predator diet when preferred prey decrease. However, when the abundance of the preferred prey A is low (poor environment), the alternative prey B then become the second order preferred prey and apparent competition occurs between alternative prey and other less profitable alternative prey (C). In systems where the alternative prey are distributed patchily throughout the environment, such as with colonial nesting birds, this should lead to spatial aggregation of predators in patches of high alternative prey density (aggregative response). In such systems, we suggest that predation risk on prey C will be influenced by the spatial distribution of alternative prey B, as alternative prey do not often increase reproduction of predators (numerical response) but can affect their geographical distribution (aggregative response), especially after a drop in preferred prey numbers (Holt and Kotler 1987, Schmitt 1987). When prey C is an incidental prey (defined as not being the focus of a directed predator search, Cornell 1975), this effect will be pronounced as the abundance and distribution of prey C should not have any effect on predator foraging behaviour. We explore this incidental prey hypothesis experimentally by measuring spatial variation in predation risk on an incidental prey species (artificial shorebird nests) in relation to the abundance of a patchily distributed alternative prey (goose nests) in years of varying preferred prey (lemming) abundance.

In the Canadian Arctic, a numerical and functional response of predators to preferred prey (lemmings) affects the breeding output of alternative prey such as geese (Bêty et al. 2001, 2002, Gauthier et al. 2004). In addition, an aggregative response of arctic foxes *Vulpes lagopus* has been documented in proximity to large goose colonies (Giroux et al. 2012). Shorebirds and geese share several natural enemies and the arctic fox is the primary egg predator for both species (Bêty et al. 2002, Lecomte et al. 2008, McKinnon and Bêty 2009). Shorebird eggs can be considered incidental prey as there are likely not the 'focus' of a directed predator search (Cornell 1975). As a prey item, shorebird eggs are also much less profitable than goose eggs as clutch sizes are generally smaller, eggs are up to 17 times smaller (i.e. lower caloric content per egg), and the nests are more difficult to find (less conspicuous in general and found in low densities in the goose colony). Given evidence of an aggregative response by the arctic fox (Giroux et al. 2012), we hypothesized that predation risk for incidental prey would increase as goose nest density increased due to apparent competition. Furthermore, we predicted that such effects would be stronger during low lemming years (poor environment) than during high lemming years (rich environment). To test for this relationship, we measured predation risk by monitoring the survival of artificial shorebird nests in quadrats varying in goose nest density. We replicated the study across three summers with contrasting lemming abundance. Results from our study support the incidental prey hypothesis, as in years of low preferred prey (lemming) abundance, apparent competition via aggregative response occurred between the alternative prey (goose eggs) and the incidental prey (artificial shorebird eggs).

Methods

Study area

The study was conducted from 2007–2009 on the south plain of the Bylot Island Migratory Bird Sanctuary in Sirmilik National Park (72°53′N, 78°55′W), Nunavut territory, Canada. The south plain is characterized by lowlands composed of mesic tundra and wetlands and uplands dominated by mesic and xeric tundra (Tremblay et al. 1997). Each summer, approximately 50 000 greater snow geese *Chen caerulescens atlantica* nest in one main colony covering approximately 65 km^2. Two species of lemming are present year round throughout the entire south plain (~425 km^2), the brown lemming *Lemmus trimucronatus* and the collared lemming *Dycrostonyx groenlandicus* (Szor et al. 2008). Populations of both species exhibit cycles at three to four year intervals, though cycles are much more pronounced for the brown lemming which ranges in abundance from four individuals per 100 trap nights in peak phase summers to zero during low phase summers (Gruyer et al. 2008). Collared lemming populations range from one individual per 100 trap nights during the peak phase to 0 during the low phase (Gruyer et al. 2008). A total of 83 arctic fox dens are distributed throughout the south plain and up to one third can be used in a high lemming year (Szor et al. 2008). Shared predators of lemmings and goose eggs include, in decreasing order of importance, arctic fox, parasitic jaegers *Stercocarius parasiticus*, glaucous gulls *Larus hyperboreaus* and common ravens *Corax corax* (Bêty and Gauthier 2001, Bêty et al. 2002). Shorebirds nesting throughout the study area included American golden plover *Pluvialis dominica*, black-bellied plover *Pluvialis squatarola*, Baird's sandpiper *Calidris bairdii*, white-rumped sandpiper *C. fuscicollis*, red phalarope *Phalaropus fulicarius* and ruddy turnstone *Arenaria interpres*. Shorebird eggs are also mainly taken by arctic foxes (McKinnon and Bêty 2009).

