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Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory Arctic herbivorous bird

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Several driving forces can affect recruitment rates in bird populations. However, our understanding of climate-induced effects or bottom–up vs top–down biological processes on breeding productivity typically comes from small-scale studies, and their relative importance is rarely investigated at the population level. Using a 31-year time series, we examined the effects of selected environmental parameters on the annual productivity of a key Arctic herbivore, the greater snow goose *Anser caerulescens atlanticus*. We determined the extent to which breeding productivity, defined as the percentage of juveniles in the fall population, was affected by 1) climatic conditions, 2) fluctuations in predation pressure caused by small rodent oscillations, and 3) population size. Moreover, we took advantage of an unplanned large-scale manipulation (i.e. management action) to examine the potential non-lethal carry-over effects caused by disturbance on spring staging sites. The most parsimonious model explained 66% of the annual variation in goose productivity. The spring North Atlantic Oscillation and Arctic snow depth were the primary climatic parameters inversely affecting the production of juveniles, likely through bottom–up processes. Indirect trophic interactions generated by fluctuations in lemming abundance explained 18% of the variation in goose productivity (positive relationship). Mean temperature during brood-rearing and disturbance on staging sites (carry-over effects) were the other important factors affecting population recruitment. We observed a strong population increase, and found no evidence of density-dependent effects. Spatially restricted studies can identify factors linking environmental parameters to local bird reproduction but if these factors do not act synchronously over the species range, they may fail to identify the relative importance of mechanisms driving large-scale population dynamics.

Identifying and understanding what factors drive animal population dynamics is a central and difficult ecological question because a large number of parameters can interact. Since we cannot manipulate environmental parameters on a large scale, controlled experiments are virtually impossible when studying their effects on vertebrate populations. Most progress in this field is achieved by observational science or natural (unplanned) experiments, and the use of a mechanistic-based approach to analyse long-term data series is essential to understanding the interactions between climatic forcing, and biotic and abiotic factors (Jenouvrier et al. 2005, Krebs and Berteaux 2006).

Empirical evidence suggests that climate, indirect trophic interactions mediated by predators and density-dependent effects are all potential forces that can affect recruitment rate of terrestrial arctic-nesting birds. Indeed, their reproductive success appears strongly affected by climatic conditions early in the breeding season, typically via changes in food and nest site availability (bottom–up processes; Madsen et al. 2007). Fluctuations in small mammal populations in the tundra can also indirectly affect the breeding success of some bird species through indirect interactions mediated by shared predators (top–down processes; Ims and Fuglei 2005). Moreover, density-dependent effects on key reproductive components (e.g. clutch size, juvenile growth and survival) have been reported in populations that have increased considerably, such as those of several arctic-nesting goose species (Cooch et al. 1989, Williams et al. 1993). Finally, events occurring outside the breeding season can also play an important role (Norris and Taylor 2006). For instance, changes in nutrient reserves acquired during migration can affect the breeding performance of Arctic migratory birds (Alisauskas 2002). Although these potential driving forces of recruitment rate are well known, our understanding typically comes from small-scale studies and their relative importance (and interactions) are rarely investigated at the population level.

Using a 31-year time series, we investigated the relative effect of several environmental factors on the annual breeding productivity of a key High-Arctic herbivore, the greater snow goose *Anser caerulescens atlanticus*. Previous studies on this species have highlighted the importance of climatic conditions on numerous reproductive components. Spring climatic conditions, for instance, are considered a major factor affecting goose breeding propensity, an important determinant of annual productivity (Reed et al. 2004, Dickey et al. 2008). Other studies have also looked at the importance of indirect effects linking lemming population cycles to predation rates (Bêty et al. 2002) and density-dependent effects on body size (Reed and Plante 1997). As proposed by Krebs and Berteaux (2006), we based our study on mechanisms previously proposed or documented at small spatial-scales to investigate the relative effects of several potential driving forces at the population level. Our main goal was to examine to what extent annual breeding productivity (percentage of juveniles in the post-breeding population) was affected by 1) climatic conditions at different periods of the breeding cycle (analysed through variations of large-scale phenomena and local weather parameters), and 2) fluctuations in predation pressure caused by rodent population oscillations. By taking advantage of an unplanned large-scale manipulation (via management actions), we also investigated the impact of human disturbance on the main staging sites, as it can generate carry-over effects on goose fecundity (Mainguy et al. 2002, Reed et al. 2004). Finally, we examined if the recent substantial population increase, which is associated with higher densities on the breeding areas (Reed et al. 2002, Gauthier et al. 2005), generated negative feedback on population breeding productivity.

