Are goose nesting success and lemming cycles linked? Interplay between nest density and predators

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The suggested link between lemming cycles and reproductive success of arctic birds is caused by potential effects of varying predation pressure (the Alternative Prey Hypothesis, APH) and protective association with birds of prey (the Nesting Association Hypothesis, NAH). We used data collected over two complete lemming cycles to investigate how fluctuations in lemming density were associated with nesting success of greater snow geese (*Anser caerulescens atlanticus*) in the Canadian High Arctic. We tested predictions of the APH and NAH for geese breeding at low and high densities. Goose nesting success varied from 22% to 91% between years and the main egg predator was the arctic fox (*Alopex lagopus*). Nesting associations with snowy owls (*Nyctea scandiaca*) were observed but only during peak lemming years for geese nesting at low density. Goose nesting success declined as distance from owls increased and reached a plateau at 550 m. Artificial nest experiments indicated that owls can exclude predators from the vicinity of their nests and thus reduce goose egg predation rate. Annual nest failure rate was negatively associated with rodent abundance and was generally highest in low lemming years. This relationship was present even after excluding goose nests under the protective influence of owls. However, nest failure was inversely density-dependent at high breeding density. Thus, annual variations in nest density influenced the synchrony between lemming cycles and oscillations in nesting success. Our results suggest that APH is the main mechanism linking lemming cycles and goose nesting success and that nesting associations during peak lemming years (NAH) can enhance this positive link at the local level. The study also shows that breeding strategies used by birds (the alternative prey) could affect the synchrony between oscillations in avian reproductive success and rodent cycles.

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In arctic tundra and northern Europe, vole (*Clethriono-mys* and *Microtus* spp.) and lemming (*Lemmus* and *Dicrostonyx* spp.) populations vary enormously in size over time and these fluctuations follow fairly regular cycles of three to five years (Krebs 1964, Hanski and Korpimäki 1995). Marked between-year variations in the reproductive success of several species of arctic ground-nesting birds have also been observed and related to cyclical changes in the abundance of small mammals (e.g. Summers 1986, Martin and Baird 1988, van Impe 1996). Two non-exclusive hypotheses have been proposed to explain this potential link.

The Alternative Prey Hypothesis (APH) states that the link is caused by a varying annual predation pressure on alternative prey resulting from the functional and numerical responses of predators to rodent densi-

ties (Lack 1954, Angelstam et al. 1984). When rodent (main prey) densities are high, predators primarily feed on them, reach high breeding densities and produce large litter. When the main prey populations decrease, predators turn to eggs and young of birds (alternative prey) and produce few or no young. Consequently, alternative prey should suffer most from predation during the decline and low phase of the rodent cycle.

The Nesting Association Hypothesis (NAH) states that some arctic bird species improve their reproductive success by nesting in association with birds of prey (Underhill et al. 1993, Lepage et al. 1996). Enhanced protection of eggs against predators gained by arctic geese and ducks nesting within the territories of aggressive birds of prey such as rough-legged hawks (or buzzards; *Buteo lagopus*) and snowy owls (*Nyctea scandiaca*) is well documented (e.g. Syroechkovskiy et al. 1991, Summers et al. 1994, Kostin and Mooij 1995). These nomadic, specialist predators are common in an area when lemmings are abundant but rare or absent when lemmings are scarce (Potapov 1997, Wiklund et al. 1998). Consequently, this opportunistic, protective association could be a mechanism driving the relationship between fluctuations in reproductive success of arctic birds and lemming cycles.

Density of breeding birds may also influence the link between rodent cycles and nest predation rate. Nest density affects predation rate (i.e., depredated nests/total) in numerous bird species (Newton 1998) and fluctuations in the availability of alternative prey for predators can lead to selection for different nesting densities (e.g. solitary vs colonial nesters: Hogstad 1995). Moreover, foraging theory predicts that changes in the predator-prey community could potentially determine the range of nest densities that results in profitable foraging by nest predators and thus influence the spatial and temporal patterns in nest predation rate (Schmidt 1999).

The suggestion of a link between lemming cycles and reproductive success of arctic birds is mostly based on winter observations of bird populations. Direct observations on the impact of fluctuations in lemming populations on bird nest predation pressure are scarce (Spaans et al. 1998), and the potential effects of varying predation pressure (APH) and association with birds of prey (NAH) are confounded in many studies (e.g. Syroechkovskiy et al. 1991, Underhill et al. 1993, Kostin and Mooij 1995). We studied the highly dynamic interaction between lemmings, predators and birds in a high-arctic-nesting species, the greater snow goose (*Anser caerulescens atlanticus*). We used data collected over two complete lemming cycles to investigate whether oscillations in lemming population and goose nesting success were linked at both low (small colonies) and high (large colony) breeding densities. We tested predictions of the APH and NAH to evaluate which of these two mechanisms could best explain the relation-

ship between lemming cycles and nest predation rate. Based on the APH, we predicted that predation rate on goose nests would be related to lemming abundance even in absence of birds of prey. More specifically, we expected that predation on nests would be lower during peak lemming years than during years of low lemming abundance. Based on the NAH, we predicted that predation rate would be lower for geese nesting in association with birds of prey than for those nesting without association in high lemming years.

Material and methods

Study area and species

We conducted the study at the Bylot Island migratory bird sanctuary, Nunavut Territory, Canada (73° 08′ N, 80° 00′ W), the most important breeding site of greater snow geese (> 25000 pairs in 1993: Reed et al. 1998). Data were collected at two nesting areas separated by 30 km, Site-1 (ca 50 km²) and Site-2 (ca 16 km²). Geese nested at low density at Site-1 (typically in groups of 10 to 20 nests, occasionally up to 300; also isolated nests) in comparison to high density at Site-2 (large patchy colony, typically > 4000 nests). The Site-1 area is a large glacial valley (2–5 km wide) bordered by steep hills to the north and southeast, and rolling hills to the southwest. The Site-2 area is located around a narrow valley (ca 0.5 km wide) surrounded by low hills with gentle slopes and extensive upland habitats (see Lepage et al. 1996 and Tremblay et al. 1997 for details of the areas). Density of other land birds at these two sites is low compared to geese (see Lepage et al. 1998, Gauthier et al. 1996).

The greater snow goose is a ground-nesting precocial species. It is single-brooded and does not renest after a failure of a clutch (Lepage et al. 2000). Nest desertion is rare (estimated at < 2%, Tremblay et al. 1997) and predation is the main cause of nest failure on Bylot Island (Lepage et al. 1996, Bêty and Gauthier 2001). As laying progresses, nest attentiveness by the female increases and time spent on the nest by incubating females averages 92% (Poussart et al. 2000). During the brief incubation recesses, females are accompanied by their mate, remain close to their nest (usually < 20 m) and feed most of the time (Reed et al. 1995).

Goose egg predators in the two study areas include glaucous gulls (*Larus hyperboreus*), common ravens (*Corvus corax*), parasitic and long-tailed jaegers (or skuas; *Stercorarius parasiticus* and *S. longicaudus*), and arctic foxes (*Alopex lagopus*). All avian predators are generalist except breeding long-tailed jaegers which depend primarily on lemmings (Maher 1970, Hussell and Holroyd 1974, Fitzgerald 1981, Wilson 1999). Arctic foxes are also generalists although their diet is heavily dependent on lemmings (Macpherson 1969, Angerbjörn et al. 1999).