Lemming abundance

An index of lemming abundance was obtained each year based on snap trapping conducted between 10 and 14 July (Gruyer et al. 2008). Lemming transects were located within the 20 km^2 area in the goose colony where we placed our artificial nest quadrats. Museum special snap traps baited with peanut butter were placed along two sets of two parallel transect lines placed 100 m apart (four transect lines in total). Transect lines had a total of 68 stations in 2007 and 80 stations in 2008 and 2009. Each station consisted of three traps placed within a 2 m radius of the transect and each station was spaced 15 m apart. Each transect was checked daily for three to four days for a total of 780 trap nights in 2007 to 597.5 trap nights in 2008 and 949 in 2009. This calculation of trap nights included a correction of −0.5 trap nights when traps misfired, or when captures occurred. An index of lemming abundance was calculated as the number of lemmings trapped per 100 trap nights.

Predation risk and goose nest density

In order to measure the relative risk of predation on shorebird nests in relation to goose nest density, artificial shorebird nests were monitored in ten 0.25 km^2 quadrats (500×500 m in size) of varying goose nest density within a 20 km^2 (4×5 km) area in the center of the goose colony. Artificial nests were used to provide a reliable measure of relative predation risk in quadrats varying in goose density, as they permitted us to control for the heterogeneity associated with real nests (temporal, spatial, inter-specific and intra-specific behavioural differences; McKinnon et al. 2010a). Artificial shorebird nests on Bylot Island are also depredated primarily by the arctic fox (McKinnon and Bêty 2009). Each artificial nest consisted of four Japanese quail *Coturnix japonica* eggs placed in a small depression made in the ground. Quail eggs resemble those of shorebirds in colouration and size, and the depressions made are similar to the simple nest scrapes used by shorebirds. Unlike the colonial nesting snow geese which make large, down-filled nests that are conspicuous and aggressively defended during incubation, shorebird nests are very well camouflaged on the tundra whether the birds are incubating or not, and are not often aggressively defended. Therefore, it was safe to assume that the artificial nests used here were providing a relative measure of predation risk on incidental prey such as shorebirds, not on geese. Four artificial nests were randomly deployed within each quadrat during the late shorebird and goose incubation period (2, 5 and 4 July in 2007, 2008 and 2009 respectively); the distance between nests within the same quadrat ranged from 110 m to 564 m. Nests were deployed within the same time period (evening), and were relocated by small sticks or natural objects (rocks or feathers) placed at 5 and 7 m from the nest. Once deployed, artificial nests were checked at 12 h, 24 h, 72 h, and then every three days up to 12 exposure days. For visit intervals greater than 24 h, failure times were assumed to occur at the midpoint between sampling intervals as the exact date of failure was not known. Nest failure was defined as the depredation of one or more eggs from the artificial nest, as partial predation of clutches of natural shorebird nests has never been recorded during the five years of shorebird reproduction studies on Bylot Island.

To select locations for the 10 artificial nest quadrats and ensure sufficient variation in goose nest density, a helicopter survey of the main goose colony was conducted to qualitatively identify areas of low, medium and high goose nest density in 2007. These areas were then surveyed by foot and the 10 artificial nest quadrats were distributed among areas varying in goose nest density (3 low, 4 medium, 3 high). In order to increase spatial independence among quadrats, quadrats in low, medium and high goose nest density areas were segregated (i.e. not all low density quadrats were clumped together) and the distance between quadrat centres was on average 2.4 ± 0.2 km in 2007 (range: 0.76 to 5 km) and 1.9 ± 0.1 km in 2008 and 2009 (range: 0.74 to 4 km). In all years, quadrats were confined within the same 20 km^2 (4×5 km) study area. The location of 5 of the 10 quadrats changed slightly between 2007 and 2008 due to annual spatial variation in goose nest distribution. Quadrat locations did not change between 2008 and 2009.

