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Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese

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Summary

1. We investigated the hypothesis that cyclic lemming populations indirectly affect arctic-nesting greater snow geese (*Anser caerulescens atlanticus* L.) through the behavioural and numerical responses of shared predators.

2. The study took place on Bylot Island in the Canadian High Arctic during two lemming cycles. We recorded changes in foraging behaviour and activity rate of arctic foxes, parasitic jaegers, glaucous gulls and common ravens in a goose colony during one lemming cycle and we monitored denning activity of foxes for 7 years. We also evaluated the total response of predators (i.e. number of eggs depredated).

3. Arctic foxes were more successful in attacking lemmings than goose nests because predators were constrained by goose nest defence. Predators increased their foraging effort on goose eggs following a lemming decline.

4. Activity rates in the goose colony varied 3·5-fold in arctic foxes and 4·8-fold in parasitic jaegers, and were highest 2 and 3 years after the lemming peak, respectively. The breeding output of arctic foxes appeared to be driven primarily by lemming numbers.

5. Predators consumed 19–88% of the annual goose nesting production and egg predation intensity varied 2·7-fold, being lowest during peak lemming years. Arctic foxes and parasitic jaegers were the key predators generating marked annual variation in egg predation.

6. Our study provides strong support for short-term, positive indirect effects and long-term, negative indirect effects of lemming populations on arctic-nesting geese. The outcome between these opposing indirect effects is probably an apparent competition between rodents and many terrestrial arctic-nesting birds.

Key-words: apparent competition, apparent mutualism, arctic ecosystem, behavioural response, numerical response.

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Introduction

The role of trophic interactions in determining the distribution and abundance of organisms is a long-standing debate among ecologists. Traditionally, community models have emphasized the role of direct interactions. Indirect interactions, in which a species can indirectly alter the abundance of another species through its direct interactions with a third species, may also be important (Strauss 1991). Despite an increase in interest, the actual role of indirect effects in natural communities is still far from clear (Menge 1995; Chase 2000).

Prey that share the same predators can indirectly interact via the functional (changes in kill rates) as well as the numerical response (changes in reproduction, survival or aggregation) of predators (Holt 1977). Prey availability can influence the behaviour of predators and modulate the predation rate experienced by a prey species through the functional response of predators. An increase in the density of a focal prey may reduce predation rate on an alternative prey because of predator saturation or selectivity (Abrams & Matsuda

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1996). This type of short-term, indirect interaction is called apparent mutualism (Abrams & Matsuda 1993). In patchy environments where predators are mobile and prey items are not uniformly distributed, co-occurring prey may also indirectly interact via the aggregative response of predators (Holt 1984). If predators select patches with the preferred prey type (i.e. local numerical response), predation rate of prey located in other patches may be reduced, again leading to short-term apparent mutualism among prey (Holt & Lawton 1994). Alternatively, an increase in the density of one prey may eventually lead to an increase in predator numbers and thus enhance predation on alternative prey. This long-term indirect interaction mediated by the numerical response of shared natural enemies could lead to a reduction in the number of the alternative prey, an effect called apparent competition (Holt 1977).

Indirect interactions mediated by predators have not been well studied in natural systems that exhibit periodic fluctuations (Abrams, Holt & Roth 1998). Parallel cyclic fluctuations in the abundance of small mammals and the abundance or the breeding success of some bird species have been taken as evidence of indirect interactions mediated by shared predators in northern communities (Angelstam, Lindström & Widén 1984). However, the relative importance of the numerical and functional responses of different predator species on the avian community is still largely unknown (e.g. Norrdahl & Korpimäki 2000; Wilson & Bromley 2001). A better understanding of the role of indirect interactions in these communities requires a detailed knowledge of long- and short-term responses of predators to changes in prey availability (Holt & Lawton 1994).

We studied direct and indirect interactions among herbivore prey and predators in the Canadian High Arctic where the assemblage of terrestrial vertebrate species is relatively simple. In our study area, the annual nesting success of greater snow geese (*Anser caerulescens atlanticus* L.) is associated positively with the overall abundance of brown lemmings (*Lemmus sibiricus* Kerr) and collared lemmings (*Dicrostonyx groenlandicus* Traill) (Bêty *et al.* 2001). Primary goose egg predators are, in decreasing order of importance, arctic foxes (*Alopex lagopus* L.), parasitic jaegers (*Stercorarius parasiticus* L.), glaucous gulls (*Larus hyperboreus* Gunnerus) and common raven (*Corvus corax* L.) (Bêty *et al.* 2001). All four predator species are highly opportunistic omnivores that also eat lemmings (Fitzgerald 1981).

Our main objective was to test the hypothesis that lemmings, the focal prey, indirectly affect snow geese, an alternative prey, through the responses of shared predators. We tested several predictions of this hypothesis with respect to the response of predators to lemming population cycles. First, if predators show a preference for lemmings, they should hunt them primarily until their density declines. Secondly, abundance of predators in goose nesting areas should be lower at high lemming densities and increase following lemming declines. Thirdly, the breeding production of predators should be higher at high than at low lemming density. Finally, the total response of predators (i.e. the product of the number of predators and the number of eggs taken per predator) should be cyclic and lowest in peak lemming years.

To test these predictions, we looked first at inter-annual changes in foraging behaviour and activity rate of nest predators in a goose colony during a complete lemming cycle. Secondly, we examined denning activity and litter sizes of the main nest predator, the arctic fox, under fluctuating lemming densities. Finally, we evaluated the total response of nest predators using surveys of goose nests and artificial nest experiments.