Nesting associations with snowy owls and rough-legged hawks occur on our study area (Lepage et al. 1996, Tremblay et al. 1997). The presence of snowy owls has a strong effect on the location of goose colonies at Site-1. Owl nests are initiated ≥ 2 weeks earlier than goose nests (Lepage et al. 1996). Two species of lemmings co-exist on our study area. The brown lemming (*Lemmus sibiricus*) occurs in wet lowlands (polygon fen) whereas the collared lemming (*Dicrostonyx groenlandicus*) prefers dry upland habitat (Gauthier et al. 1996). Adults brown and collared lemmings weigh 40–100 g (Krebs 1964, Wilson 1999) and a fresh goose egg 90–130 g.

Goose nesting parameters

Goose nests were monitored from 1993 to 1999 at Site-1 and from 1994 to 1999 at Site-2. Nests were found by systematic searches during laying or early incubation period and mapped with a Global Positioning System receiver ($\pm$ 25 m). Nests were marked with orange wood sticks at a distance of 10 m and eggs were individually marked with waterproof black ink. Nests were revisited in the first half of incubation, during the hatching period and after goslings had left in order to determine their fate. Nesting parameters are not biased by our visits (Bêty and Gauthier 2001). A nest was considered successful if at least one egg hatched. Total clutch size was defined as the maximum number of eggs found in a nest, after the start of incubation. For nests found after the laying period, laying date (date for laying the first egg) was determined by estimating incubation stage, or by backdating from hatching date (see Lepage et al. 1999 for details). Nest density was defined for each goose nest as the number of nests within a 1-ha circle centred on the focal nest (minimum nest density according to this method was thus 1 nest ha^{-1}). Mean nest density was calculated separately for each nesting area and year. This provided an index of spatial and temporal variations in nest aggregation and genuine nest density. Some nests found during late incubation period were not used for the calculation of nesting parameters (e.g. success, clutch size) but were used to characterise nest distribution and evaluate nest density. Including all nests found at any time during the nesting season provides a better estimate of the maximum nest density.

Nest predators

From 1996 to 1999, we conducted behavioural observations at Site-2 during the incubation period in a plot (ca 50 ha) where conditions (habitat and nest dispersion) were typical of those encountered in the goose colony monitored. This allowed us to observe a large number of goose nests (> 125). Each year, we did 24 4-h observation sessions systematically rotated throughout the 24-h cycle. We recorded all attacks by predators attempting to rob goose nests. We used binoculars (7 $\times$ 35) to detect and identify predators and a spotting scope (20 $\times$ –60 $\times$) to determine the outcome of their attacks. Nest attacks were considered successful if at least one egg was preyed upon. The low nest density precluded direct observations at Site-1. However, previous observations suggest that the relative importance of predators is similar at both sites (Lepage et al. 1996, Tremblay et al. 1997).

Lemming abundance

Lemming abundance was estimated in July from 1994 to 1999 with snap-trap censuses at Site-1. Trapping was done in two study plots representing the two main habitat types (wet lowland and dry upland), except in 1994 (only one plot in wet lowland). In each plot, 50 Museum Special traps baited with peanut butter and rolled oat were set every 10 m on two line transects (100 m apart) for 10–11 d and were checked once a day (Shank 1993). We standardised the total number of lemmings trapped over the whole period to the number of animals caught per 100 trap-nights (= lemming index). We subtracted 0.5 night for each sprung trap to improve estimates of sampling effort and control for site-specific rates of trap-springing (Beauvais and Buskirk 1999). Similar trapping conducted from 1997 to 1999 at Site-2 showed a high spatial synchrony in the phase of the lemming cycle between the two goose nesting areas (see Results). Synchrony at the regional scale is typical in lemmings (Erlinge et al. 1999). We therefore considered our estimate of lemming abundance obtained at Site-1 as a general index of lemming abundance on the two study areas.

In 1993, lemming abundance was based on density of lemming winter nests which is well correlated with early summer lemming density (Wilson 1999; see also Sittler 1995). Lemming nest surveys were conducted on Bylot Island in 1993 and 1996 at two sites of 100 ha and 50 ha, respectively (3.72 and 2.52 nests ha^{-1}, respectively: Olivier Gilg unpubl.; see Sittler 1995 for details of the method). The ratio of lemming abundance to nest survey obtained in 1996 was applied to the 1993 nest survey to estimate lemming abundance that year.

Artificial nest experiments

Goose eggs were simulated with domestic chicken eggs, which are smaller but similar in shape and colour. Three eggs were placed in simulated nest bowls and covered with goose down collected in nests during previous years. Nest locations were marked with short

bamboo canes. Rubber gloves were worn during nest deployment and visit. Artificial nests were not used to estimate predation rate on natural nests but were used in conjunction with real nest data to provide an index of spatial variation in predation risk (see Berg 1996, Valkama et al. 1999).

We conducted an experiment to test the hypothesis that owls reduce predation risk on goose eggs around their nest. The experiment was replicated around two snowy owl nests. In each replicate, five artificial nests were distributed at 5, 30, 50, 100 and 150 m along four perpendicular transects starting at the owl nest and twenty other nests were similarly placed in a control area 2 km away from the owl nest. To avoid straight patterns of distribution, we placed nests at varying distance on either side of line transects. Nests were located in upland habitats and checked after 1, 2, 3, 4, 6, 8, 11 and 17 d of exposure. A nest was considered depredated when at least one egg had been destroyed or removed.

We tested at Site-2 the hypothesis that geese can protect conspecific nests at high breeding density by defending their own nest surroundings. Four artificial nests were placed at 5, 10, 20 and 30 m along 30-m-long transects, each transect starting at a different goose nest and running away from it. The minimum distance of 5 m was used because over 98% of goose nests were separated by > 5 m at both nesting areas. Transects were oriented so that minimum distance with other goose nests was > 30 m. We placed ten transects at mid-incubation and repeated the experiment 6 d later with 20 additional transects for a total of 120 artificial nests at 30 different goose nests. Transects were set from 19.00 to 21.00. All nests were revisited after 2 and 5 h of exposition to predators.

Statistical analyses

Laying dates (expressed in Julian date, $1 = 1$ January) were compared using Kruskal-Wallis test (Siegel and Castellan 1988). We used t-test to compare mean clutch size and nest density. When variances were heteroscedastic, an approximate t-test based on unequal variances was used. Correlation analyses were made using Spearman rank correlation (r_s). To increase sample size in the correlation analysis of mean nest density and median laying date, we combined our data to those of Lepage et al. (1996) collected at the same study sites.

We used multiple linear regression (procedure GLM of SAS Institute 1996) to examine the relationship between relative laying date (deviation from the median laying date in each year), relative clutch size (deviation from mean clutch size) and distance from

the nearest snowy owl nest. Models also included year as independent variable. Generalised Linear Models (procedure GENMOD of SAS) with logit link function were used to perform logistic regression analyses. We first evaluated the relationship between goose nesting success (success = 1, failure = 0) and distance from owls using logistic regression model including variables distance, year and nest density. Type 3 contrasts using the likelihood ratio statistics were used to test the significance of a variable in models with other variables already included. If an interaction term was not significant, it was deleted and the model was rerun. Interactions were deleted one at a time from higher to lower levels, until only significant interactions remained (Christensen 1990).

We used a logistic regression with an inflection point to test for the presence of a threshold distance (distance from owl) beyond which the protective influence of breeding owl was absent. The approach is analogous to method used to estimate transition point in linear regression (Bacon and Watts 1971). The logistic model (run with procedure GENMOD of SAS with logit link function) included variables distance-f, year and nest density. The variable distance-f took the value of the distance from the nearest owl for goose nests located at distance ≤ inflection point and took the value of the inflection point if distance > inflection point. Models were run with inflection point varying from 100 to 2000 m, incrementing this value by 25 to 200 m each time. The position of the inflection point associated with the best fitting model, which was the model with the lowest deviance (Agresti 1996), was selected as the threshold distance. Models were also run separately for each year to examine differences between years.