To provide a quantitative estimate of goose nest density within each artificial nest quadrat, a survey of goose nests was conducted via distance sampling (Thomas et al. 2010) within each quadrat after the artificial nest monitoring was concluded. In 2007, four 500 m transects, placed 100 m apart within each quadrat, were surveyed for goose nests. In 2008 and 2009, only two 500 m transects, placed approximately 250 m apart, were surveyed due to logistical constraints. All goose nests seen from the transect line were counted and the perpendicular distance from each nest to the transect line was recorded. Transect surveys were conducted at the end of the goose incubation period (between 10 and 17 July each year), while nests were still intact and detectable but disturbance to nesting geese could be reduced. Goose nest density in each artificial nest quadrat was determined by compiling line transect data from all three years and determining the distance at which probability of nest detection was 100% using the program Distance ver. 5.0 (Thomas et al. 2010). Once determined, the total number of nests within this distance on either side of the transect line were summed and then converted to nests per hectare.

The effect of goose nest density on predation risk of artificial shorebird nests was tested in each of the three years varying in lemming abundance using Cox proportional hazards regression models (PROC PHREG in SAS) which test for a relationship between Kaplan–Meier survival estimates and explanatory variables (Cox 1972). The parameter estimate provided for covariates in the Cox proportional hazards model can be exponentiated to provide an estimate of the hazard ratio (or risk ratio), which is a measure of the risk of predation relative to a baseline measure of risk. One assumption of the Cox approach is that the survival and hazard functions being compared are proportional to each other. Violation of this assumption was tested by regressing the Schoenfield residuals across time, a significant result indicating violation of the assumption (Hess 1995).

Predator activity

To account for the confounding effect of variation in spatial proximity to reproductive dens of arctic fox on predation risk, a variable indicating the number of reproductive dens in proximity to each quadrat was included in the Cox proportional hazards model described above. Preliminary home range analyses on arctic fox at Bylot Island (DB, A. Tarroux unpubl.) indicated that summer movements of foxes are generally limited to 7 km from their dens. Based on these data, a quadrat extending out 7 km in the four cardinal directions from the centre of each artificial nest quadrat was constructed and the total number of reproductive dens in this area was counted. Reproductive status of dens was confirmed by sightings of young at the dens as in Szor et al. (2008).

To provide evidence that any increase in predation risk on artificial nests in quadrats of high goose nest density was due to the attraction of predators to areas of high goose nest density, the effect of goose nest density on arctic fox activity was also tested. In 2008, fox activity was quantified for each artificial nest quadrat by placing a camera in the centre of each quadrat at the beginning of each experiment. Cameras were programmed to take five photos when triggered via motion for a period of 72 h. In general these motion detectors will trigger when an animal passes < 10 m from the camera. Predator activity was estimated based on the total number of motion triggered events caused by a fox across the entire 72 h period. The effect of goose nest density on predator activity rate was determined via linear regression analysis using the lm function in R ver. 2.11.0.

All statistical tests are two-sided and statistical significance and confidence intervals (CI) are based on a type 1 error of less than 0.05. All means are presented with standard error unless otherwise noted.

Results

Lemming abundance

During the three years of the study, the index of lemming abundance was high in 2007 (0.89 individuals captured per 100 trap nights) and 2008 (0.84) but low in 2009 (0.21).

Predation risk and goose nest density

Transect surveys conducted within each artificial nest quadrat showed that the distance at which detection rate of goose nests was 100% was 10 m (combining all transects and the three years). Within the 20×500 m survey transects, goose density varied from 0 to 7 nests ha^{-1} in 2007, 1 to 24 nests ha^{-1} in 2008 and 0 to 12 nests ha^{-1} in 2009.

