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RESEARCH ARTICLE

Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis

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ABSTRACT

The alternative prey hypothesis (APH) suggests that the functional and numerical response of predators to fluctuating rodent populations may drive annual variation in predation pressure on other available prey such as bird eggs. Most studies that have provided evidence supporting the APH in arctic bird populations have been conducted in the eastern hemisphere, and considerably less evidence for APH has emerged from western hemisphere populations. We tested the hypothesis that predation pressure on shorebird nests would increase as lemming abundance decreases due to apparent competition between lemmings and shorebirds via their shared predators in the eastern Canadian High Arctic. Over a period of 5 years on Bylot Island, Nunavut, Canada, we found that lemming abundance had a significant negative effect on predation risk as measured by artificial nests. Survival probabilities of artificial nests were also negatively related to fox abundance but positively associated with the abundance of breeding avian predators, likely due to predator exclusion around avian predator nests. Models of daily nest survival for real nests also indicated that interannual variation in nest survival was best explained by lemming abundance. Combined results from both artificial and real nests indicate that fluctuations in lemming populations likely have an indirect effect on predation pressure on shorebird eggs in the Canadian High Arctic, although mechanisms explaining the observed relationship require further investigation.

Keywords: apparent competition, arctic, artificial nests, Baird's Sandpiper, nest success, nest survival, White-rumped Sandpiper

Interactions impliquant des prédateurs entre les lemmings et les limicoles: Un test de l'hypothèse des proies alternatives

RÉSUMÉ

L'hypothèse des proies alternatives (HPA) suggère que la réponse fonctionnelle et numérique des prédateurs à la fluctuation des populations de rongeurs peut conduire à une variation annuelle de la pression de prédation sur d'autres proies disponibles telles que les œufs d'oiseaux. La plupart des études qui ont fourni des preuves appuyant l'HPA chez les populations d'oiseaux arctiques ont été réalisées dans l'hémisphère est; beaucoup moins de preuves supportant l'HPA ont émergé des populations de l'hémisphère ouest. Nous avons testé l'hypothèse selon laquelle la pression de prédation sur les nids de limicoles augmente à mesure que l'abondance des lemmings diminue, en raison de la compétition apparente entre les lemmings et les limicoles via leurs prédateurs communs dans l'est du Haut-Arctique canadien. Sur une période de 5 ans sur l'île Bylot, au Nunavut, Canada, nous avons trouvé que l'abondance des lemmings avait un effet négatif significatif sur le risque de prédation, tel que mesuré par les nids artificiels. Les probabilités de survie des nids artificiels étaient reliées de façon négative à l'abondance des renards mais elles étaient positivement associées à l'abondance des prédateurs aviens nicheurs, probablement en raison de l'exclusion des autres prédateurs autour des nids de prédateurs aviens. Les modèles de survie quotidienne des vrais nids indiquaient aussi que la variation interannuelle de la survie des nids était mieux expliquée par l'abondance des lemmings. Les résultats combinés des vrais nids et des nids artificiels indiquent que les fluctuations dans les populations de lemmings semblent avoir un effet indirect sur la pression de prédation sur les œufs de limicoles dans le Haut-Arctique canadien mais les mécanismes expliquant la relation observée requièrent des études plus poussées.

Mots-clés: compétition apparente, arctique, nids artificiels, *Calidris bairdii*, succès de nidification, survie du nid, *Calidris fuscicollis*

INTRODUCTION

Optimal foraging theory predicts that when faced with 2 prey types, predators should maximize consumption of high quality and easy to capture prey, increasing nutritional value while reducing energetic costs of capture, thus maximizing intake rates (Macarthur and Pianka 1966, Krebs et al. 1977). If 2 prey of equal nutritional value and

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equal capture costs are available, the factor determining the choice of prey will likely be the relative density of the 2 prey types. Predators may form a search image for the higher density prey and focus on this prey until it is depleted below a certain density threshold, at which time the predator will switch to another higher density prey (Murdoch 1969, Cornell 1976). While experimental (Bergelson 1985, Joern 1988, Hughes and Croy 1993) and indirect evidence (Summers et al. 1998) for predator switching has been previously documented in vertebrates, fewer studies have provided direct observations of predator switching via coupling behavioral observations with detailed studies of predator and prey abundance in systems where prey cycle naturally (Underhill et al. 1993, Bêty et al. 2002).

Systems with prey cycles provide excellent natural laboratories to study predator switching due to the marked and easily measured changes in prey density (Gilg et al. 2003). Many high arctic systems are characterized by cyclic small rodent populations (Ims and Fuglei 2005). As a result, predator switching behavior has been implicated in causing fluctuations in coexisting bird populations (Angelstam et al. 1984, Summers et al. 1998, Bêty et al. 2002, Blomqvist et al. 2002). The alternative prey hypothesis (APH) suggests that the functional and numerical response of predators to fluctuating rodent populations results in cyclic variation in annual predation pressure on other available prey such as birds eggs (Lack 1954, Angelstam et al. 1984).