The previous analyses use each goose nest as an independent observation. We tested the hypothesis that spatial patterns of predation were random, i.e. that the probability that a nest is depredated is independent of the fate of its nearest neighbours. We compared proportion of nests for which the nearest neighbour was successful versus depredated using 2×2 contingency tables and Fisher's exact tests (see Larivière and Messier 1998 for details).

To evaluate the effect of lemming abundance on annual variations in goose nesting success, we used a multiple logistic regression including the variables lemming index, nesting area and mean nest density. The CONTRAST statement of the GENMOD procedure was used to compare nesting success in a logistic model using three levels of lemming abundance (low, intermediate and high). Statistical tests were two-tailed and significance levels were set at 0.05. Values are reported as mean ± 1 standard error.

Table 1. Annual nesting parameters of greater snow goose nests monitored at two areas, Site-1 (S1, small colonies) and Site-2 (S2, large colony) on Bylot Island from 1993 to 1999. Mean ± SE.

	1993	1994		1995		1996		1997		1998		1999	
	S1	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
n	283	46	285	72[a]	69	113	246	35	291	19[a]	331[a]	5[a]	180[a]
Laying date[b]	6	7	11	11	10	12	14	11	10	10	7	12	18
Clutch size	4.5±0.1	4.5±0.2	3.6±0.1	5.1±0.5	3.7±0.1	4.0±0.1	4.0±0.1	4.9±0.3	4.2±0.1	4.7±0.5	4.0±0.1	3	3.1±0.1
Nest density[c]	3.4±0.2	1.1±0.1	6.7±0.2	1.4±0.1	5.5±0.3	1.8±0.1	4.2±0.2	1.2±0.1	5.7±0.2	1.1±0.1	6.6±0.2	1.0±0.0	4.1±0.2

[a] n for clutch sizes was smaller in those years (1995 S1, $n = 16$; 1998 S1, $n = 7$; 1998 S2, $n = 301$; 1999 S1, $n = 1$; 1999 S2, $n = 107$).
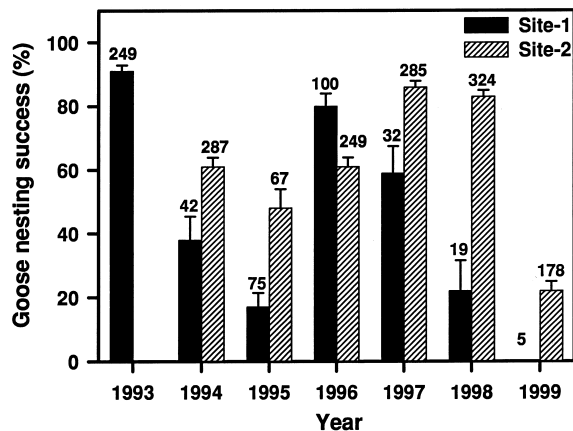[b] Median laying date in June.
[c] Nest ha^{-1}.

Fig. 1. Annual fluctuations in greater snow goose nesting success (proportion of nests where at least one egg hatched successfully) at two nesting areas, Site-1 (low breeding density, small colonies: 1993 to 1999) and Site-2 (high breeding density, large colony: 1994 to 1999), on Bylot Island. Numbers represent sample sizes and error bars are SE.

Results

Goose nesting parameters

From 1993 to 1999, nesting success was determined for 1912 goose nests found early in the nesting period. Overall annual goose nesting success varied considerably among years (22% to 91%) and success was always lower at Site-1 than at Site-2 except in 1996 (Fig. 1). From 1994 to 1999, timing of breeding was similar at both nesting areas (median laying date 11 June: $\chi^2 = 0.007$, df $= 1$, $p = 0.93$) and clutch size was slightly higher at Site-1 (4.3 ± 0.1) than at Site-2 (3.8 ± 0.1: $t = 6.5$, df $= 1580$, $p < 0.001$; Table 1). Nest density was highly variable among years but was always higher at Site-2 than at Site-1 (2.3 to 6.2 times higher, all $p < 0.001$; Table 1). Annual mean nest density and median laying date were not related at Site-1 ($r_s = -0.04$, $n = 10$, $p = 0.92$). However, mean nest density was lower in late nesting season at Site-2 colony ($r_s = -0.78$, $n = 7$, $p = 0.05$).

Importance of nest predators

A total of 318 attacks by predators on goose nests were observed during 384 h of observation and 66 (21%) of them were successful. Each year, arctic fox was the main predator and was responsible for 44% of all attacks on nests and for 45% of successful ones. Other important egg predators were parasitic jaegers, glaucous gulls and common ravens that accounted for 30, 16 and 10% of the attacks and 18, 21 and 14% of successful ones, respectively. Contrary to avian predators, successful attacks by foxes generally resulted in predation of more than one egg and often in total nest
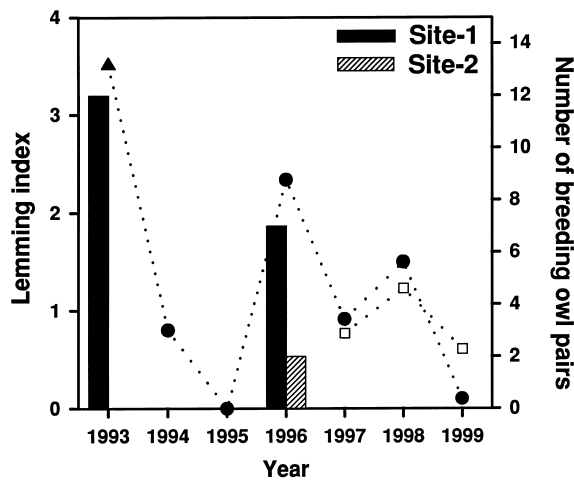
Fig. 2. Index of lemming abundance (pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights) at Site-1 from 1994 to 1999 (●) and at Site-2 from 1997 to 1999 (□), Bylot Island. Lemming index at Site-1 in 1993 (▲) was estimated from lemming nest survey data, based on the ratio lemming nest survey/lemming abundance obtained in 1996 (see Methods). The number of breeding snowy owl pairs recorded at Site-1 (ca 50 km²: 1993 to 1999) and at Site-2 (ca 16 km²: 1994 to 1999) is also shown (bars).

predation. Out of 27 successful attacks by foxes with a known number of eggs preyed upon, 15 (56%) resulted in loss of ≥ 2 eggs (2.5 ± 0.2 eggs) comparatively to only two out of 18 for avian predators. Nesting geese were capable of defending their nests against predators. When parents were close to their nests (≤ 10 m), successful attacks by predators were rare [8% ($n = 121$) for arctic foxes and 2% ($n = 83$) for avian predators].

Lemming cycle and nesting association

Peak in lemming abundance occurred in 1993 and 1996 and owl nests ($n = 21$) were found only in these two years
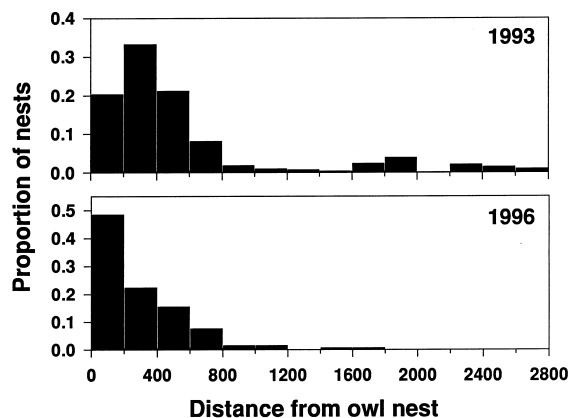

Fig. 3. Distribution of snow goose nests found at Site-1 area in relation to distance (m) from the nearest snowy owl nest in 1993 ($n = 351$) and 1996 ($n = 115$).