During the high lemming year of 2007 (rich environment), goose nest density had no significant effect on predation risk (coefficient 0.082, SE 0.084, $\chi^2 = 0.96$, $p = 0.33$, hazard ratio = 1.085; Fig. 1A). In 2008 when lemming abundance was still high but in a declining phase, predation risk increased by 5.9% with an increase from zero to one goose nests ha^{-1} (coefficient 0.058, SE 0.025, $\chi^2 = 5.24$, $p = 0.02$, hazard ratio = 1.059; Fig. 1B). When lemming populations crashed in 2009 (poor environment), the effect of goose nest density on predation risk was much stronger with predation risk increasing by 17.7% with an increase from 0 to 1 goose nests per hectare (coefficient 0.163, SE 0.048, $\chi^2 = 11.63$, $p = 0.0006$, hazard ratio = 1.177; Fig. 1C). This meant that, when applied to the maximum change in goose nest density (0 to 12 nests ha^{-1}), the increase was over 600% (hazard ratio = 7.07). Due to the fact that goose nest density doubled during 2008 (maximum of 24 goose nests ha^{-1} compared to 7 and 12 in 2007 and 2009 respectively), analyses were re-conducted on a subsample of data spanning a similar range of goose nest density each year. When limited to a maximum of 12 nests ha^{-1} (the maximum for 2009), the effect of goose nest density on predation risk was no longer significant in 2008 (coefficient 0.014, SE 0.06, $\chi^2 = 0.056$, hazard ratio = 1.014, $p = 0.81$). No violations of assumptions were detected for any of the models (2007: $F_{1,21} = 4.21$, $p = 0.053$, 2008: $F_{1,33} = 0.38$, $p = 0.541$, 2009: $F_{1,23} = 0.05$, $p = 0.818$).