Materials and methods

STUDY AREA AND SPECIES

We conducted the study at the Bylot Island migratory bird sanctuary, Nunavut, Canada (72°53′N, 78°55′W), the most important breeding site of greater snow geese (> 25 000 pairs in 1993: Reed, Giroux & Gauthier 1998). Density of most terrestrial bird species is low relative to snow geese (estimated to be < two pairs per 100 ha in most species; Lepage, Nettleship & Reed 1998). Nesting geese are concentrated mainly in two areas (< 100 km^2) on the South plain of Bylot Island (*c.* 1600 km^2; see Lepage *et al.* 1998 and Bêty *et al.* 2001). We made observations and nest monitoring in a large goose colony (typically > 4000 nests over *c.* 16 km^2) located around a narrow valley (*c.* 0·5 km wide) surrounded by gently slopping hills (see Lepage, Gauthier & Reed 1996 and Tremblay *et al.* 1997 for details of the areas). Two species of lemmings coexist on Bylot Island and, in contrast to nesting geese, they occur over all the South plain. The brown lemming prefers wetlands (polygon fen) and feeds primarily on graminoids (grasses and sedges) (Gauthier, Rochefort & Reed 1996; Negus & Berger 1998). By contrast, the collared lemming prefers dry upland habitat and feeds mainly on dicotyledonous plants (Negus & Berger 1998). Adult brown and collared lemmings weigh 40–100 g and a fresh goose egg 90–130 g.

The greater snow goose is a strict herbivore. Like brown lemmings, geese depend mainly on wetland graminoids for their food (Gauthier *et al.* 1996). However, even in years of peak abundance, lemmings consume a small proportion of above-ground biomass compared to geese, as shown by the long-term monitoring of vegetation in goose and lemming exclosures (G. Gauthier, unpublished data). Geese are single-brooded and do not renest after failure of a clutch (Lepage, Gauthier & Menu 2000). Nest initiation occurs in June and is typically very synchronized (about 90% of nests initiated within 8 days; Lepage *et al.* 1996). Low nest density occurred in late nesting seasons and is probably a consequence of reduction in overall geese breeding effort under unfavourable climatic conditions (Gauthier *et al.* 1996; Lepage *et al.* 1996; Bêty *et al.* 2001). As laying progresses, nest attentiveness by the female increases and time spent on the nest by incubating females averages 92% and does not vary seasonally (Poussart, Larochelle & Gauthier 2000). The duration of incubation period is approximately 24 days (Poussart *et al.* 2000). During the brief incubation recesses, females are accompanied by their mate and feed most of the time (Reed, Hughes & Gauthier 1995). Nest desertion is rare (estimated at < 2%, Tremblay *et al.* 1997) and predation is the main proximate cause of nest failure (Lepage *et al.* 1996; Bêty *et al.* 2001). Egg predators can raise no more than one litter/brood per year (Fitzgerald 1981).

LEMMING ABUNDANCE

Index of lemming abundance was obtained in July from 1994 to 2000 with snap-trap censuses. Trapping was carried out in two study plots (wet lowland and dry upland), except in 1994 (only one plot in wet lowland). In each plot, we set 50 baited traps for 10–11 days (see Bêty *et al.* 2001 for details of the methods). Study plots were located in a goose brood-rearing area 30 km from the monitored goose colony. Similar trapping conducted from 1997 to 2000 at the goose colony showed a spatial synchrony in the fluctuation of lemming abundance at the regional scale (Bêty *et al.* 2001; Bêty and Gauthier, unpublished data).

BEHAVIOUR AND ACTIVITY OF PREDATORS

From 1996 to 1999, we conducted detailed behavioural observations during the incubation period in a plot (*c.* 50 ha) where conditions (habitat and nest dispersion) were typical of those encountered in the whole monitored goose colony. The number of goose nests located in the observation zone was estimated at the beginning of the incubation by visual counts of breeding pairs. This was used as an index of nest density in foraging behaviour analyses (see below). Each year, we performed 24 4-h observation sessions systematically rotated throughout the 24-h cycle and spread throughout the incubation period. The photoperiod is 24-h daylight during the goose nesting period. We conducted observations from a blind and predators appeared unaffected by our presence once we were inside the blind. We recorded the number of predators staying at least 1 min within the plot (including predators flying over). The 1-min criterion was used to eliminate the few observations of avian predators that were travelling at high speed across the plot and clearly not foraging. To calculate the annual activity rate of predators (number of presences per 24 h), we randomly assigned each 4-h observation session to form a total of 4 days of observation (i.e. four replicates of a complete 24-h cycle). We used binoculars (7 × 35) to detect and identify predators and a spotting scope (20–60 ×) to determine the outcome of their attacks.

Nest attacks were defined as any attempt by a predator to rob goose eggs. Avian predators most often tried to reach goose nests from the air (rapid and direct flight toward a nest) but sometimes on foot (mainly ravens). Foxes usually initiated attacks from a distance of > 10 m and ran at high speed straight towards a goose nest. At the time of the attack, we noted the presence or absence of protecting adults around the nest and scored the distance to the nest of the nearest goose if present [0 m (female incubating), 1–10 m and > 10 m]. Nest attacks were considered successful if at least one egg was preyed upon. From 1997 to 1999, we recorded systematically attacks of arctic foxes on lemmings during their presence in the goose colony. Generally, when a fox spotted a lemming, it stopped moving, swayed its head and jumped or dug rapidly to capture the prey. Attack rates on lemmings are not available for avian predators because it was too difficult to confirm their attacks by direct observation.