(Fig. 2). At Site-1, nesting association with owls was observed in both years that owls nested (see also Lepage et al. 1996). We found goose nests around (< 600 m) all owl nests but two in 1993. The median number of goose nests per owl nest was ten ($n = 18$, range 1 to 270). Goose nests at Site-1 were clustered around owl nests with 75% and 87% of nests at ≤ 600 m in 1993 and 1996, respectively (Fig. 3). At Site-2, only one of the two owls was located in the goose colony (38% of monitored goose nests were at ≤ 600 m). However, this owl abandoned its nest during incubation at a time when geese were finishing laying. The other owl nest was at > 2 km from the colony and hatched successfully.

There was a weak relationship between laying date and distance from owl at Site-1 in both 1993 and 1996 ($\beta = 7.2 \times 10^{-4} \pm 2.6 \times 10^{-4}$, $r^2 = 0.02$, $p = 0.006$, $n = 383$; year and interaction term, $p > 0.3$). Similarly, clutch size slightly declined as distance from owl increased ($\beta = 3.1 \times 10^{-4} \pm 1.0 \times 10^{-4}$, $r^2 = 0.02$, $p = 0.003$, $n = 369$; year and interaction term, $p > 0.4$). Nest failure was lower close to owl nests than further away (distance, $\chi^2 = 4.50$, $p = 0.03$; year, $\chi^2 = 11.13$, $p = 0.008$; nest density, $\chi^2 = 0.07$, $p = 0.79$; all interaction terms, $p > 0.40$; df $= 1$, $n = 337$). Because distance to owls and nest density were correlated (1993, $r_s = -0.43$, $p < 0.001$, $n = 283$; 1996, $r_s = -0.36$, $p < 0.001$, $n = 108$), we repeated analyses excluding the variable distance from the model (Agresti 1996). Risk of nest failure was not significantly related to nest density ($\chi^2 = 0.38$, df $= 1$, $p = 0.54$). At Site-2, the single owl nest that was abandoned in early incubation in 1996 had no effect on goose nesting success (distance, $\chi^2 = 0.23$, df $= 1$, $p = 0.63$, $n = 247$). In 1994, some geese nested close to a rough-legged hawk nest at Site-1 (see Lepage et al. 1996). The proportion of successful nests tended to be higher for nests located at < 550 m from the hawk (60%, $n = 10$) compared to nests located further away (31%, $n = 32$; Fisher's exact test, $p = 0.14$).

We examined if the protective effect of owls on goose nests disappeared beyond a certain distance at Site-1. The use of an inflection point in the logistic regression model improved the fit compared to a model without it (reduction in deviance up to 1.7, Δ df $= 0$). The best fitting model had an inflection point located at 550 m (deviance $= 213.7$, df $= 334$, Fig. 4). The inflection point was remarkably similar in both years, indicating that goose nesting success progressively declined as distance from owls increased but reached a plateau beyond 550 m (Table 2, Fig. 5). Overall failure rate of nests located in the estimated protective area of owls was 7% lower compared to nests located outside (9%, $n = 269$ vs 16%, $n = 68$, respectively).

Artificial nest experiments

Results from the two artificial nest experiments conducted around snowy owls at Site-1 further supported
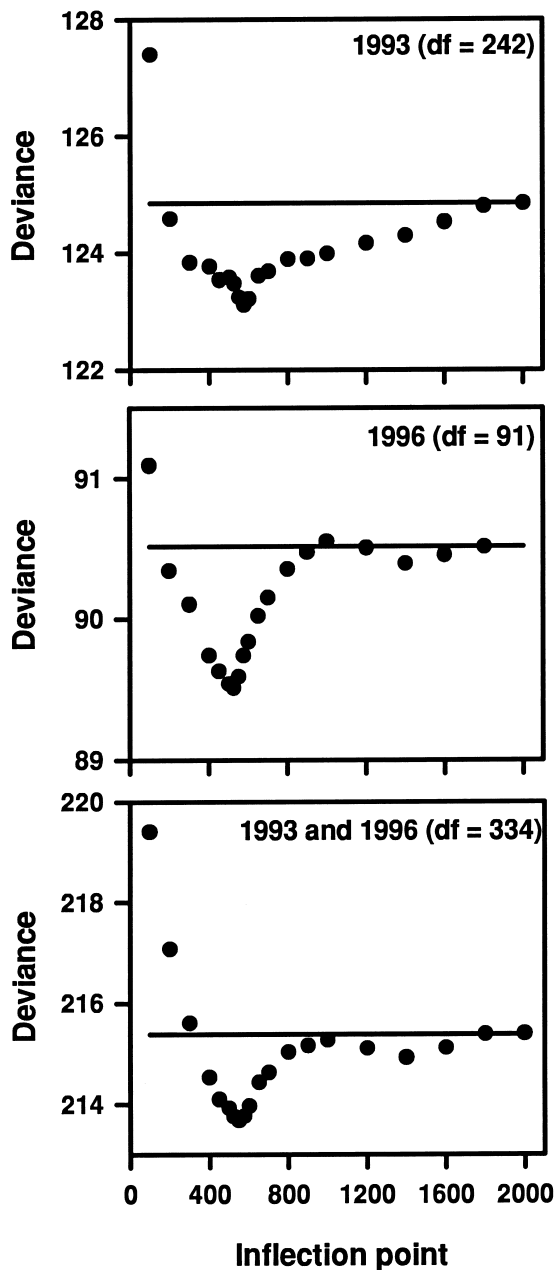
Fig. 4. Change in model fit in relation to the inflection point (distance from nearest owl nest in m) used in logistic regression analyses to test for a threshold distance beyond which the protective influence of owls on goose nesting success was absent (see Methods). Solid lines represent deviance for logistic models without inflection point. The degrees of freedom were the same for all models presented in a panel.

the hypothesis that owls reduced predation risk on goose nests located around their nest. For nests ($n = 40$) located in control areas, 88% were preyed upon after 3 d and 100% after 6 d. In comparison, for nests ($n = 40$) located around owls, only 13% were depredated after

3 d and 38% over the full length of the experiment (17-d exposition period). Eighteen goose nests were located at < 550 m from owl nests used for the experiment. Mean distance between goose and artificial nests was 61 ± 6 m (range 10 to 164 m).

Predation rate on artificial nests placed around goose nests at Site-2 colony in 1998 was also very high. After only 2 h, overall predation rate was 73%, 66%, 70% and 53% on artificial nests placed at 5, 10, 20 and 30 m, respectively (distance, $\chi^2 = 2.18$, $p = 0.14$; date, $p = 0.33$, and interaction term, $p = 0.43$, were dropped; df = 1, $n = 120$). All nests were destroyed after 5 h of exposure to predators. No egg was depredated in the 30 real goose nests during these experiments. Direct observations showed that artificial nest predation was mostly ($> 90\%$) confined to arctic foxes.

Randomness of predation patterns

We found no evidence for spatial dependence in goose nest survival at both nesting areas from 1993 to 1999 except in 1996 (Site-1 only) and 1994 (Table 3). The significant spatial dependence observed twice at Site-1 occurred in two years where geese nested in association with birds of prey (owls in 1996 and hawk in 1994). By creating protective areas around their nests, birds of prey could cause a non-random pattern of predation among geese nests leading to a significant spatial dependence. However, we did not detect significant spatial dependence at Site-1 in 1993 despite the presence of owls (Fisher's exact test, $p = 0.37$), possibly due to the very low predation rate (9%) observed that year. We have no explanation for the weak but significant spatial dependence observed at Site-2 in 1994. Nevertheless, an overall test including all years showed no significant spatial dependence in failure rate at Site-2 ($\chi^2 = 10.79$, df = 6, $p = 0.10$).