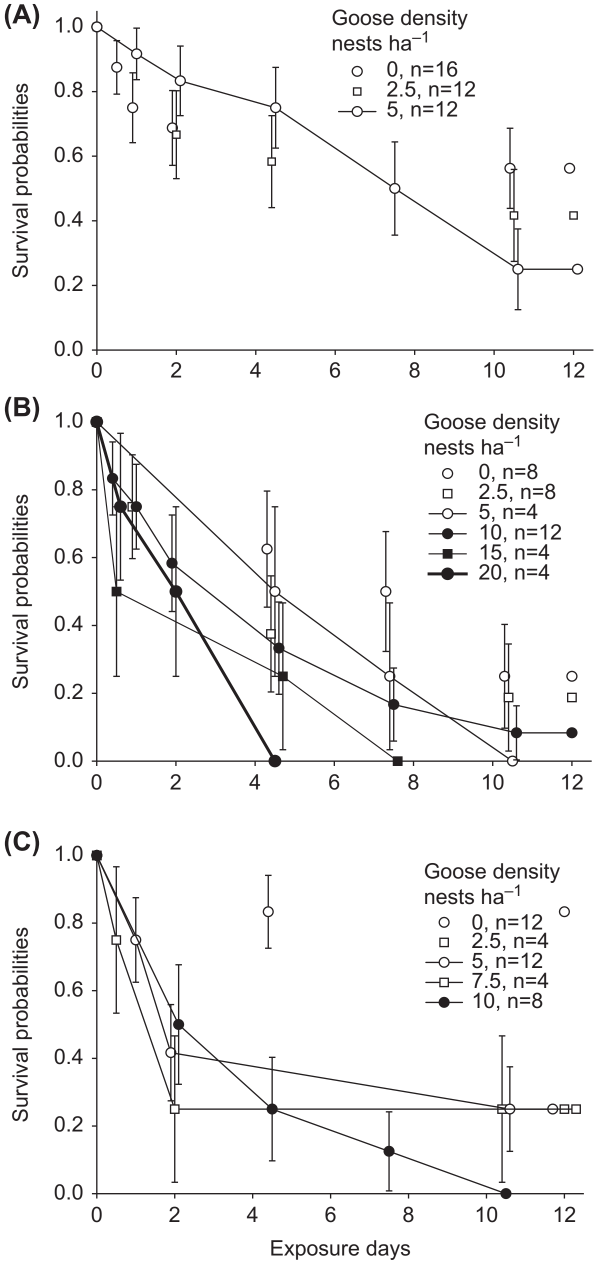

Figure 1. Kaplan–Meier survival probabilities over 12 exposure days for artificial shorebird nests placed in quadrats of varying goose nest density (nests ha^{-1}) in 2007 ((A); high lemming abundance), 2008 ((B); high but declining lemming abundance) and in 2009 ((C); low lemming abundance). Each data point on the curve represents the Kaplan–Meier survival estimate at time t (± SE), which provides the probability that a nest will survive past time t. For ease of graphical presentation, data are grouped by intervals of 2.5 goose nests per hectare (0 = 0 to 2.4, 2.5 = 2.5 to 4.9, 5 = 5 to 7.4 etc.) up to 10 nests per hectare after which data are grouped by intervals of 5 goose nests per hectare (10 = 10 to 14.9, 15 = 15 to 19.9 etc.). Sample sizes indicated refer to the number of artificial nests deployed in each goose nest density interval graphed.

Predator activity

The number of active fox reproductive dens (hereafter dens) within the 7 km limit from each quadrat was consistent across all quadrats in 2007 (five dens) and almost all quadrats in 2009 (three dens for 9 of the 10 quadrats, zero dens for the other). In 2008, the number of dens located within 7 km of each quadrat ranged from 2 to 10 (mean 8.7 ± 0.8). Due to the lack of variation in 2007 and 2009, this variable was only tested in the 2008 dataset and there was no effect of proximity to fox dens on predation risk (coefficient -0.022, SE 0.079, $\chi^2 = 0.08$, hazard ratio $= 0.979$, $p = 0.78$). No violations of assumptions were detected for this model ($F_{1,33} = 1.16$, $p = 0.289$).

In 2008, arctic fox activity was monitored in 9 of the 10 artificial nest quadrats due to technical difficulties with one camera. Motion triggered fox activity was recorded in 6 of the 9 quadrats, and ranged from zero to three sightings per 72 h period. All motion triggered events were considered independent as the time between successive triggered events ranged from 40 min to 11 h (mean $= 5.4 \pm 1.6$ h). The number of motion triggered fox sightings increased with goose nest density ($y = 0.19 + 0.1x$, $R^2 = 0.42$, $F = 5.8$, DF = 1,8, $p = 0.04$; Fig. 2).

Discussion

When presented with several prey items of decreasing profitability, it is not surprising that a hierarchical chain of indirect interactions between preferred prey and different classes of alternative prey may result (Holt 1977). Few empirical studies have investigated interactions between preferred, alternative and incidental prey in a natural setting. Here we took advantage of a naturally cycling population of lemmings to provide experimental evidence of a second order indirect interaction between goose nest density and predation risk on artificial shorebird nests in a system in which apparent competition between lemmings and geese has already been documented (Bêty et al. 2001, 2002, Gauthier et al. 2004). On Bylot Island, predation risk on artificial shorebird nests increased as goose nest density increased and the relationship was much stronger at low lemming abundance (poor environment). This is consistent with our predictions that predation risk for artificial shorebird nests would increase as goose nest density increases especially in years of low lemming abundance due to short-term apparent competition via an aggregative response of their main shared predator, the arctic fox. Camera monitoring of predator activity confirmed that arctic fox activity increased as goose nest density increased. Overall, our data support our incidental prey hypothesis which suggests that when preferred prey decrease in abundance, short-term apparent competition via aggregative response can occur between alternative and incidental prey.