In the presence of a strong functional response, when small rodents are abundant, predation pressure on alternative prey should be low, whereas when small rodent populations decline, predation pressure on alternative prey should increase. In effect, predation pressure on alternative prey should be inversely correlated with small rodent abundance. This relationship can be accentuated in the presence of a strong numerical response of the predator to the preferred prey. For example, predation pressure on alternative prey should be higher in a year of low small rodent abundance that immediately follows a year of high small rodent abundance, if predator populations increased due to successful reproduction in the previous year (i.e. 1-year time lag).

Correlations between small rodent population fluctuations and bird breeding productivity have been documented for arctic-nesting geese in Siberia (Summers et al. 1998, Nolet et al. 2013) and Canada (Morrissette et al. 2010) and shorebirds in Siberia (Summers et al. 1998, Blomqvist et al. 2002). These correlations were hypothesized to be caused by the functional and numerical response of the arctic fox (*Alopex lagopus*) to their preferred small rodent prey, yet most of the studies did not directly measure (a) whether foxes were an important predator of bird eggs and chicks or (b) variation in predation risk and/or nest success of arctic-nesting birds. Instead, correlations between indices of predation pressure (fox population densities and/or lemming abundance) and indices of breeding productivity of birds (proportion of juveniles caught during migration or on wintering grounds) were frequently used to implicate predator switching as the mechanism causing population cycles in arctic-nesting birds (Summers et al. 1998). Moreover, the few studies that directly measured changes in predation risk and/or nest survival of birds on the breeding grounds dealt with large-bodied prey species like geese (Bêty et al. 2002).

Finally, most studies that have provided evidence supporting the APH in arctic bird populations were conducted in the eastern hemisphere (Underhill et al. 1993, Summers et al. 1998, Blomqvist et al. 2002). Of the 4 studies testing APH in arctic bird populations in the western hemisphere (Bêty et al. 2001, Smith et al. 2007a, Smith 2009, Reiter and Andersen 2011), only half have found evidence to support the hypothesis (Bêty et al. 2001, Smith et al. 2007a). The main objective of this study was to investigate the indirect relationship between shorebird reproduction and lemming abundance in the eastern Canadian High Arctic. On Bylot Island, Nunavut, previous studies have confirmed lemmings as the primary prey of arctic foxes (Giroux 2007, Giroux et al. 2012), while camera monitoring of shorebird nests has revealed that arctic foxes are the primary predator of shorebird nests (McKinnon and Bêty 2009). We therefore predicted that predation risk on shorebird nests (as measured by artificial nests) would increase as lemming abundance decreases due to apparent competition between lemmings and shorebirds via their shared predator, the arctic fox. Similarly, we predicted that survival of real shorebird nests would decrease as lemming abundance decreases.

METHODS

Study Area and Species

The study was conducted during summers 2005–2009 in 2 study sites located within the Bylot Island Migratory Bird Sanctuary in Sirmilik National Park, Nunavut territory, Canada. The first 8 km^2 site (Site 1) was located within the Qarlikturvik Valley (72°53′N, 78°55′W), and the second 4 km^2 site (Site 2) was located 30 km south within proximity of a large Greater Snow Goose (*Chen caerulescens*) colony. We chose a larger search area for Site 1 because we had twice as many nest searchers available at that site each year (2 nest searchers for Site 1, 1 nest searcher for Site 2). Due to the lower nest searching effort at Site 2, not enough real nests were found to merit analysis of nest survival. Both sites were characterized by lowlands composed of mesic tundra and polygonal wetlands and uplands dominated by mesic and xeric tundra (Duclos 2002).

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On Bylot Island, the most abundant nesting shorebirds during the study period were Baird's Sandpiper (*Calidris bairdii*) and White-rumped Sandpiper (*Calidris fuscicollis*). Both species nest on the ground in small scrapes devoid of nest cover at relatively low densities (<10 nests km^{-2}). As previously mentioned, camera monitoring of nests has revealed that the arctic fox is by far the main predator of shorebird nests on Bylot Island (McKinnon and Bêty 2009). Other potential nest and chick predators at our study sites may include, in suspected order of importance; Long-tailed Jaegers (*Stercorarius longicaudus*), Glaucous Gulls (*Larus hyperboreus*), Sandhill Cranes (*Grus Canadensis*; 2 cases recorded via camera in 2010; Bêty personal observation), Parasitic Jaegers (*S. parasiticus*), Common Ravens (*Corvus corax*), and ermine (*Mustela erminea*).

Brown (*Lemmus sibiricus*) and collared (*Dicrostonyx groenlandicus*) lemmings occur year-round in the study area (Duchesne et al. 2011). Populations of both species have exhibited cycles at 3 to 4 year intervals, although cycles are more pronounced for the brown lemming (Gruyer et al. 2008). All potential predators of shorebirds can consume lemmings (Therrien et al. 2014) and can thus be considered shared predators (Bêty et al. 2002).