Lemming abundance, nest density and failure rate

At both nesting areas, goose nesting success was positively related to lemming abundance (Fig. 6A). However, differences emerged between nesting areas where geese used different nesting strategies (as shown by the significant interaction terms; Table 4). First, the relationship between lemming abundance and nesting success was steeper at Site-1 than at Site-2. Second, nest failure rate was inversely density-dependent at Site-2 (large colony) whereas no effect of nest density was detected at Site-1 (small colonies; Fig. 6B). At Site-1, inter-annual variations in nest success closely tracked the cyclic fluctuations in lemming population. The proportion of successful nests was 87.7% ($n = 349$), 42.4% ($n = 93$) and 16.2% ($n = 80$) during years of high (1993, 1996), intermediate (1994, 1997, 1998) and low (1995, 1999) lemming abundance, respectively (Contrasts:

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Table 2. Logistic model with inflection point testing the effect of distance from the nearest breeding owl on goose nesting success at Site-1 in 1993 and 1996 ($n = 337$). We used the inflection point (distance-550) associated with the best fitting model. The variable distance-550 was equal to the actual distance from the nearest owl for a nest located at ≤ 550 m and was set at a constant value of 550 m for nests located at > 550 m. Nest density and interaction terms were not significant and were dropped from the model.

Variables	df	β	SE	χ²	p
Intercept	1	2.27	0.46		
Year	1	1.31	0.37	12.02	<0.001
Distance-550	1	−0.0027	0.0011	6.19	0.01

$df = 1$, $p < 0.001$ in all cases). At Site-2, the combined effects of fluctuations in nest density and lemming abundance created a different pattern. Despite high lemming abundance, nesting success was lower in 1996 (61.4%, $n = 249$), a year of relatively low nest density, than during years with intermediate lemming abundance but high nest density (1994, 1997 and 1998; 76.8%, $n = 896$; $p < 0.001$). As in Site-1, nesting success was lowest during low lemming years (1995 and 1999; 29.4%, $n = 245$; $p < 0.001$).

Mean nest density was not linearly related to lemming index (Site-1: $r_s = 0.60$, $p > 0.15$, $n = 7$; Site-2: $r_s = 0.14$, $p > 0.50$, $n = 6$, see Table 1). Nonetheless, density was higher during the two peak lemming years at Site-1 (2.93 ± 0.14 nests ha^{-1}) compared to other years (1.22 ± 0.04 nests ha^{-1}; $t = -12.2$, df $= 444.3$, $p < 0.001$). The clustering of goose nests around owls mainly explains why density was higher during peak lemming years as mean density of goose nests located at > 550 m from owls (1.26 ± 0.05 nests ha^{-1}) was similar to density observed in other years ($t = -0.72$, df $= 284$, $p = 0.47$).

To eliminate the confounding effect of nesting association with owls in the relationship between lemming abundance and nest success at Site-1, we analysed data excluding nests ($n = 269$) in the estimated protective area of owls (< 550 m) during peak lemming years. In contrast to the model with all nests, the influence of lemming abundance on nesting success no longer differed between nesting areas (interaction nesting area × lemming index: $\beta = -0.31$, 95% CI: -0.81 to 0.16, $\chi^2 = 1.66$, df $= 1$, $p = 0.20$; dropped from the final model in Table 5; Fig. 6). Analyses using the overall density of nests at Site-1 or the density calculated only for nests located outside the protective area gave similar results. Therefore, the link between lemming and nest success was present in both nesting areas even after excluding the confounding positive effect of nesting association with owls in peak lemming years.

Discussion

The main finding of this study was that abundance of lemmings is closely associated with nest predation rate in arctic-nesting greater snow geese but that nesting strategies used by geese can affect this relationship. Other studies have also reported reduced failure rate on bird nests during peak lemming years but were unable to discriminate the confounding effects of varying predation pressure (APH) and association with birds of prey (NAH) (e.g. Syroechkovskiy et al. 1991, Underhill et al. 1993, Summers et al. 1994, Kostin and Mooij 1995, Spaans et al. 1998). In this study, we were able to assess these hypotheses independently.

Alternative Prey Hypothesis (APH)

Our results are in accordance with the prediction of APH that predation pressure on goose nests is low at peak lemming abundance and high during the low phase of the rodent cycle. This general pattern was observed at both high and low goose breeding densities. Correlation between bird nesting success and rodent densities have also been described for other species in northern ecosystems and taken as evidence in favour of the APH (Newton 1998).

Annual variations in predation pressure can result from both the numerical and functional responses of predators to lemming cycles. Arctic fox, the main goose nest predator, is probably the key predator leading to cyclic fluctuations in predation pressure. Foxes are
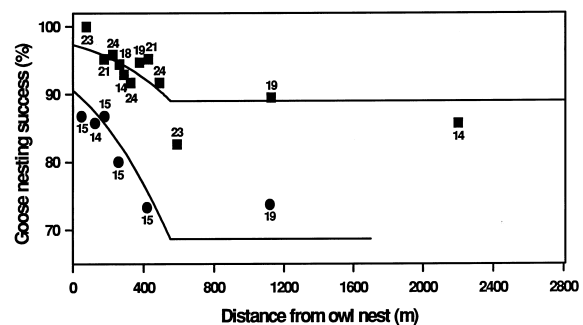

Fig. 5. Relationship between goose nesting success and distance from nearest owl nests at Site-1 during the two peak lemming years (1993, ■: 1996, ●). The regression curves (solid lines) were obtained with the best fit logistic model with an inflection point (inflection point = 550 m). To illustrate the adequacy of the model, each point represents proportion of successful nests grouped by distance interval (sample size is shown near each point).

Table 3. Ratio of observed/expected frequency of successful-successful (S-S) and failed-failed (F-F) pairs of nests used to test the hypothesis that the probability of a nest being depredated is independent from the fate of its neighbour. Values > 1 indicate higher than expected frequencies (i.e. the fate of a nest is linked to the fate of its nearest neighbour). P-values for Fisher's exact tests are indicated with asterisk (** $p<0.01$, *** $p<0.001$, otherwise $p>0.05$). The number of nests used for these analyses are shown in parenthesis for Site-1 and Site-2, respectively.

Year (n)	Site-1				Site-2			
	S-S		F-F		S-S		F-F	
1993 (231, –)	1.0		0.0[a]		[b]		[b]	
1994 (31, 287)	2.6	***	1.5		1.1	**	1.3	
1995 (68, 171)	1.7		1.0		1.0		0.8	
1996 (91, 239)	1.1	***	3.0		1.0		1.0	
1997 (24, 269)	1.0		1.0		1.0		0.9	
1998 (17, 314)	4.2		1.1		1.0		1.1	
1999 (5, 175)	–[c]		–[c]		1.2		1.0	

[a] Number of F-F observed in 1993 at Site-1 = 0 (expected = 1.3).
[b] No data available at Site-2 in 1993.
[c] Sample size too small to perform statistical analysis.

considered generalist predators but their breeding success and population dynamics are strongly affected by lemming populations where the species co-exist (Macpherson 1969, Angerbjörn et al. 1999). Foxes reproduce only once a year and their reproductive output is generally high when lemming are abundant and negligible when lemming populations crash (Tannerfeldt and Angerbjörn 1998). Thus, the numerical response of foxes to varying densities of lemmings will often have a 1-yr time lag (Angerbjörn et al. 1999). On the other hand, a diet shift (type III functional response, Holling 1959) is typical for generalist predators when their prey populations change. The potential of vertebrate predators to shift on alternative preys has been well demonstrated in northern ecosystems (e.g. Angelstam et al. 1984, Korpimäki et al. 1990, O'Donoghue et al. 1998). However, when bird breeding density is high, eggs could still be the primary prey of arctic foxes during the nesting period even if the rodent abundance is relatively high (Stickney 1991). Therefore, the relative impacts of the numerical and functional responses of predators to lemming cycles on bird egg predation still remain to be investigated.