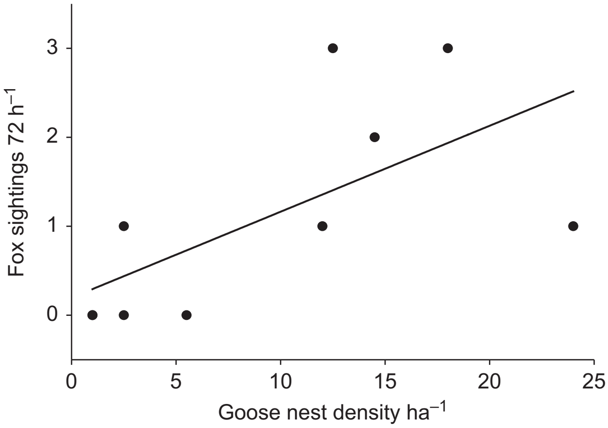

Figure 2. Relationship between fox activity (number of sightings over a 72 h period based on motion triggered camera monitoring within artificial nest quadrats) and goose nest density per quadrat in 2008.

We attributed the significant elevated risk of predation on incidental prey, in the presence of increasing alternative prey density when preferred prey were less available, to an increase in predator activity. As we were only able to record fox activity during one year of the study when lemmings were relatively high (2008), more observations are needed to support our interpretation. However, another study at the same site has provided evidence that reproductive activity of foxes (probability of a den being used for reproduction) increased with proximity to the goose colony in years of lower lemming abundance (Giroux et al. 2012). Results from the motion triggered camera data also indicate that fox activity increased in quadrats of increasing goose nest density. The abrupt increase in predator activity above 10 goose nests ha^{-1} is consistent with current models of patch use by foragers (Schmidt and Brown 1996), whereby the foragers/predators over-exploit patches where the density of resources is greater than the mean density of resources across all patches. In 2008, the mean goose nest density across all patches was 9.4 nests ha^{-1}. Zero fox activity was recorded using automatic cameras in three of the four patches falling below this mean. We may also interpret these results as evidence that the quadrat size (and inter-quadrat distances) used in this study sufficiently represented distinct foraging patches for our main predator, the arctic fox. It is important to note that the average goose nest density in our sampled patches in 2008 was higher than the long term average for the colony (10 year average: 3.5 nests ha^{-1}, Gauthier unpubl.). Therefore, it is possible that the significant relationship between goose nest density and predation risk found in this year was influenced more by the higher range of goose nest density, as opposed to a declining abundance of lemmings. Indeed, when artificial nest data were reanalyzed using a similar maximum goose nest density across years, nest predation risk on artificial nests increased with goose nest density only in the year of low lemming abundance (2009) as predicted.

Most studies documenting increased predation (Roseberry and Klimstra 1970, Vickery et al. 1992) or an increased risk of predation (James et al. 2004) due to an aggregative response of predators to preferred prey have been based on classic 1 predator: 2 prey (1 preferred, 1 alternative) systems (Roseberry and Klimstra 1970, Vickery et al. 1992, Hoi and Winkler 1994, James et al. 2004, Schmidt 2004). For example, in ungulates, apparent competition via aggregative response has been suggested based on documented avoidance of habitat favourable to alternative prey; woodland caribou *Rangifer tarandus caribou* avoid high quality moose *Alces alces* habitat in order to decrease predation risk from wolves, the principal predator of moose (James et al. 2004). When the same effect has been documented in avian prey, studies were also conducted in a 1 predator: 2 prey system (Roseberry and Klimstra 1970, Vickery et al. 1992, Hoi and Winkler 1994, Schmidt 2004). For example, nest predation of ground nesting birds increased when racoon activity increased due to an aggregative response of racoons to their preferred rodent prey (Roseberry and Klimstra 1970). To our knowledge, our results provide the first experimental evidence of an hierarchical interaction between preferred, alternative and incidental prey in a 1 predator: 3 prey system. Though our inferences may be limited by the fact that our data included only one year of low preferred prey abundance, we were successfully able to conduct the same field experiment in three years during which lemming populations crashed after two years of high abundance. In addition, we conducted these experiments at a study site where numerical and aggregative responses of foxes to lemmings and geese, respectively, have been shown extensively over several lemming cycles, providing additional support for the interpretation of our results.