Lemming Abundance

We estimated an index of lemming abundance each year based on snap trapping (as described in Gruyer et al. 2008) conducted between July 23 and August 3 at Site 1 and July 11 and July 14 at Site 2, corresponding to the late incubation and brood rearing period for shorebirds. Sampling dates differed between sites due to logistical reasons (Site 2 closed earlier in the season). Museum special snap traps were placed along 2 transect lines in each of 2 plots at Site 1 (1 in wet meadow habitat, 1 in mesic habitat) and in 1 plot at Site 2 (mesic habitat). For the first 2 years at Site 1, each transect line had 25 stations placed 15 m apart, with each station consisting of 1 trap within a 2 m radius, for a total of 25 traps. We checked traps daily for 10 days, totalling ~1000 trap nights (TN).

From 2007 onward, the number of stations per transect at both sites was increased to 68 (2007–2008) and then to 80 (2009) by lengthening the transects, and the number of traps per station increased to 3 within a 2 m radius. Traps were checked daily for 3 to 4 days, totalling 1224–1920 TN at Site 1 and 612–960 TN at Site 2. Based on our knowledge of lemming home range size on Bylot Island (~7 and 14 ha for brown and collared lemmings, respectively; Gruyer 2007), increasing trapping effort via lengthening transects could introduce bias in estimates by increasing the probability of captures; however, our trapping effort continued to increase after 2007, but captures per trap night decreased, providing some support that the consequences of this bias were minimal.

The index of lemming abundance was calculated as the number of lemmings trapped per 100 TN, caluculated separately for each site.

Predator Abundance

We calculated an index of fox abundance separately for both study sites based on (1) confirmation of natal fox dens and (2) captures and observation of individually identified adult arctic foxes. Preliminary home range analyses on arctic fox at Bylot Island (D. Berteaux and A. Tarroux personal observation) indicated that summer movements of foxes are limited to ~7 km from their dens. Based on these data, we constructed a quadrat extending up to 7 km in the 4 cardinal directions on each side of each study site. Due to areas of unsuitable (ocean, glaciers) and/or inaccessible habitat (cliffs), however, the zones were restricted to a smaller geographical area (182 km^2 centred on Site 1 and 165 km^2 centred on Site 2) within which fox dens have been surveyed intensively since 2003 (see details in Szor et al. 2008).

We confirmed reproductive status of dens via sightings of young, as in Giroux (2007). The minimum number of adults in the defined study areas was calculated based on the assumption of 2 adults per natal fox den and the number of other individuals captured or observed that were not associated with a natal den. Data were then converted to individuals per 100 km^2. Although we monitored the fox population intensively each year through a capture–mark–recapture program and detailed den surveys (Cameron et al. 2011), it is always possible that transient foxes went undetected in the study areas; however, we found no evidence that such events were distributed so as to strongly bias our results.

We also tested the effect of avian predator abundance (jaegers and gulls; *Stercocarius* spp. and *Larus* spp., respectively) on predation risk of artificial nests. An index of avian predator abundance was generated by multiplying by 2 (number of adults per nest) the number of jaeger and gull nests found within the 182 km^2 predator study area centered on Site 1 and the 165 km^2 predator study area centered on Site 2, described earlier. We then converted data to individuals per 100 km^2. Because we were not able to provide an estimate of the number of nonreproductive individuals, our index may be an underestimate of the actual avian predator abundance; however, it provided the best available estimate of interannual variation in nesting predator abundance at both study sites.

Shorebird Reproduction

Predation risk. We conducted artificial nest monitoring from 2005 to 2009 at Site 1 and 2007 to 2009 at Site 2. In the Arctic, artificial nests can provide a reliable measure of relative predation risk because they allow the control of heterogeneity associated with real nests (temporal, spatial,

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and inter- and intraspecific behavioral differences; McKinnon et al. 2010a). Problems of external validity may arise when using artificial nests as a surrogate measure of nest success for real birds if they attract a different suite of predators (Moore and Robinson 2004, Faaborg 2010). In our study, this problem was accounted for by identifying predators with cameras placed at both real and artificial nests during the study period (McKinnon and Bêty 2009). Our camera monitoring results revealed the arctic fox as the dominant predator at real and artificial nests (McKinnon and Bêty 2009), with jaegers and gulls depredating artificial nests in smaller proportions. At other arctic sites, camera monitoring has revealed that real shorebird nests were depredated by arctic fox, jaegers, and gulls (Cartar and Montgomerie 1985, Liebezeit and Zack 2008).