Nesting Association Hypothesis (NAH)

Although our results support the Alternative Prey Hypothesis, they also show that nesting associations with birds of prey during peak lemming years (NAH) can enhance the positive link between lemming cycles and nest success. Nesting associations have often been reported, but are especially common among tundra birds. This might be due to the varying and sometimes intense predation pressure suffered by arctic-nesting birds

(Larsen and Grundetjern 1997). As predicted by the NAH, failure rate of nests located close to owl nests was lower than for nests located further away, even though nesting associations occurred in peak lemming years. The main explanation for this relationship is likely the protective influence of owls that chase preda-
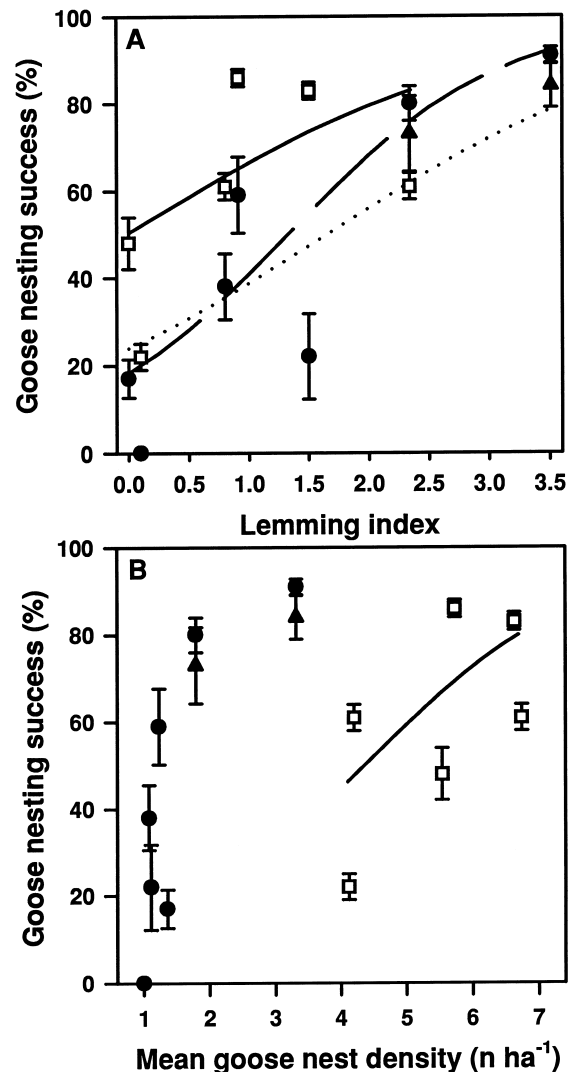

Fig. 6. Relationship between goose nesting success and (A) lemming density index (pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights) or (B) mean goose nest density at two nesting areas. To illustrate the adequacy of the model, annual nesting success (mean ± SE) are given for each area (Site-1, ●, from 1993 to 1999; Site-2, □, from 1994 to 1999; Site-1 excluding nests under the protective influence of owls in 1993 and 1996, ▲). Regression curves obtained with multiple logistic regression analyses are shown. Models either include all nests, solid line (Site-2) and long dash line (Site-1, $n = 1912$ in total), or exclude nests within the estimated protective influence of owls at Site-1 during the two peak lemming years, dotted line (in this model, regression lines at Site-2 remained almost the same; $n = 1643$ in total).

Table 4. Multiple logistic regression model testing the effect of nesting area, lemming abundance and mean nest density on goose nesting success from 1993 to 1999 ($n = 1912$ nests). Correlation between predicted and observed annual nesting success at a given nesting area was significant ($r_s = 0.89$, $p < 0.001$, $n = 13$). Interaction terms that were not significant were dropped from the model.

Variables	df	β	SE	χ^2	p
Intercept	1	−1.34	0.30		
Nesting area	1	−1.99	0.46	18.68	<0.0001
Lemming index	1	1.13	0.20	84.48	<0.0001
Mean nest density	1	−0.07	0.28	3.14	0.08
Area × Lemming index	1	−0.46	0.21	4.86	0.03
Area × Mean nest density	1	0.66	0.28	5.48	0.02

tors away from the vicinity of their nests (Litvin et al. 1985, Underhill et al. 1993, Tremblay et al. 1997). Our results obtained with artificial nests are the first experimental evidence supporting this hypothesis.

Because owl nests were at the centre of goose colonies (Lepage et al. 1996), the spatial distribution of goose nests could have affected their vulnerability (i.e. nests close to owls were in a central position at high density whereas those located further from owls were at the periphery at low density). However, we found no significant effect of nest density on the risk of predation around owls. Experiments with artificial nests also showed that 1) geese did not protect conspecific nests by defending their own nest surroundings and 2) foxes could easily reach and prey upon nests located in a dense colony. Thus, it seems that edge or density effects had little influence on nest predation rate around owl nests.

Litvin et al. (1985) reported that snowy owls could exclude foxes within a 200–300 m radius of their nests, and up to 500 m during years of high lemming abundance. Our estimation of the threshold protective distance around owl nests (550 m) using an objective criterion (inflection point logistic regression) is in accordance with these previous suggestions. Nesting near owls during peak lemming years probably entails little cost because owls do not prey on eggs and rarely on young birds (Lepage et al. 1996). However, when lemming availability decreases, nesting associations with lemming predators can be unreliable (Larsen and Grundetjern 1997) as young and adult ducks and geese could then become more susceptible to attacks by owls (Dorogoi 1990).

The impact of the positive nesting association with owls at the goose population level remains unknown, but it may be small. First, owls nested in our study area only in peak lemming years. Second, even in those years density of nesting owls was generally < 0.2 pairs per km² at our study area (Lepage et al. 1998), a density comparable to other arctic regions (Fitzgerald 1981). Thus, the size of the protective area and the low availability of breeding owls considerably limit the number of birds that can use this strategy. Moreover,

the timing and pattern of snowmelt are additional constraints that may limit the ability of arctic birds to take full advantage of nesting association with owls (Lepage et al. 1996).

Predation rate and nest density

We found that predation rate was inversely density-dependent at high breeding density. Annual variations in nest density were more likely a consequence of variations in the number of birds attempting to breed in the area than of variations in nest dispersion (see also Lepage et al. 1996). Climatic conditions on the breeding grounds are considered as a dominant factor affecting the breeding effort of arctic and sub-arctic nesting geese. When late snow-melt and low spring temperature prevail, the breeding effort is low (Barry 1962, Gauthier et al. 1996, Skinner et al. 1998). When predation rate is inversely density-dependent, a reduced breeding effort (hence, low nest density) due to poor spring weather conditions will thus lead to increased nest predation rate in colonial birds.

In colonies, the dilution effect (predators swamping) is probably the main mechanism causing inversely density-dependent nest predation rate (Wittenberger and Hunt 1985). Even if predators show a strong functional response to the availability of eggs, the number of eggs depredated will be restricted by the density of predators and thus explain why the proportion of eggs depredated is lower at high nest density (Newton 1998). Group defence and mutual vigilance are additional factors that may account for a reduced predation risk at high nest density (Wittenberger and Hunt 1985). However, our artificial nest experiments showed that geese could not efficiently protect a conspecific nest against foxes, although mutual protection could be more effective against avian predators. Because nest density is lower in late nesting years, other factors correlated with the timing of breeding, such as nest attentiveness by females, could contribute to high predation rate at low nest density. However, Poussart (1997) found no relationship between nest initiation date and nest attentiveness in greater snow geese.