BREEDING ACTIVITY OF PREDATORS

From 1994 to 2000, we searched for and monitored arctic fox dens in the vicinity (up to 40 km) of the goose colony. Dens were visited at least once in June or early July to check for signs of fox presence (i.e. fresh scats, tracks, prey remains or recent digging). Dens with signs of activity were revisited later during the summer (July and August) to determine the presence and number of pups. Litter size was defined as the highest number of pups observed at any visit. These estimates must be regarded as a minimum number (Garrott, Eberhardt & Hanson 1984). New dens were found every year, because the size of the surveyed area increased during the study (*c.* 240 km^2 at the end of the study). We are confident that we found the majority of dens present in the surveyed area. We assumed that the annual proportion of breeding dens among those surveyed was representative of the total number of dens present over the entire area. The proportion of breeding dens multiplied by the mean litter size and the density of dens was used as an index of the yearly breeding production of foxes. The low breeding density of glaucous gulls and parasitic jaegers in the study area (estimated at < 0·3 pairs per 100 ha) precluded adequate monitoring of their breeding activity and little evidence for breeding was reported for common ravens (Lepage *et al.* 1998).

PREDATION ON GOOSE EGGS

We monitored goose nests from 1996 to 2000. Nests were found by systematic searches mainly during the laying or early incubation periods and mapped with a Global Positioning System receiver (±25 m). Eggs were marked individually and signs of nest predation were noted on each visit (see Bêty *et al.* 2001). Although jaegers and gulls may be temporally attracted by the presence of investigators in the goose colony, nesting parameters are not biased by our visits (Bêty & Gauthier

2001). A nest was considered successful if at least one egg hatched. We estimated nest density (nests per 50 ha) by dividing the number of nests found by the area of the search zone measured with RANGES V using concave polygons (Kenward & Hodder 1996). The extent of the search zone ranged from 91 to 268 ha and was higher in years of low nest density to permit the location of an adequate number of nests (> 175). We considered both total and partial nest predation in our estimation of the total number of eggs depredated (ED) as follows:

$$\mathrm{ED} = [(\mathrm{NMR} \times \mathrm{TCL}) + (1 - \mathrm{NMR}) \times (\mathrm{TCL} - \mathrm{CSH})] \times \mathrm{ND}$$

where NMR is the nest mortality rate for the entire nesting period, TCL is the total clutch laid (total number of eggs marked in a nest), CSH is the clutch size at hatch (number of eggs in successful nests) and ND is the nest density. This statistic is an index of the total response of predators, i.e. the product of the number of predators and the number of eggs taken per predator. However, total or partial nest predation during laying (i.e. before nests were found by investigators) could lead to an underestimation of ND or TCL. Thus, our evaluation of ED is a minimum estimate of egg predation and may be negatively biased at high predation rate.

We estimated the relative contribution of each predator species to the total response (i.e. the number of eggs depredated by each species i, ED_i) using the nest attack rates observed in the colony. We assumed that the proportion of successful attacks by avian predators was similar to arctic foxes in a given year, as found for all years combined (see results). Finally, we weighted attacks by allowing twice as many eggs for each successful attack by foxes compared to avian predators (based on data from Bêty *et al.* 2001 and Bêty & Gauthier, unpublished data). The estimated relative contribution of predator species i was thus defined as:

$$\mathrm{ED}_i = \left[\frac{(AR_i \times W_i)}{\sum(AR_i \times W_i)}\right] \times \mathrm{ED}$$

where AR is the attack rate (number of nest attacks per 96 h) and W is the weighted factor (1 for avian predators and 2 for arctic foxes).

ARTIFICIAL NEST EXPERIMENT

We used artificial nests to assess experimentally the interannual variation in predation pressure on goose nests and as an additional index of the total response of egg predators. Goose eggs were simulated with domestic hen eggs. Three eggs were placed in simulated nest bowls and covered with goose down collected in old nests. Nest locations were marked with small, inconspicuous bamboo canes. Rubber gloves were worn during nest deployment and visits. A nest was considered depredated when at least one egg had been destroyed or removed. In 1997 and 1998, artificial nests were distributed in three plots (*c.* 300 m × 300 m) separated by > 1 km and located in the patchy goose colony. The experiment was performed in the same three plots in both years. Within each plot, nests were placed in three habitat types (mesic flat tundra, mesic hilly tundra and wet polygon fen). Two 80-m-long transects separated by 50 m were positioned in each habitat type. Five nests separated by 20 m were placed on each transect (total 30 nests/plot). Nests were set from 19.00 to 21.00 h and checked after 2, 5, 8 and 12 h of exposure to predators. We used nest remains to identify predators (birds or arctic fox). Nests depredated by foxes were characterized by a small hole in the goose down covering eggs, the absence of eggshell around the nest and sometimes fresh fox faeces in the nest. In contrast, scattered goose down and, generally, broken eggs or eggshells were found around nests depredated by avian predators. We calibrated our method by coupling direct observations from a blind and analyses of artificial nests remains. These observations confirmed (i) that predators of artificial nests were the same as those of real goose nests and (ii) the validity of our nest remains criteria to identify predator type (100% concordance for 101 nests where predators were observed; 81 by arctic foxes, 20 by parasitic jaegers and glaucous gulls).