We positioned 40 artificial nests randomly in suitable shorebird nesting habitat, covering an area of $\sim$4 km^2 at each site. This density of artificial nests was within the range of observed nesting densities of shorebirds on Bylot Island. Each artificial nest consisted of 4 Japanese Quail (*Coturnix japonica*) eggs placed in a small depression made in the ground. To reduce human scent at artificial nest sites, researchers made nest depressions using the heel of their rubber boots, did not kneel at the nests, and wore rubber gloves when handling eggs. Quail eggs resemble those of shorebirds in coloration and size, and the depressions made are similar to the simple nest scrapes used by shorebirds. Nests were deployed within the same time period and were relocated by small sticks or natural objects (rocks or feathers) placed between 5 and 7 m from the nest. Once deployed, artificial nests were checked at 12, 24, and 72 hr, and then every 3 days up to 9 exposure days. For visit intervals $>$24 hr, failure times were assumed to occur at the midpoint between sampling intervals because the exact date of failure was not known. Artificial nest monitoring occurred twice during the breeding season, corresponding to the early and late incubation periods.

Nest success. We searched for shorebird nests during the early laying and incubation periods, early June through early July, each year. Nest searchers walked a set of transects throughout the early laying and incubation period each year to ensure systematic coverage of the entire study area. In later years of the study (2007–2009), additional smaller study plots (400 $\times$ 400 m) within the study area were searched more intensively via rope dragging. Nests were marked by small sticks or natural objects (rocks or feathers) placed between 5 and 7 m from the nest.

Incubation stage was estimated for each nest using the flotation method (Liebezeit et al. 2007). The duration of the incubation period is 21 days for Baird's and White-rumped sandpipers (Moskoff and Montgomerie 2002, McKinnon and Bêty 2009). Chicks of both species generally leave the nest within 24 hr of hatching (L. McKinnon and J. Bêty personal observation). Nests were visited every 2–5 days during incubation. Within 2 days of the estimated hatch date, nests were visited daily to maximize the probability of recording nest outcome. If an empty nest was found near the date of hatching, determining if the nest was successful or had been depredated just prior to hatching was difficult because there are generally no obvious signs of hatch in a successful nest (i.e. no large egg remains or membranes as found in duck and goose nests). Nests were considered successful (at least one egg hatched) if one or more of the following criteria were met: (1) chicks were found in the nest, (2) remnants of egg shells were found in the nest material close to the estimated hatch date (Mabee et al. 2006), (3) eggs were hatching (starred and/or pipped) on the last date visited and the nest was empty on the next visit, and/or (4) the nest was empty on the last visit and the banded adult was later seen with chicks. Nests that were abandoned or depredated during laying were not included to simplify the analyses (by not including different nesting stages); these cases did not represent an important proportion of the sample sizes ($n = 6$ of 126 nests across the 5-year study period).

Statistical Analyses

Predation Risk. The effects of (1) lemming abundance, (2) fox abundance, and (3) avian predator abundance on artificial nest survival were tested using a Cox proportional hazards regression model (PROC PHREG in SAS; Cox 1972) that tests for a relationship between Kaplan-Meier survival estimates and explanatory variables. Analyses were stratified by site to control for differences between the 2 sites that would likely influence the relationship between lemmings and predation risk on shorebirds (e.g., generally higher density of foxes and avian predators, higher densities of alternative prey such as Snow Geese, and differences in habitat). 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 graphically for each variable (Hess 1995).

Nest Success. Daily nest survival estimates for real nests were estimated using the nest survival option in program MARK (Dinsmore and Dinsmore 2007). Exposure days began the day the nest was found; however, only exposure days during the incubation period were included to decrease heterogeneity associated with nesting stage. Models of daily nest survival were generated separately for each species because sample sizes (Table 1) were not large enough to generate complex models with multiple interactions. Sample sizes of real nests at Site 2 never surpassed 1 per species each year, so nest survival models were only generated for nests found

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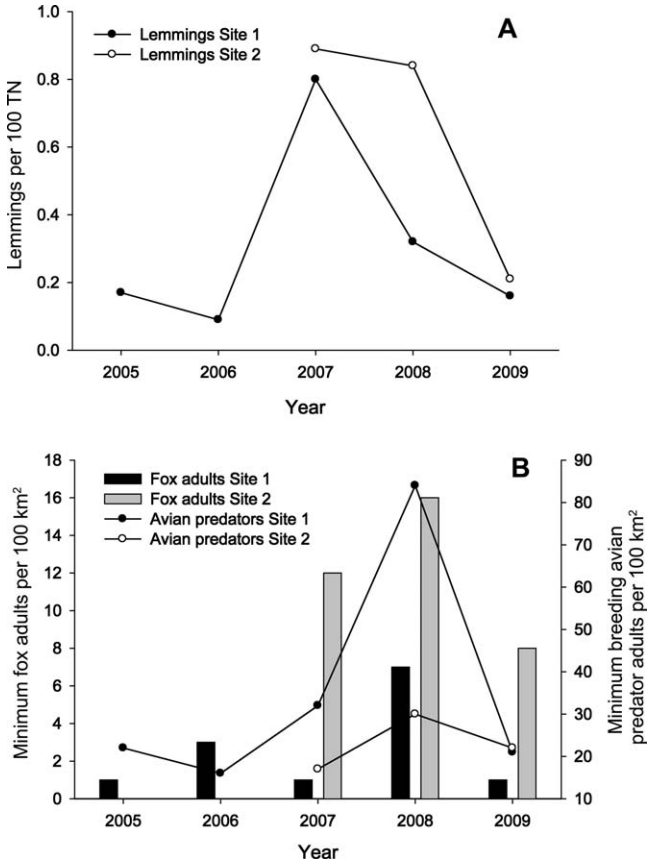