Table 5. Multiple logistic regression model testing the effect of nesting area, lemming abundance and mean nest density on goose nesting success from 1993 to 1999 ($n = 1643$). Model excludes nests under the protective influence of breeding owls at Site-1 during the two peak lemming years. Correlation between predicted and observed annual proportion of successful nests at a given nesting area was significant ($r_s = 0.87$, $p = 0.001$, $n = 13$). Interaction terms that were not significant were dropped from the model.

Variables	df	β	SE	χ^2	p
Intercept	1	−1.16	0.32		
Nesting area	1	−2.24	0.50	20.33	<0.0001
Lemming index	1	0.70	0.08	90.33	<0.0001
Mean nest density	1	0.0009	0.20	9.26	0.002
Area × Mean nest density	1	0.59	0.21	7.35	0.007

Bird productivity, nest density and lemming cycles

Some authors have suggested that climatic conditions (Angelstam et al. 1985) and the breeding range of a species (van Impe 1996) could influence the relationship between small mammal population cycles and annual bird productivity. We showed that nesting strategies of birds is another important factor that can contribute to the different patterns of annual fluctuations observed in the breeding productivity of arctic nesting species.

For instance, the breeding productivity (percentage of first-year birds in the winter population) of several arctic-nesting waders and the brent geese (*Branta b. bernicla*) follows fairly regular three-year cycles and was associated to the lemming cycles (Summers and Underhill 1987, Summers et al. 1998). These species breed at low nest density and their eggs are highly vulnerable to arctic foxes (Sutton 1932 cited in Summers and Underhill 1987, Underhill et al. 1993, Spaans et al. 1998). A cyclic pattern in reproductive success was also reported in the white-fronted geese (*Anser a. albifrons*, van Impe 1996), a large body-size goose which can efficiently defend its nest against foxes but which also nests at low density (Syroechkovskiy et al. 1991, Rogacheva 1992). At low density, nest predation rate either increases with density of nests, particularly when birds are unable to defend their nests against predators (e.g. Hoi and Winkler 1994; see also Larivière and Messier 1998), or is density-independent (e.g. Niemuth and Boyce 1995). In these cases, annual variations in predation pressure could be the dominant factor generating oscillations in breeding productivity.

In greater snow geese, annual breeding productivity varies considerably (25-fold amplitude) but with no evidence of cyclic patterns (Gauthier et al. 1996, Reed et al. 1998). We showed that oscillations in snow geese nesting success were synchronised with lemming cycles only at low breeding density. For geese nesting at high density (large colony), nest failure rate was inversely density-dependent and annual variations in mean nest density were independent of lemming abundance. In such cases, factors affecting nest density dampened the effect of lemming cycles on nest predation rate and thus explain why the overall breeding productivity is not cyclic even though the predation pressure is still dependent on lemming abundance.

The synchrony in fluctuations of rodent populations over the whole breeding range of a species could also influence the breeding productivity at the population level (Angelstam et al. 1985). For instance, spatial synchrony in lemming population growth can disappear between sites separated by > 400 km, and cyclic patterns across the whole Palaearctic tundra are considered asynchronous (Erlinge et al. 1999). In greater snow geese, the latitudinal and longitudinal breeding range exceeds 1000 km over the Canadian arctic archipelago, and is broken up by many physical barriers such as mountain ranges, ice caps and sea channels (Reed et al. 1998). Consequently, lemming cycles and predation pressure may vary asynchronously throughout the breeding range. Therefore, we may not detect cyclic fluctuations in breeding productivity at the population level even if predation pressure and goose nesting success are locally driven by rodent cycles.

Conclusion

We suggest that varying predation pressure (APH) is the main mechanism linking lemming cycles and nest predation rate although nesting association with birds of prey (NAH) can further enhance the link at the local level. However, independent variations in breeding effort (hence nest density) could mask an otherwise cyclic pattern in bird productivity. Our results indicate that breeding strategies used by birds (the alternative prey) could modify the link and the synchrony between oscillations in avian reproductive success and rodent cycles.

References

Agresti, A. 1996. An introduction to categorical data analysis. – John Wiley and Sons.

Angelstam, P., Lindström, E. and Widén, P. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. – Oecologia 62: 199–208.

Angelstam, P., Lindström, E. and Widén, P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia – occurrence and distribution. – Holarct. Ecol. 8: 285–298.

Angerbjörn, A., Tannerfeldt, M. and Erlinge, S. 1999. Predator-prey relationships: arctic foxes and lemmings. – J. Anim. Ecol. 68: 34–49.

Bacon, D. W. and Watts, D. G. 1971. Estimating the transition between two intersecting straight lines. – Biometrika 58: 525–534.

Barry, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. – J. Wildl. Manage. 26: 19–26.

Beauvais, G. P. and Buskirk, S. W. 1999. Modifying estimates of sampling effort to account for sprung traps. – Wildl. Soc. Bull. 27: 39–43.

Berg, A. 1996. Predation on artificial, solitary and aggregated wader nests on farmland. – Oecologia 107: 343–346.

Bêty, J. and Gauthier, G. 2001. Effects of nest visits on predator activity and predation rate in a snow goose colony. – J. Field Ornithol. (in press).

Christensen, R. 1990. Log-linear models. – Springer-Verlag.

Dorogoi, I. V. 1990. Factors affecting communal nesting of Snowy Owl and Anseriforme on Wrangle Island. – Ornithologia 24: 26–33 (in Russian with English summary).

Erlinge, S., Danell, K., Frodin, P. et al. 1999. Asynchronous population dynamics of Siberian lemmings across the Palaearctic tundra. – Oecologia 119: 493–500.

Fitzgerald, B. M. 1981. Predatory birds and mammals. – In: Bliss, L. C., Heal, O. W. and Moore, J. J. (eds), Tundra ecosystem: a comparative analysis. Cambridge Univ. Press, pp. 485–508.

Gauthier, G., Rochefort, L. and Reed, A. 1996. The exploitation of wetland ecosystems by herbivores on Bylot Island. – Geosci. Can. 23: 253–259.

Hanski, I. and Korpimäki, E. 1995. Microtine rodent dynamics in the northern Europe: parameterized models for the predator-prey interaction. – Ecology 76: 840–850.

Hogstad, O. 1995. Do avian and mammalian nest predators select for different nest dispersion patterns of Fieldfares *Turdus pilaris*? A 15-year study. – Ibis 137: 484–489.

Hoi, H. and Winkler, H. 1994. Predation on nests: a case of apparent competition. – Oecologia 98: 436–440.

Holling, C. S. 1959. The component of predation as revealed by a study of small-mammal predation of the European pine sawfly. – Can. Entomol. 91: 293–320.

Hussell, D. J. T. and Holroyd, G. L. 1974. Birds of the Truelove Lowland and adjacent areas of northeastern Devon Island, NWT. – Can. Field-Nat. 88: 341–344.

Korpimäki, E., Huhtala, K. and Sulkava, S. 1990. Does the year-to-year variation in the diet of eagle and Ural owls support the alternative prey hypothesis? – Oikos 58: 47–54.

Kostin, I. O. and Mooij, J. H. 1995. Influence of weather conditions and other factors on the reproductive cycle of Red-Breasted Geese *Branta ruficollis* on the Taymyr Peninsula. – Wildfowl 46: 45–54.