STATISTICAL ANALYSES

The foraging behaviour of predators was analysed using generalized linear models (GLM) with logit link function. Type 3 contrasts with the likelihood ratio statistics were used to test the significance of a variable in models with other variables already included. Non-significant interactions were removed, one at a time from higher to lower levels, until only significant interactions remained (Christensen 1990). There are potential sources of lack of independence in some analyses of foraging behaviour of predators. First, we were unable to properly distinguish all individuals, and therefore we could not calculate the true (i.e. interindividual) variances of our measures of foraging behaviour. Secondly, attacks on different nests performed by the same predator during a single visit at the colony are repeated measures. In these cases, we used generalized estimating equation (GEE) with the logit link function (procedure GENMOD of SAS using the statement REPEATED, SAS Institute Inc. 1999). This analysis considers each predator visit as statistically independent but assumes that multiple attacks by the same predator are correlated (see Horton & Lipsitz 1999). The number of attacks per visit was low and unbalanced. Consequently, we used an exchangeable structure to model the working correlation matrix (i.e. matrix with one correlation coefficient for all individuals and repeated attacks; Horton & Lipsitz 1999). Annual variations in activity rate of predators were analysed with one-way ANOVA (year). The Mayfield method was used to calculate daily nest mortality rate and the product method was used to evaluate nest mortality rate for the whole nesting period (Johnson 1979). We calculated nest losses and exposure following Klett & Johnson (1982). We used two periods delimited by nest visits sequence: 'early' nesting stage (laying and first 7 days of incubation) and 'mid/late' nesting stage (8th day of incubation until hatching). Pairwise comparisons of nest mortality rates were made with Z-tests (Johnson 1979). We considered each goose nest as independent because the fate of a goose nest is independent of the fate of its nearest neighbours (Bêty *et al.* 2001). We calculated hourly mortality rate in artificial nests (Mayfield estimate) using the plot (not the nest) as the sampling unit. Annual variations in artificial nest mortality rate and relative importance of predators were analysed with Kruskal–Wallis tests. All statistical tests were performed with SAS statistical software version 8. All probabilities are two-tailed and significance levels were set at 0·05. Values are reported as mean ± 1 SE.

Results

LEMMING CYCLES AND FORAGING BEHAVIOUR OF PREDATORS

Our study spanned two lemming cycles (periods of 3 and 4 years) with three peaks and two declines in abundance (Fig. 1). The number of collared lemmings trapped remained low over this period and only brown lemmings exhibit marked annual variation in abundance. The number of goose nests located in the observation plot at the beginning of incubation varied considerably during the lemming cycle, with 150, 413, 448 and 124 nests from 1996 to 1999, respectively. Over this period, a total of 2431 observations of nest predators were made during 384 h of observations. Based on short-term recognizable patterns of pelt colour, we estimated the minimum number of arctic foxes foraging in the goose colony at four to six each year from 1996 to 1999.

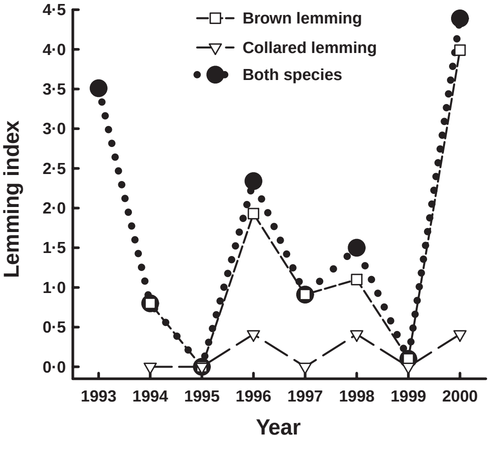

Fig. 1. Index of lemming abundance (number caught per 100 trap-nights) in July on Bylot Island from 1994 to 2000. Lemming index in 1993 was estimated using lemming nest surveys (see Bêty *et al.* 2001 for details).

Foxes were much more successful in capturing lemmings than goose eggs. Success rate of attacks was 21% (n = 141) on eggs and 92% (n = 26) on lemmings (P < 0·0001, median number of attacks per visit to the colony = 2, range 1–9). Success rate of attacks by avian predators on eggs was also low (20%, n = 176, median number of attacks per visit = 1, range 1–3). Because geese can defend their nests against predators, the fate of nest attacks was strongly influenced by the distance of the birds from their nest. Fox attacks were much less successful when geese were incubating (8% success, n = 118) than during incubation recesses (91% success when parents were at > 1 m from the nest, n = 23; P < 0·0001). Avian predators never attacked when females were sitting on the nest and they were 10 times as likely to rob eggs when geese were at > 10 m from their nests (21% success, n = 63) than when they were at a distance of 1–10 m (2% success, n = 83; P = 0·001, data pooled for all avian predator species).

The proportion of attacks by foxes while goose females were on the nest incubating was related negatively to lemming abundance, ranging from 91% (n = 47) at low lemming abundance to 76% (n = 42) at high lemming abundance (lemming index, P = 0·02; nest density, P = 0·68). Similarly, the proportion of attacks by avian predators in presence of parents near the nest decreased from 97% (n = 107) at low lemming abundance to 80% (n = 44) at high lemming abundance (lemming index, P = 0·02; nest density, P = 0·0001). Increases in frequency of attacks with low probability of success indicate that predators put more effort into robbing eggs at low lemming abundance. Lemming abundance did not influence the success rate of attacks by foxes when geese were close to their nests (P = 0·52; sample size was too small for a similar analysis with avian predators). Consequently, the overall success of attacks on goose nests decreased at low lemming abundance (Fig. 2). Thus, despite an apparent increase in foraging effort on goose nests at low lemming abundance, predators were less successful due to effective nest defence by geese.