In our study system, the three prey species represented preferred, alternative and incidental prey. Though it is an assumption that shorebird eggs are incidental prey, the artificial nests used here can certainly be considered incidental prey as they were a foreign, randomly placed prey item in the environment and were only available to predators for a short period of time each year. In other systems, where a variable number of alternative prey species can be the object of a directed predator search, the hierarchical chain of interactions between preferred prey and multiple alternative prey may be easy enough to predict, yet much more difficult to document with empirical data. In this case, any of the alternative prey may influence the spatial patch use of predators when preferred prey are low or absent, and, if the prey items are of equal profitability, the strength by which each alternative prey influences the spatial patch use will likely be determined by the density of each prey species (Holt 1977, Holt and Kotler 1987). This differs in the case of incidental prey, as the spatial availability of incidental prey should theoretically have no effect on patch use by predators.

Using artificial nests, which can provide a controlled measure of relative predation risk for arctic-nesting shorebirds (McKinnon et al. 2010a, b), we estimated that predation risk was over 600% higher in areas where goose nest densities surpassed 12 nests ha^{-1} relative to areas without goose nests when lemmings were scarce. Given this magnitude of change, and provided that shorebirds are known to avoid areas of high predation risk (Cresswell et al. 2010), one would predict the exclusion (local extinction) of shorebird nests within high density goose nesting areas (Holt 1984). Throughout the three years of our study, we found a much smaller number of shorebirds nesting within proximity (2 km radius) to the goose colony versus a site approximately 30 km from the colony, although nest densities were too low for systematic comparisons between the two sites (McKinnon and Bêty unpubl.). Further investigations are needed to evaluate the potential effect of geese on shorebird distribution.

Indeed, if habitats in proximity to goose colonies are characterized by an elevated risk of predation on incidental prey, this could imply that incidental prey nesting outside of these patchily distributed and localized goose colonies would experience lower predation risk. The latter will essentially depend on whether, in the absence of nesting geese, shorebirds remain in the functional role of incidental prey, or take on a role more akin to the alternative prey. Decreasing shorebird nest densities in the presence of high goose nest densities has been reported at other arctic study sites. At the Egg River snow goose colony on Banks Island, Nunavut, one study concluded that shorebird numbers increased as distance from the snow goose colony increased (up to 10 km; Hines et al. 2010). Results from our study suggest that an increase in predation risk in the presence of increasing goose nest densities could be one of the mechanisms driving the potential exclusion of shorebirds in the presence of high goose nest densities. Though other mechanisms, such as changes in habitat due to increased goose grazing or increased trampling of nests by foraging geese may have been important at some sites, previous studies did not confirm any indirect effect mediated by predators (Jehl 2007, Sammler et al. 2008).

Across the entire Arctic, populations of nesting geese have been increasing exponentially since the 1960s (Gauthier et al. 2005) whereas throughout the same range populations of shorebirds have been decreasing (Morrison et al. 1994, 2006). On the local patch scale on Bylot Island, we provide evidence that predation risk on shorebird nests increases in the presence of increasing goose nest densities, especially at low lemming abundance. These results are in accordance with Holt and Lawton's hypothesis that short-term apparent competition occurs in poor environments defined by low densities of preferred prey (Holt and Lawton 1994) and could indicate that in areas of low lemming abundance, increases in arctic-nesting goose populations may lead to decreases in enemy-free space (Jeffries and Lawton 1984) for incidental prey such as shorebirds and songbirds. Population level consequences of the short-term negative effects of apparent competition documented in our study cannot be revealed without investigating the potential long-term positive effects such as increases in equilibrium population size of alternative prey (Abrams and Matsuda 1996). We encourage other researchers to investigate these hierarchical interactions at a larger spatial scale (i.e. landscape level) in order to provide a more comprehensive understanding of the long-term effects of predator mediated indirect interactions between preferred, alternative and incidental prey.

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