Krebs, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. – Arct. Inst. N. Am. Tech. Pap. 15: 1–104.

Larivière, S. and Messier, F. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? – Oikos 83: 12–20.

Lack, D. 1954. The natural regulation of animal numbers. – Oxford Univ. Press.

Larsen, T. and Grundetjern, S. 1997. Optimal choice of neighbour: predator protection among tundra birds. – J. Avian Biol. 28: 303–308.

Lepage, D., Gauthier, G. and Reed, A. 1996. Breeding-site infidelity in greater snow geese: a consequence of constraints on laying date? – Can. J. Zool. 74: 1866–1875.

Lepage, D., Nettleship, D. N. and Reed, A. 1998. Birds of Bylot Island and adjacent Baffin Island, Northwest Territories, Canada, 1979 to 1997. – Arctic 51: 125–141.

Lepage, D., Desrochers, A. and Gauthier, G. 1999. Seasonal decline of growth and fledging success in snow geese *Anser caerulescens*: an effect of date or parental quality? – J. Avian Biol. 30: 72–78.

Lepage, D., Gauthier, G. and Menu, S. 2000. Reproductive consequence of egg-laying decisions in snow geese. – J. Anim. Ecol. 69: 414–427.

Litvin, K. E., Pulyaev, A. I. and Syroechkovsky, E. V. 1985. Colonies of the Snow Goose (*Anser caerulescens*), Brent Goose (*Branta bernicla*) and Eider (*Somateria mollissima*) near the Snowy Owl (*Nyctea scandiaca*) nests on the Wrangle Island. – Zool. Zh. 64: 1012–1023 (in Russian with English summary).

Macpherson, A. H. 1969. The dynamics of Canadian arctic fox populations. – Can. Wildl. Serv. Rep. Ser. 8.

Maher, W. J. 1970. Ecology of the long-tailed jaeger at Lake Hazen, Ellesmere Island. – Arctic 23: 112–129.

Martin, A. P. and Baird, D. 1988. Lemming cycles – which Palearctic migrants are affected. – Bird Study 35: 143–145.

Newton, I. 1998. Population limitation in birds. – Academic Press.

Niemuth, N. D. and Boyce, M. S. 1995. Spatial and temporal patterns of predation of simulated sage grouse nests at high and low nest densities: an experimental study. – Can. J. Zool. 73: 819–825.

O'Donoghue, M., Boutin, S., Krebs, C. J. et al. 1998. Behavioural responses of coyotes and lynx to the snowshoe hare cycle. – Oikos 82: 169–183.

Potapov, E. R. 1997. What determines the population density and reproductive success of rough-legged buzzards, *Buteo lagopus*, in the Siberian tundra? – Oikos 72: 362–376.

Poussart, C. 1997. Patron d'incubation et régime thermique des oeufs chez la Grande oie des neiges. – MSc thesis, dépt. biologie, Univ. Laval.

Poussart, C., Larochelle, J. and Gauthier, G. 2000. The thermal regime of eggs during laying and incubation in greater snow geese. – Condor 102: 292–300.

Reed, A., Hughes, J. R. and Gauthier, G. 1995. Incubation behavior and body mass of female Greater Snow Geese. – Condor 97: 993–1001.

Reed, A., Giroux, J.-F. and Gauthier, G. 1998. Population size, productivity, harvest and distribution. – In: Batt, B. D. J. (ed.), The Greater Snow Geese: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, pp. 5–31.

Rogacheva, E. V. 1992. The birds of central Siberia. – Husum Druck, Husum.

SAS Institute 1996. SAS/STAT user's guide. Release 6.12. – SAS Inst., Inc., Cary, NC.

Schmidt, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. – Oikos 85: 151–160.

Shank, C. C. 1993. The Northwest Territories small mammal survey: 1990–1992. – Dept of Renewable Resources, Government of the Northwest Territories, Yellowknife, NWT, Manuscript Report No 72.

Siegel, S. and Castellan, N. J. Jr. 1988. Non-parametric statistics for the behavioral sciences. 2nd ed. – McGraw-Hill.

Sittler, B. 1995. Response of stoats (*Mustela ermina*) to fluctuating lemming (*Dicrostonyx groenlendicus*) population in North East Greenland: preliminary results from a long-term study. – Ann. Zool. Fenn. 32: 79–92.

Skinner, W. R., Jefferies, R. L., Carleton, T. J. et al. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. – Glob. Change Biol. 4: 3–16.

Spaans, B., Blijleven, H. J., Popov, I. U. et al. 1998. Dark-bellied Brent Geese *Branta bernicla bernicla* forego breeding when Arctic Foxes *Alopex lagopus* are present during nest initiation. – Ardea 86: 11–20.

Stickney, A. 1991. Seasonal patterns of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. – Can. J. Zool. 69: 2853–2859.

Summers, R. W. 1986. Breeding production of Dark-bellied Brent Geese *Branta bernicla bernicla* in relation to lemming cycles. – Bird Study 33: 105–108.

Summers, R. W. and Underhill, L. G. 1987. Factors related to breeding production of Brent Geese *Branta b bernicla* and waders (Charadrii) on the Taimyr Peninsula. – Bird Study 34: 161–171.

Summers, R. W., Underhill, L. G., Syroechkovski, E. E., Jr. et al. 1994. The breeding biology of Dark-bellied Brent Geese *Branta b. bernicla* and King Eiders *Somateria spectabilis* on the northeastern Taimyr Peninsula, especially in relation to Snowy Owl *Nyctea scandiaca* nests. – Wildfowl 45: 110–118.

Summers, R. W., Underhill, L. G. and Syroechkovski, E. E. 1998. The breeding productivity of dark-bellied brent geese and curlew sandpipers in relation to changes in the numbers of arctic foxes and lemmings on the Taimyr Peninsula, Siberia. – Ecography 21: 573–580.

Syroechkovskiy, Y. V., Litvin, K. E. and Ebbinge, B. S. 1991. Breeding success of Geese and Swans on Vaygach Island (URSS) during 1986–1988; interplay of weather and Arctic Fox predation. – Ardea 79: 373–382.

Tannerfeldt, M. and Angerbjörn, A. 1998. Fluctuating resources and the evolution of litter size in the arctic fox. – Oikos 83: 545–559.

Tremblay, J.-P., Gauthier, G., Lepage, D. and Desrochers, A. 1997. Factors affecting nesting success in greater snow geese: effects of habitats and association with snowy owls. – Wilson Bull. 109: 449–461.

Underhill, L. G., Prys-Jones, R. P., Syroechkovski, E. E., Jr. et al. 1993. Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. – Ibis 135: 277–292.

Valkama, J., Currie, D. and Korpimäki, E. 1999. Differences in the intensity of nest predation in the curlew *Numenius arquata*: a consequence of land use and predator densities? – Ecoscience 6: 497–504.

van Impe, J. 1996. Long-term reproductive performance in White-fronted Geese *Anser a. albifrons* and Tundra Bean Geese *A. fabalis rossicus* wintering in Zeeland (The Netherlands). – Bird Study 43: 280–289.

Wiklund, C. G., Kjellén, N. and Isakson, E. 1998. Mechanisms determining the spatial distribution of microtine predators on the Arctic tundra. – J. Anim. Ecol. 67: 91–98.

Wilson, D. J. 1999. Effects of predation on the population dynamics of lemmings and loss of goose nests. – PhD thesis, Univ. of British Columbia, Vancouver.

Wittenberger, J. F. and Hunt, G. L. Jr. 1985. The adaptive significance of coloniality in birds. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds), Avian biology, vol. 8. Academic Press, pp. 2–79.