From 1997 to 1999, 44% (n = 152) of visits by foxes in the goose colony resulted in the attack of a least one prey (lemming or goose nest). Foxes always attacked only one type of prey in a given visit. Overall, 80% (n = 124) of fox attacks in the goose colony were directed toward goose nests and 20% toward lemmings. We analysed separately the effects of nest density and lemming abundance on the probability of nest attacks during a visit because both variables varied in parallel way during the three years. The proportion of visits with attacks by foxes did not vary with lemming abundance (P = 0·51) or nest density (P = 0·82) and was similar among years (yearly mean = 0·46 ± 0·03, P = 0·27). Moreover, when foxes attacked prey, the mean number of attacks performed during a visit did not vary among years (yearly mean: 1·8 ± 0·1 attacks

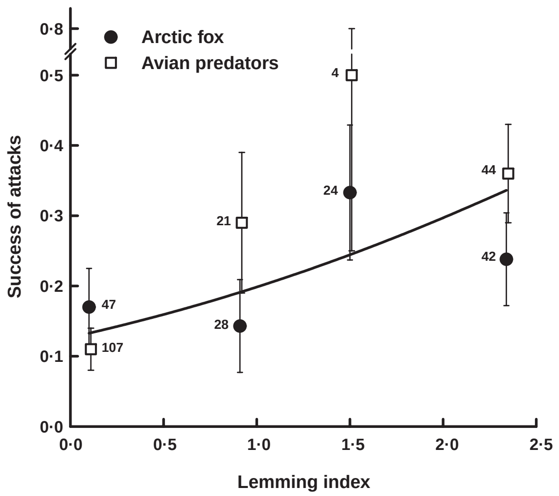

Fig. 2. Proportion of nest attacks by predators that were successful in relation to the index of lemming abundance (both species), Bylot Island (1996–99). To illustrate the adequacy of the model, annual success of predators are given for the two types of predators (arctic fox or avian predators). Number of attacks is shown and error bars are 1 SE. Lemming index, $P = 0{\cdot}0004$; nest density, $P = 0{\cdot}22$; type of predators, $P = 0{\cdot}46$.

per visit, Kruskal–Wallis test, $P = 0{\cdot}76$). The probability that attacks were directed toward nests instead of lemmings was related negatively to lemming abundance, ranging from 100% ($n = 47$) at low lemming abundance to 50% ($n = 48$) at moderate lemming abundance ($P < 0{\cdot}0001$). As the overall probability of attack remained stable among years, this indicates that at high lemming abundance foxes reduced their foraging effort on goose eggs when visiting the colony. The proportion of attacks directed toward goose nests also decreased with increasing nest density ($P < 0{\cdot}0001$). However, this negative association likely resulted from the parallel variation of nest density and lemming abundance. We suggest that lemming abundance primarily influenced foraging decisions of arctic foxes because at low lemming abundance foxes concentrated their foraging effort on nests despite their low availability, and at high lemming abundance foxes partially ignored nests despite their high availability.

ACTIVITY RATE AND REPRODUCTION OF PREDATORS

During one lemming cycle (1996–99), changes in activity rate of predators in the goose colony varied among species (Fig. 3). Annual activity rate varied 3·5-fold in arctic foxes ($F_{3,12} = 23{\cdot}7$, $P < 0{\cdot}001$, data log-transformed) and 4·8-fold in parasitic jaegers ($F_{3,12} = 124{\cdot}9$, $P < 0{\cdot}001$). The highest activity of foxes occurred 2 years after the lemming peak density, whereas highest activity of parasitic jaegers occurred in the low phase, 3 years after the lemming peak. In contrast, activity rates of common ravens and glaucous gulls showed little variation throughout the lemming cycle (variations of < 1·6-fold: gulls, $F_{3,12} = 2{\cdot}9$, $P = 0{\cdot}08$; ravens, $F_{3,12} = 0{\cdot}9$, $P = 0{\cdot}47$).

From 1994 to 2000, a total of 37 arctic fox dens were found (overall estimated density of 15·4 dens per 100 km^2). Presence of breeding foxes was confirmed in 5 out of 7 years but not in 1994 and 1995, when the number of monitored dens was small (Table 1). A total of 77 cubs were observed in 21 dens (mean = 3·67 ± 0·39). Arctic foxes showed a numerical response

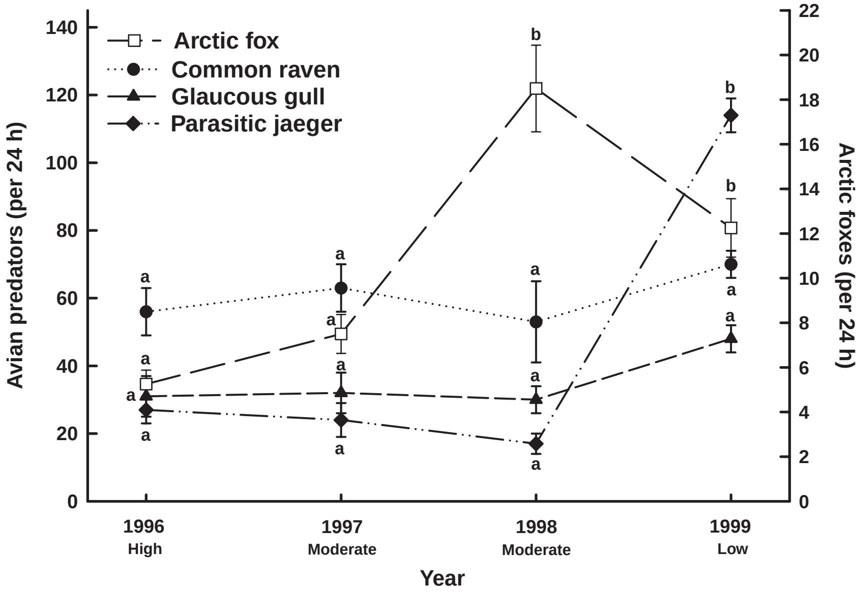

Fig. 3. Annual variations in activity rate of nest predators in a snow goose colony during one complete lemming cycle on Bylot Island (mean ± 1 SE, $n = 4$ complete 24-h cycle for each data point). Years accompanied by different letters differed significantly within species (a posteriori multiple comparisons with Tukey's adjustment, $P < 0{\cdot}05$). Relative lemming abundance is indicated under corresponding years.