FIGURE 1. (**A**) Index of lemming abundance based on snap-trap data at Site 1 (closed circle) and Site 2 (open circle). (**B**) Minimum number of adult arctic fox per 100 km^2 within Site 1 (black bar) and Site 2 (gray bar) and the minimum number of breeding adult avian predators per 100 km^2 at Site 1 (closed circle) and Site 2 (open circle).

at Site 1. A suite of 3 a priori models (including 1 constant) were generated for each species to evaluate the effects of (1) lemming abundance and (2) fox abundance. Estimates of nest survival were derived from the model that best fit the data based on the lowest AIC_c value (Burnham and Anderson 2002, Arnold 2010). Models with <2 delta AIC_c from the top model were considered competitive.

All statistical tests are 2-sided, and statistical significance and confidence intervals (CI) are based on a Type 1 error <0.05.

RESULTS

Lemming Abundance

At Site 1, lemming abundance ranged from lows of 0.09 to 0.16 individuals per 100 TN (2006 and 2009) to a maximum of 0.80 individuals per 100 TN (2007; Figure 1A). Lemming abundance was higher at Site 2, ranging from 0.21 during the low phase (2009) to a maximum of 0.89 during the peak phase (2007) of the cycle.

Predator Abundance

The minimum number of adult fox was lowest at Site 1, ranging from 1 to 7 adults per 100 km^2, whereas at Site 2 the minimum number of adult fox ranged from 8 to 16 adults per 100 km^2 (Figure 1B). The minimum number of breeding adult avian predators was highest at Site 1, ranging from 16 to 84 adults per 100 km^2, and lower at Site 2, ranging from 17 to 30 adults per 100 km^2 (Figure 1B). There was no significant correlation among the 3 variables when used together in later analyses (fox/avian $r = 0.09$, $P = 0.84$; fox/lemming $r = 0.59$, $P = 0.12$; avian/lemming $r = -0.003$, $P = 0.99$); however, given the low sample sizes ($n = 8$ yr), the power to detect significant correlations is relatively low.

Shorebird Reproduction

Predation risk. When stratified by site, the abundance of lemmings had a significant negative effect on predation risk (coefficient = –0.776, $\chi^2_1 = 18.70$, $P < 0.001$; Figure 2), with predation risk decreasing by 50% with each increase of 1 lemming per 100 TN. The 2 indices of predator abundance also had significant but opposing effects on predation risk. Predation risk increased by 8% with each increase of 1 adult fox per 100 km^2 (coefficient = 0.078, $\chi^2_1 = 11.43$, $P < 0.001$); however, predation risk decreased by 1% with each increase of 1 breeding avian predator per 100 km^2 (coefficient = –0.012, $\chi^2_1 = 16.62$, $P < 0.001$).

Nest success. The number of real nests monitored each year varied considerably, ranging from 0 to 30 nests per species at Site 1 (Table 1). Daily nest survival was best described by lemming abundance for both Baird's Sandpiper and White-rumped Sandpiper (Table 2). As lemming abundance increased, daily nest survival increased (Figure 3).

DISCUSSION

The APH suggests that the functional and numerical response of predators to fluctuating rodent populations

TABLE 1. Sample size of nests used in real shorebird nest survival analyses at Site 1.

Species	2005	2006	2007	2008	2009	TOTAL
Baird's Sandpiper	16	30	10	8	10	74
White-rumped Sandpiper	27	12	6	1	0	46
TOTAL	43	42	16	9	10	120