Material and methods

Study population

The greater snow goose breeds principally in the eastern Canadian High-Arctic, from northern Baffin Island to northern Ellesmere Island (Gauthier et al. 2005). In fall, birds migrate from the Arctic to their main staging areas in southeastern Canada (Québec) and then to their wintering grounds on the mid-Atlantic coast of the United States. The largest known breeding colony (> 14% of the entire adult breeding population) is located on Bylot Island, Sirmilik National Park of Canada, Nunavut Territory, Canada (73°08’N, 80°00’W; Reed et al. 2002; Fig. 1).

The greater snow goose is a strict herbivore and nest initiation occurs in early June (Lepage et al. 2000). Geese are single-brooded, do not renest after clutch failure, and those nesting earlier achieve the highest reproductive success (lay more eggs and have higher gosling survival; Lepage et al. 2000). Nest desertion is rare (estimated at < 2%) and predation is the main cause of nest failure (Bêty et al. 2001).

Study design and selected environmental factors

We estimated the annual breeding productivity of the population using the percentage of juveniles (i.e. young of the year, which are easily distinguishable from adults ⩾1 year of age on the basis of plumage colouration) in the fall population. Age ratio counts of flocks were conducted at several sites in southern Québec (47°04’N, 70°47’W, Fig. 1), their main fall staging area, following Lynch and Singleton (1964). At the beginning of October, only small numbers of geese, mainly non-breeding adults, are present in staging areas. Numbers then build up rapidly as the bulk of family groups and other adults arrive, and large numbers are present until the end of October. Field surveys to determine flock age ratios were collected by the Canadian Wildlife Service from 1976 to 2006, focusing on the first two to three weeks of October to ensure sampling of both breeding and non-breeding segments of the population. This early timing, which was consistent across years, minimized possible underestimation of productivity resulting from hunting, which removes more vulnerable juveniles at a higher rate than adults (Calvert et al. 2005). The sampling effort was adapted to changes in goose distribution (i.e. new areas used by geese) and increased population size (number of birds counted each year increased from about 10 000 in mid 1970s to 25 000–30 000 in recent years). Our productivity index is strongly correlated with the juvenile:adult ratio at the end of the breeding season on Bylot Island (1990–2007: r = 0.83; Gauthier unpubl.) and thus reflects changes in the average number of juveniles produced per adult.

Figure 1. Map showing the breeding grounds (enclosed by a dotted line and including the locations of nesting colonies in dark grey), the main staging areas and the wintering ground of the greater snow goose.

The main potential mechanisms linking the studied environmental factors to annual breeding productivity are summarized in Fig. 2, and reflect bottom–up and top–down forces, as well as carry-over and density-dependent effects. Details concerning selected parameters and associated processes are outlined below.

Climatic effects

It has been shown that local climatic conditions encountered during the breeding season have strong and variable influences on several components of reproductive success (Table 1). Based on previous studies, we thus separated the breeding cycle into five time periods in order to investigate the relative impacts of climatic conditions on population productivity (Table 2). We chose climatic variables that were previously linked with components of goose reproductive success, and we formulated specific hypotheses related to annual productivity (Table 1). Variation through time of climatic effects can be captured by local measures of weather on the main goose breeding site or by large-scale climatic indices, which may better represent conditions met by birds over their larger breeding range (both categories of variables appear in Table 1).

The North Atlantic Oscillation (NAO) is a major source of atmospheric mass balance measured as the mean deviation in average sea level pressure between the subarctic and subtropical Atlantic (Hurrell 1995). This climatic phenomenon is sometimes described as a regional manifestation of the Arctic Oscillation (AO; Thompson and Wallace 1998). By influencing the speed and direction of westerly surface winds across the North Atlantic, the NAO has an impact on local weather in the Arctic (Hurrell et al. 2003). Although it is commonly viewed as a winter phenomenon, recent atmospheric pressure reductions have also been observed during spring, summer and fall months but with less vigorous variation (Hurrell et al. 2003). We obtained daily values of the NAO and AO indices from the Climate Prediction Center of the National Weather Service (<www.cpc.ncep.noaa.gov>).