Table 1. Breeding production of arctic foxes on Bylot Island from 1994 to 2000. Litter sizes (mean ± 1 SE) are minimum estimates of the number of cubs

Year	Relative lemming abundance	No. of dens monitored	No. of breeding dens	Breeding dens per 100 km^2	Litter size	Breeding production (cubs per 100 km^2)
1994	Moderate	11	0	0	–	0
1995	Low	11	0	0	–	0
1996	High	18	3	2·6	5·7 ± 0·8	14·6
1997	Moderate	23	3	2·0	5·0 ± 0·3	10·0
1998	Moderate	31	8	4·0	2·9 ± 0·2	11·5
1999	Low	35	2	0·9	2·0 ± 0·7	1·8
2000	High	37	5	2·1	3·6 ± 0·3	7·5

Table 2. Annual variations in snow goose nesting parameters on Bylot Island from 1996 to 2000. Nest mortality rate (NMR) for the entire nesting period was calculated from daily nest mortality rates estimated for the early and mid/late nesting periods (see Methods) using the product method (Johnson 1979). Years accompanied by different letters indicate significant differences in NMR ($\alpha = 0·005$, Bonferroni correction). Mean ± 1 SE

			Clutch size[b]		Nesting production[c]		
Year	*n*	Density[a]	TCL	CSH	NMR	Potential	Real
1996	237	50	4·0 ± 0·1	3·6 ± 0·1	0·38 ± 0·03^{a}	200	112
1997	284	132	4·2 ± 0·1	4·0 ± 0·1	0·15 ± 0·02^{b}	554	450
1998	326	179	4·0 ± 0·1	3·7 ± 0·1	0·18 ± 0·02^{b}	716	544
1999	179	55	3·1 ± 0·1	2·4 ± 0·2	0·85 ± 0·03^{c}	171	20
2000	198	82	3·5 ± 0·1	3·3 ± 0·1	0·17 ± 0·03^{b}	287	224

[a] Nests per 50 ha.

[b] TCL = total clutch size, and CSH = clutch size at hatching.

[c] Estimated nesting production (eggs per 50 ha): potential = nest density × TCL, real = nest density × (1-NMR) × CSH.

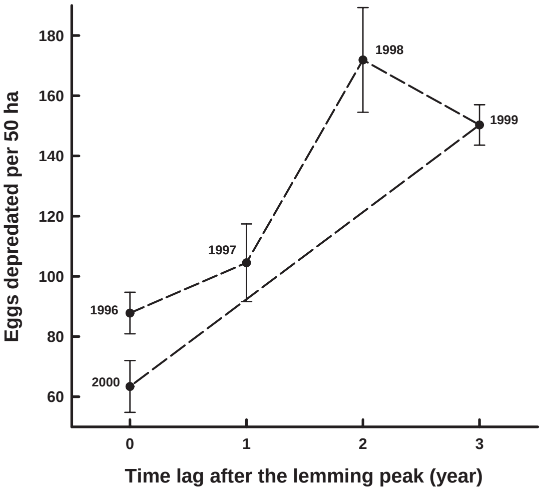

Fig. 4. Annual variations in the number of goose eggs depredated (total response of predators) with respect to the phase of the lemming population cycle on Bylot Island. Years are indicated near each data point (mean ± 1 SE).

to rodent densities as their lowest breeding output occurred at low lemming abundance (Table 1).

TOTAL RESPONSE OF PREDATORS

From 1996 to 2000, we determined the fate of 1224 goose nests. There were large annual variations in both nest density (3·6-fold) and daily nest mortality rate (12- and 24-fold difference during the early and mid/late nesting periods, respectively; Table 2). The total response of predators varied by 2·7-fold and the lowest predation pressure on nests occurred in peak lemming years (Fig. 4). On average, the total number of eggs depredated represented 39 ± 13% of the estimated annual potential nesting production, reaching 88% in 1999, a year of low lemming abundance and low nest density (Table 2, Fig. 1). The estimated relative contribution of each predator species to the total response indicates that arctic foxes and parasitic jaegers together caused between 75% (1996) and 94% (1998) of all egg predation (Fig. 5). The relative contribution of foxes and jaegers to the total number of eggs depredated varied markedly among years (2·8- and 17·7-fold variation, respectively). In contrast, estimated egg predation by glaucous gulls and common ravens was low and relatively constant despite large fluctuations in prey availability. Their combined impact reduced by < 13% the yearly potential goose nesting production.

Results from artificial nest experiments are consistent with those obtained from real goose nests. The mortality rate of artificial nests during the first 5 h of exposure was 2·6 times higher in 1998, 2 years after the lemming peak, than in 1997 (0·31 ± 0·07 vs. 0·12 ± 0·03, *n* = 3 plots per year, *P* = 0·05, Fig. 6). Mortality after 12 h of exposure was very high in both years (> 90%), which reflects the high vulnerability of nests in the absence of protecting adults. As in real

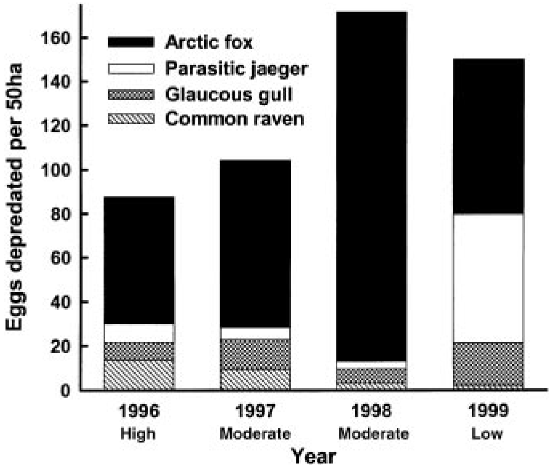

Fig. 5. Estimated relative contribution of each predator species to the total number of goose eggs depredated during one lemming cycle on Bylot Island. These estimates were calculated using the relative nest attack rates ($n = 317$ attacks) and the total response of predators (see methods). Relative lemming abundance is indicated under corresponding years.