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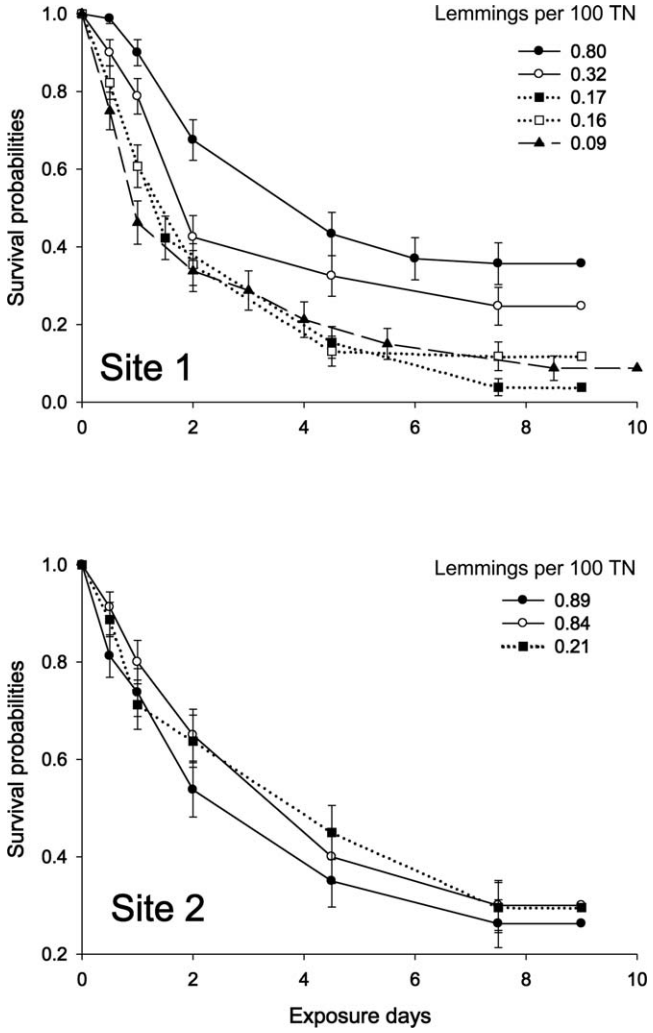


FIGURE 2. Kaplan-Meier survival curves (±SE) for artificial nests for Site 1 and Site 2. Curves are provided per year with the abundance of lemmings (N per 100 TN) for each curve in the legend.

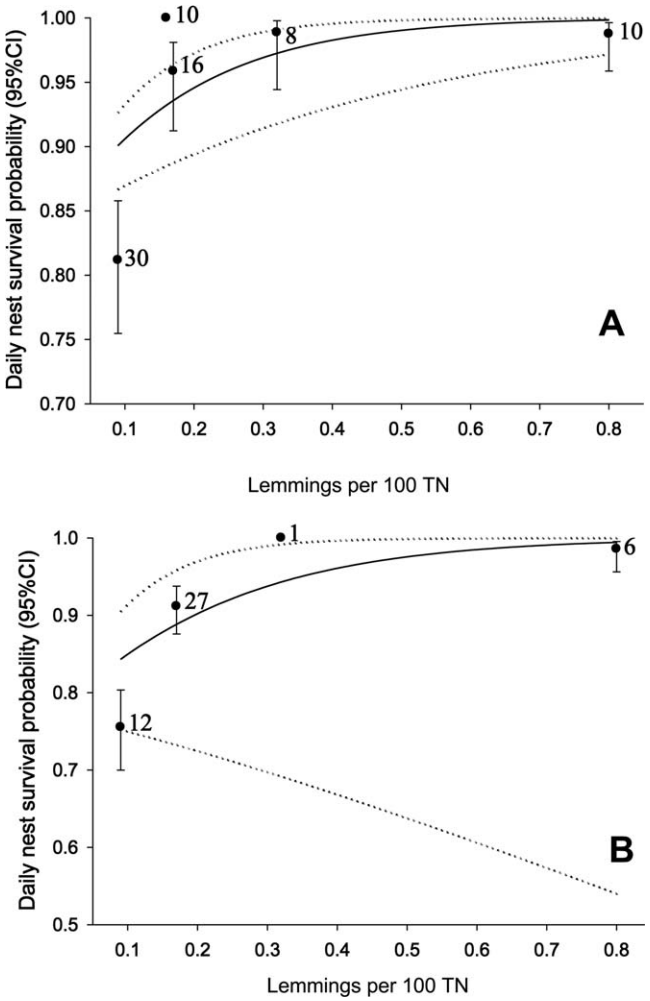


FIGURE 3. Model of daily nest survival (solid line) ±95% CI (dotted lines) derived from the top model for Baird's Sandpiper (**A**) and White-rumped Sandpiper (**B**) for Site 1 only. Annual estimates of daily nest survival (±95% CI) on which the models are based are also provided for each species along with the sample sizes.

may drive annual variation in predation pressure on other available prey such as birds eggs (Lack 1954, Angelstam et al. 1984). Over a period of 5 years on Bylot Island, we found that the abundance of lemmings had a significant effect on interannual variation in predation risk, as measured by artificial shorebird nests. Lemming abundance also explained interannual variation in daily nest survival of 2 species of shorebirds, despite small sample sizes in the later years of the study. For real nests, there was no support for an effect of fox abundance on nest survival; however, for artificial nests, the risk of predation increased by 8% with each additional adult fox per 100 km^2 and decreased by 1% with each additional breeding avian adult predator per 100 km^2. Combining the results from both real and artificial nests suggests that fluctuations in rodent populations do have an effect on predation pressure on shorebird eggs.