From 1994 to 2006, we used local climatic data acquired with an automated weather station installed 20 m above sea level on the main greater snow goose breeding site, Bylot Island. Mean temperatures on Bylot Island are strongly correlated with those recorded in eastern High-Arctic communities (e.g. spring mean temperature in Resolute Bay or Clyde River: $r > 0.70$). Air temperature was measured 2 m above ground using a shielded temperature probe and mean hourly values were recorded. From these data, we calculated the mean temperatures for the selected periods (Table 2). We recorded total daily rainfall (mm) manually from 3 June to 15 August using a rain gauge. We visually estimated the percentage of snow cover on Bylot Island on 5 June each year and measured snow depth (cm) at 50 stations along two 250-m transects at two day intervals during snow-melt. We used data from the Environment Canada weather station located at the Pond Inlet airport, approximately 60 km from the Bylot Island goose colony, to cover the period preceding the installation of the weather station on Bylot Island. The weather data from the two stations were highly correlated (Table A1 in Appendix 1). Nevertheless, data recorded on Bylot Island are better to predict key goose reproductive parameters (such as timing of breeding; Dickey et al. 2008). Predictive equations were thus used to estimate climatic parameters on Bylot Island for the period 1976–1993. Because Pond Inlet snow cover was not available, we used mean daily snow depth (1 to 13 June) as snow condition index. Snow cover and snow depth data from Bylot Island were positively correlated ($r = 0.64$, $p = 0.006$, $n = 17$). No data were available from either Bylot or Pond Inlet for the year 1994 and this year was not considered in the analyses.

To estimate climatic conditions during the goose fall migration, we used local mean temperature recorded at the Environment Canada weather station located in Cape Dorset (64°13’N, 76°31W; Fig. 1). This community is located along the first leg of the migration route, where climatic conditions seem to affect survival of juveniles (Menu et al. 2005).

Predation pressure effects

Annual variation in predation pressure on geese (mostly eggs and goslings) is mainly due to complex interactions between arctic foxes *Vulpes lagopus*, parasitic jaegers *Stercorarius parasiticus* and lemmings *Lemmus sibiricus* and *Dicrostonyx groenlandicus*. In years of low lemming abundance,

Table 1. Potential climatic effects (variables and mechanisms documented in previous studies; see references in footnote) on the annual breeding productivity of the greater snow goose population according to different time periods of their Arctic breeding cycle (Table 2). The right column details hypotheses.

Periods	Variables	Mechanisms	Hypotheses
Spring	temperature snow cover NAO/AO*	influence breeding propensity[1,3], laying date[2,3] and gosling growth[3] mostly through food availability	(A) early spring (warm temperature and low snow cover) increases food availability and is thus positively associated with breeding productivity (linear relationship) (B) very early spring causes a mismatch between peak food quality and hatch date, reducing breeding productivity (quadratic relationship)
Early summer	precipitations	influence egg predation rate by affecting water availability and distance traveled from the nest by females during incubation recesses[3,4]	(C) high precipitation increases water availability during incubation and is positively associated with breeding productivity
Mid summer	temperature NAO/AO*	influence gosling survival and growth by affecting costs of thermoregulation, exposure to cold and food availability[3]	(D) higher temperatures decrease costs of thermoregulation, reduce exposure to cold temperatures and increase the availability of food, and are thus positively associated with breeding productivity
Late summer and fall	temperature NAO/AO*	influence juvenile survival through food availability[5]	(E) higher temperatures extend the period of food availability in late summer and are thus positively associated with breeding productivity

*Previous studies looked specifically for the effects of Arctic Oscillation (AO). We used the North Atlantic Oscillation Index (NAOI) in this study.

[1]Reed et al. 2004, [2]Bêty et al. 2003, [3]Dickey et al. 2008, [4]Lecomte et al. 2009, [5]Menu et al. 2005.

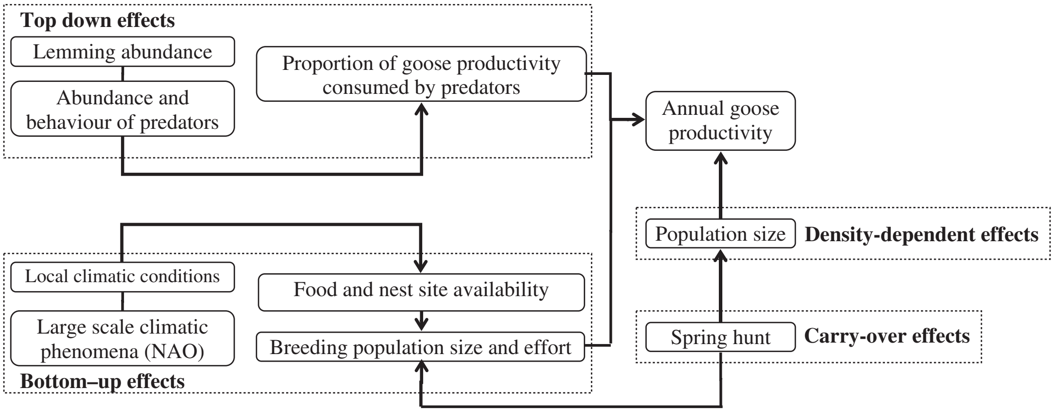

Figure 2. Flow diagram summarizing the main mechanisms that are likely to link annual greater snow goose breeding productivity (% of juveniles in fall flock) and various environmental factors, including climatic conditions (mainly through bottom–up effects; see mechanisms and complete list of potential effects in Table 1), fluctuations in predation pressure caused by lemmings cycles, population size and spring hunt on the main staging areas.