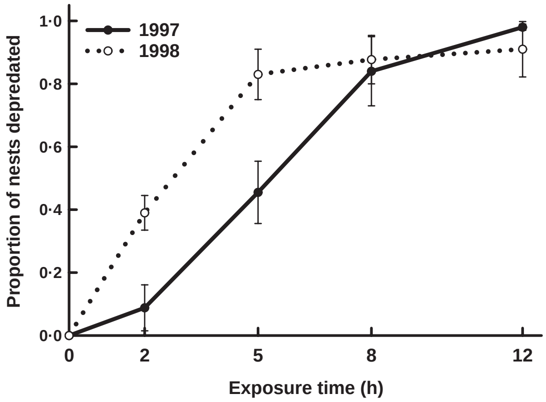

Fig. 6. Predation rate on artificial nests in relation to the time that nests were exposed to predators in a snow goose colony 1 (1997) and 2 (1998) years after a peak of lemming abundance (mean ± 1 SE, $n = 3$ plots for each data point).

goose nests, arctic fox was the main predator and its relative importance was lower in 1997 than in 1998 (mean proportion of nests depredated by foxes was 77 ± 11% and 100 ± 0%, respectively, $n = 3$ plots per year, $P = 0{\cdot}04$). These experiments showed that annual variations in nest predation rate and in the relative importance of different predators were not related to behavioural changes by geese such as nest attentiveness or nest defence intensity.

Discussion

The predictions of the hypothesis that cyclic lemming populations affect the breeding production of snow geese indirectly through direct interactions with shared predators were supported by our results. First, predators appeared to hunt primarily lemmings (the focal prey) although attack rates on geese increased in low lemming years. Secondly, activity rates of predators in the goose colony were generally reduced in peak lemming years. Thirdly, arctic foxes showed a numerical response to rodent densities. Finally, the predation pressure on goose eggs was cyclic and lowest in peak lemming years. It appears that the indirect interaction is mediated by both the behavioural and numerical responses of shared predators to oscillations in rodent abundance. This is one of the first field evidences of such interactions. Although our analysis is based mainly on data from one study area and one lemming cycle, our study provides strong support for the occurrence of both short-term and long-term indirect effects mediated by shared predators in an arctic tundra community.

SHORT-TERM INDIRECT EFFECTS AND BEHAVIOURAL MECHANISMS

Several mechanisms can generate short-term indirect effects among prey. Constraints on predator foraging such as the time required to handle prey may lead to mutually positive indirect effects, because time spent handling one prey may reduce the time available for capturing other prey (Holt 1977). Changes in predator behaviour that affect its relative and/or absolute effort in capturing different prey may also generate apparent mutualism (Abrams & Matsuda 1993).

In arctic foxes, we showed that the overall frequency of attack on prey (either lemming or goose nest) when visiting the goose colony remained relatively constant among years despite fluctuations in prey availability. Therefore, it appears that attacks directed on eggs are at the expense of those directed on lemmings, and vice versa. Our results also suggest that lemming availability primarily drives foraging decisions in arctic foxes and that predators increase their foraging effort on goose nests when lemmings, their preferred prey, are not as abundant. These observations indicate that predators attacked prey selectively and that changes in foraging behaviour during the lemming cycle could be part of a prey-switching behavioural response.

The most profitable foraging strategy for a predator is often to maximize the trade-off between energy reward and foraging costs rather than to maximize energy gain alone (Stein 1977). Foraging costs may include risk of injury, energy expenditure or missed foraging opportunities. The risk of injury can be an important cost for predators foraging within colonies of birds that perform active defence (Gilchrist, Gaston & Smith 1998). Therefore, predators foraging in snow goose colonies may be facing a trade-off between energy gain and foraging costs (e.g. Samelius & Alisauskas 2001), and lemming abundance may influence the fitness benefits of eggs (see Schmidt 1999). The increase in attack rate when geese were in a position of defending their nest (i.e. a more costly and potentially risky situation) indicates that predators increased their foraging effort on nests at low lemming abundance. We suggest that the indirect effect resulting from these behavioural mechanisms is a reciprocal positive–positive apparent mutualism between lemmings and geese on a short time scale (e.g. within a single predator generation). Nevertheless, intensive predator studies with marked individuals are required to better evaluate the behavioural responses under fluctuating prey availability.

NUMERICAL RESPONSE OF PREDATORS

A time lag in the increased activity of arctic foxes and parasitic jaegers in the goose colony with respect to the lemming peak may result from a delayed increase in predator population due to improved reproduction at high lemming densities (reproductive numerical response). Alternatively, or additionally, these fluctuations may be due to aggregative movements of predators to more profitable foraging areas with decreasing lemming abundance (aggregative numerical response). We suggest that both of these mechanisms occurred at our study site.