Although the indirect effect of cycling small rodent populations on ground-nesting waterbirds has been well documented in Sweden and Siberia (Underhill et al. 1993, Summers et al. 1998, Blomqvist et al. 2002), results from other North American studies to date have been less consistent. In the Low Arctic near Churchill, Manitoba, Semipalmated Sandpipers (*Calidris semipalmatus*) suffered higher predation in low lemming years (Meltofte et al. 2007); however, Semipalmated Plovers (*Charadrius semipalmatus*) exhibited relatively little to no interannual variation in nest survival (Meltofte et al. 2007), and nest survival of Canada Geese was not affected by lemming abundance as predicted by the APH (Reiter and Anderson

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TABLE 2. Model selection results per species (Site 1 only) for the 3 a priori models of daily nest survival.

Species	Model	ΔAIC_c [a]	AIC_c weights	Model likelihood	Num. par	Deviance
Baird's Sandpiper	Lemming	0	1.00	1	2	196.88
	Constant	20.21	0.00	0	1	219.11
	Fox	20.56	0.00	0	2	217.45
White-rumped Sandpiper	Lemming	0	1.00	1	2	95.86
	Constant	11.05	0.00	0	1	108.94
	Fox	11.44	0.00	0	2	107.30

[a] The AIC_c score for the top models are 200.90 (Baird's Sandpiper) and 99.91 (White-rumped Sandpiper).

2011). Further north on Southampton and Coats islands, nest survival of several shorebirds species was lower during a lemming population crash compared with 2 years of higher lemming abundance (Smith et al. 2007a), but when studied over a longer period, interannual variation in nest survival was best explained by predator abundance (Smith 2009).

On Bylot Island, nest survival of both shorebirds (this study) and geese (Bêty et al. 2001, 2002) seem to be indirectly affected by lemming abundance. The inconsistent results between North American studies could be due to methodological differences between studies and/or ecological differences between the study sites. Lemming abundance at the Southampton and Coats sites was based on daily field observations, which is likely a sufficient method to indicate peak lemming years but may be less accurate in distinguishing moderate years from crashes due to low lemming densities during these periods. This method may also be sensitive to observer experience with small mammal sightings. On Bylot Island, lemming indices were based on standardized snap-trapping data collected each summer. Although indices based on snap trapping have limitations (i.e. small geographic area sampled over a short period of time), this method has provided a reliable quantitative index of increasing, peak, decreasing, and crash years on Bylot Island in previous studies covering more than one lemming cycle (Bêty et al. 2001, 2002).

Based on our data from real nests, the relationship between lemmings and real nest survival seems to be driven primarily by the crash year (2006) when daily nest survival rates reached as low as 0.70. Accurate identification of these important crash years may be pertinent to the detection of this relationship. Alternatively, ecological differences may exist between the North American study areas in terms of the amplitude of lemming population cycles and/or the numerical and functional responses of predators. On Bylot Island, lemming fluctuations can be pronounced, and the numerical and behavioral responses of the primary shorebird egg predator, the arctic fox, to lemmings has been previously documented (Bêty et al. 2002); however, the relationship between lemmings and fox abundance at Churchill (Reiter and Andersen 2011), Southampton, and Coats Island has yet to be studied in detail. Differences in the species traits of the dominant small rodent species at each site may also affect the numerical and behavioral responses of the primary predators (Ims et al. 2013). The striking differences in latitude between the North American sites may also play a role in these inconsistencies. Predation risk in general decreases with latitude (McKinnon et al. 2010b), and a higher diversity and/or abundance of alternative prey species at lower arctic sites could possibly diminish the effect of lemmings on birds eggs in general.

Alternative prey theory partly relies on the switching behavior of predators (Murdoch 1969). Switching by definition means that when one prey becomes more abundant, a predator will disproportionately increase its rate of consumption of that prey, incurring a functional response. Shorebird eggs may possibly be incidental prey, not the focus of a directed predator search (Vickery et al. 1992), as opposed to alternative prey that predators "switch" to prey upon. Compared with other available alternative prey on Bylot Island, such as goose eggs, shorebird eggs are less abundant, less detectable, less profitable, and likely comprise a minute proportion of the diet of arctic fox in any year, regardless of the abundance of lemmings; therefore, there is likely little incentive to adopt a search image for prey of such limited availability and profitability.

As incidental prey, predation risk on shorebirds may increase in years of low lemming abundance due to changes in fox foraging behavior other than switching. If predators increase foraging time or expand foraging area when their main prey declines (Norrdahl and Korpimäki 2000), the likelihood of detecting other prey incidentally will increase. There is some evidence that this may be the case on Bylot Island, where in years of low lemming abundance, home ranges of arctic fox increase (A. Tarroux personal communication). Alternatively, if detection by predators changes with shorebird nest density, then the indirect effect of lemmings may be density-dependent and only exist, or be detectable, at high nest densities.