Generally, arctic foxes numerically track rodent populations with a time lag of 1 year in areas where rodent populations cycle (Macpherson 1969). Variation in reproductive rates is thought to be the main factor generating time lag between lemming and arctic fox population densities (Angerbjörn, Tannerfeldt & Erlinge 1999). Our results are consistent with previous reports showing that reproductive output of foxes is primarily driven by lemming numbers (e.g. Macpherson 1969; Tannerfeldt & Angerbjörn 1998). Nevertheless, the use of an additional food source such as birds during the summer may contribute to the breeding success of foxes and may be important for the maintenance of arctic fox populations in the low phase of the rodent cycle for several reasons (see also Macpherson 1969). First, the survival of pups is related to summer food availability (Tannerfeldt, Angerbjörn & Arvidson 1994). Secondly, food caches made during the summer can be used in the fall, and even during the winter and the following spring (Bantle & Alisauskas 1998). In goose colonies, most eggs depredated by foxes are cached for future consumption (> 80%; Stickney 1991; Bêty & Gauthier, unpublished data). Cached food may enhance winter survival of adult foxes (Macpherson 1969) and the number of young born in the following year (Angerbjörn *et al.* 1991). Consequently, the resulting indirect interaction mediated by the reproductive numerical response of foxes is most probably a negative–negative long-term apparent competition between lemmings and geese.

In contrast to foxes, the intense foraging activity of parasitic jaegers in the goose colony in the low phase of the lemming cycle may result mainly from an aggregative rather than a reproductive numerical response. The high mobility of avian predators allows them to aggregate rapidly in the most profitable foraging patches (e.g. Korpimäki 1994). Non-breeding avian predators may also concentrate in areas of relatively high prey density (Norrdahl & Korpimäki 2000). Thus, a low breeding effort and/or a high breeding failure rate because of intraguild predation may lead to the concentration of avian predators in the vicinity of bird nesting areas in the low phase of the lemming cycle. If we assume that the indirect interaction with parasitic jaegers is mediated by an aggregative response, the resulting effect would be a short-term (within a single predator generation) apparent mutualism between lemmings and geese.

RODENT CYCLES AND PREDATION ON BIRDS

The foraging decisions made by shared predators will influence the resulting indirect interactions among prey (Holt 1977). In general, prey selection by a predator will depend on its preference hierarchy (e.g. Fairweather 1985), the ability of alternative prey to resist predation (e.g. Schmitt 1982) and the relative abundance of alternative prey (e.g. Murdoch 1969). The relative vulnerability of birds should therefore influence the optimal foraging decision of egg predators (Schmidt 1999), which in turn should affect the outcome of indirect interactions between cyclic rodents and birds.

If bird eggs are temporarily abundant and easy to catch, they may become the primary prey item in the summer diet of foxes in spite of a high abundance of rodents (e.g. in waterfowl nesting areas, Stickney 1991). In this case, the impact of predation should depend more on the ratio of predator/alternative prey than on the abundance of rodents (Norrdahl & Korpimäki 2000). In contrast, if the alternative prey is relatively difficult to capture, predators should concentrate their foraging activity on this prey only if the abundance of the main prey is low, and the impact of predators should depend primarily on the density of rodents (Norrdahl & Korpimäki 2000).

Our results support the latter scenario. Predators of lemmings and snow goose eggs appeared to primarily target rodents, and increased their foraging effort on eggs when rodent population declined. Active nest defence by geese was the primary factor limiting foraging success of predators. The high intensity of egg predation at low lemming abundance was not due to a higher success rate of attacks by predators but to a much higher frequency of attacks on goose nests.

SHARED PREDATORS AND ARCTIC-NESTING BIRDS

Our results indicate that both short-term, positive effects and long-term, negative effects occurred between lemmings and geese. Such conflict between indirect interactions has also been found in other systems (see Holt 1977; Holt & Lawton 1994), but the outcome of these antagonistic indirect interactions is difficult to predict in natural ecosystems (Abrams & Matsuda 1996). Mathematical models predict that cyclic population fluctuations may weaken apparent competition because the variability in prey abundance reduces the average density of predators (Abrams *et al.* 1998).

In arctic ecosystems, it has been suggested that rodent populations could have an overall long-term positive effect on birds, especially those more vulnerable to arctic foxes (e.g. ducks and waders; Larson 1960). In some areas devoid of lemmings, arctic fox populations are generally dependent on abundant localized prey such as seabird colonies or dead carcasses of large mammals (e.g. Angerbjörn, Hersteinsson & Lidén 1994). However, in most terrestrial arctic regions, foxes act as specialist lemming predators and probably none or little alternative prey can maintain fox populations (Macpherson 1969; Angerbjörn *et al.* 1999). Consequently, we suggest that apparent competition mediated by the long-term numerical response of predators may be the dominant indirect interaction between lemmings and most terrestrial arctic-nesting birds. Large-scale empirical and experimental studies of the long- and short-term responses of predators to changes in prey availability are required to better highlight indirect trophic interactions in Arctic tundra.

Our main conclusion is that shared predation has considerable effects on the nesting production of greater snow geese, although other factors (e.g. food availability and climatic conditions) may also influence their breeding success (Gauthier *et al.* 1996; Skinner *et al.* 1998). In some arctic goose populations, egg and gosling predation may significantly limit population growth (e.g. Summers 1986), but this is apparently not a general phenomenon (Krebs *et al.* 1999). Theory of food chain dynamics predicts that predators do not control herbivores in unproductive arctic environments and that the plant–herbivore interaction should be the dominant trophic interaction (e.g. Oksanen & Oksanen 2000). However, the properties of each community may depend largely on the unique adaptations of the component species (Krebs *et al.* 1999). Our study provides direct evidence that birds nesting in a high arctic region can experience high, although variable, predation pressure. Therefore, predator–prey interactions may be more important than thought previously in structuring some arctic communities.

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