During the last 3 years of the study, the sample size of shorebirds nesting at Site 1 decreased by more than half compared with the first 2 years (>40 in 2005–2006, <16 in 2007–2009; Table 1). For the 3 years with decreased

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sample sizes, nest survival was consistently high, despite one of these years (2009) having low lemming abundance. Given that search effort did not change between years (same number of nest searchers) and the principal nest searcher (L. McKinnon) was present for each year of the study, the decrease in sample size was likely a decrease in actual nesting density of shorebirds; therefore, it is likely that shorebird nest density may influence the indirect effects of lemming abundance on shorebird nest survival. Thus the indirect effects of lemming abundance on shorebirds could differ between sites due to ecological differences such as (1) the prey role of shorebird eggs (alternative vs. incidental) and/or (2) nest density.

Results from the artificial nest experiments clearly support an indirect effect of lemmings on predation risk on shorebird nests, although they also indicate an effect of predator abundance, which, interestingly, was not detected for real nests. For artificial nests, predation risk increased by up to 248% between the minimum and maximum number of adult fox estimated during the study period (1 to 16 individuals per 100 km^2). Alternatively, the abundance of avian predators in our study had the opposite effect on predation risk. Predation risk declined by 1% with each increase in breeding avian predator per 100 km^2, indicating that predation risk could decrease by up to 64% between the minimum and the maximum number of breeding avian predators recorded (16 to 84 per 100 km^2).

Although the direction of this effect was unexpected, some studies have shown that predation risk on shorebird nests actually decreases in the presence of nesting avian predators due to protection from mammalian predators (Nguyen et al. 2006, Smith et al. 2007b). In one study this effect was consistent between real and artificial nests (Nguyen et al. 2006). The lack of predator effects for real nests could be attributed to behavioral adaptations of incubating birds, such as nesting associations with avian predators, or possibly to the low nest density, as discussed earlier.

The effect of lemming abundance on predation risk of artificial nests was also considerable, with predation risk decreasing by up to 50% between the lowest recorded index of lemming abundance (0.09 lemmings per 100 TN) and the highest (0.89 lemmings per 100 TN). Results from the real nests at Site 1 indicated a similar magnitude of effect, with nest success (daily nest survival$^{21 \text{ incubation days}}$) of Baird's and White-rumped sandpipers increasing ~75% from the year of lowest lemming abundance (0.09 lemmings per 100 TN, 0–1% nest success) to the year of highest lemming abundance (0.89 lemmings per 100 TN, 74–77% nest success). A noteworthy finding was this magnitude of change in breeding parameters despite the lower than usual amplitude of the lemming cycle for Bylot Island, where years of high lemming abundance often surpass 4 lemmings per 100 TN (Bêty et al. 2002). Despite the lower amplitude of the cycle during our study, the magnitude of change in breeding parameters between high and low lemming years is consistent with studies on geese–lemming interactions during higher amplitude cycles on Bylot Island (Bêty et al. 2002), as well as studies of bird–lemming interactions in the eastern hemisphere.

On the Taimyr Peninsula, Siberia, Underhill et al. (1993) showed that daily nest survival of shorebirds (up to 10 species combined) decreased from 0.98 to 0.80, which corresponds to a 98% decrease in nest success (based on an average incubation period of 21 days) between a peak lemming year and a decreasing lemming year. Using a longer time series (more than 20 years), Summers et al. (1998) revealed an indirect effect of lemmings on a larger spatial scale by providing evidence that breeding productivity of Dark-bellied Brent geese (*Branta bernicla bernicla*) and Curlew Sandpipers (*Calidris ferruginea*), as measured by the percent of first year individuals in wintering flocks, varied by up to 50% between years of low and high lemming abundance over a larger area of the Taimyr Peninsula.

In conclusion, our evidence, based on both real and artificial nests, indicates that fluctuations in lemming populations have an indirect effect on predation pressure on shorebird nests in the Canadian High Arctic. On Bylot Island, lemming populations exhibit cycles at 3 to 4 yr intervals; therefore, our study is limited in that our 5 yrs of data only cover 1 full lemming cycle. Moreover, our index of lemming abundance was based on snap trapping and not mark–recapture methods, which could provide more accurate estimates of lemming densities. Despite these limitations, we found strong evidence for an indirect effect of lemmings on daily nest survival of real shorebirds nests and on predation risk for artificial nests monitored at 2 study sites. These results were consistent with studies of bird–lemming interactions in the eastern hemisphere but not so clearly consistent with those in the western hemisphere, providing several intriguing questions for future research. Are these differences methodological, or does the indirect relationship between lemming and birds vary by species, nest density, or amplitude of lemming cycles? Future studies should also investigate the proximate mechanisms involved and how these interactions may differ in the presence of other alternative prey species.

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