predators partially switch prey and focus more on goose eggs (Bêty et al. 2002). Arctic fox also show a reproductive numerical response to rodent densities, whereas parasitic jaegers appear to show an aggregative numerical response (more abundant around goose colonies in low lemming years; Bêty et al. 2002). Overall, direct observations conducted on the main goose breeding sites indicated that lemming abundance is a good proxy of predation pressure on geese, as it influences both the numerical and behavioural responses of the two main predators (Bêty et al. 2001). We thus expected a positive association between lemming abundance and goose productivity.

An index of lemming abundance on Bylot Island was obtained in July from 1994 to 2006 with snap-trap censuses and in 1993 with a winter lemming nest survey conducted at the main goose brood-rearing area (Bêty et al. 2002). From 1997 to 2006 a second lemming site located in the main nesting colony was monitored (30 km south of the first site; Gruyer et al. 2008). When available, we used mean abundance from both trapping sites. Lemming abundance index was calculated as the number of lemmings trapped per 100 trap-nights. Overall, this index encompasses about 1000 trap-nights per year and is adequate to track trends in lemming abundance at a regional scale (Gauthier et al. 2004). Lemming population fluctuations typically followed a three to four-year cycle on Bylot Island (Gruyer et al. 2008) and geographical synchrony is relatively high in the eastern Canadian Arctic (Krebs et al. 2002).

Periodic irruptions of certain raptors in temperate areas during winter are believed to reflect population cycles of their northern prey, small mammals (Cheveau et al. 2004). To estimate lemming abundance prior to 1993, we used the Christmas Bird Count (CBC) of snowy owls from the National Audubon Society (<www.audubon.org/bird/cbc/>). We constructed a predictive equation linking lemming abundance on Bylot Island to the number of snowy owls observed in Manitoba, Ontario and Québec over the period 1993–2005 (lemming index = $-0.310 + 60.90 \times$ snowy owl CBC index; $R^2 = 0.54$, $n = 13$, $p = 0.004$). In our analyses, we used the annual lemming index derived from this equation for the period 1976–1992.

Carry-over effects

From 1999 to 2006, a special spring hunting season was instated in the main goose staging area in southern Québec to control the growth of the population (Fig. 1). This management action generated disturbance and negatively affected accumulation of pre-migration body reserves (Féret et al. 2003) and, consequently, negatively affected some goose reproductive parameters (breeding propensity, laying date and clutch size; Mainguy et al. 2002, Bêty et al. 2003). We thus predicted a negative effect of the spring hunt on goose productivity.

Density-dependent effects

The greater snow goose population has been surveyed every spring on the main staging areas since 1965, mainly by the

Table 2. Definition of the selected time periods of the greater snow goose breeding cycle used for statistical analyses.

Periods (label)	Date	Stage
Spring (sp)	20 May to 20 June	arrival and egg-laying
Early summer (es)	21 June to 15 July	incubation and hatching
Mid summer (ms)	16 July to 15 August	brood-rearing
Late summer (ls)	16 to 31 August	fledging and early post-fledging
Fall (f)	1 to 30 September	migration (northern regions)*

*The complete migration period is longer but we only considered the early migration over the northern region because a large amount of migration mortality occurs shortly after fledging or at the beginning of fall migration (Menu et al. 2005).

Canadian Wildlife Service using photo inventory (Béchet et al. 2004). A small proportion of the flocks are missed during the survey and the method generates a reliable estimate of population size ($CV < 11\%$; Béchet et al. 2004). The population has increased considerably over the study period (Results) in part due to additional food supplies associated with agricultural lands on wintering and staging areas (Menu et al. 2002, Gauthier et al. 2005). This resulted in higher goose densities on staging and breeding areas (Reed et al. 2002). Per capita reduction in resources on the breeding grounds was identified as the main cause of recent declines in body size and condition of juveniles (Reed and Plante 1997). These declines can negatively affect survival of juveniles during the fall migration (Menu et al. 2005). We thus predicted a negative effect of population size on goose productivity.

Data analyses

Although the NAO and AO are the same physical entity and are highly correlated (Pearson correlation, $r = 0.95$, $p < 0.001$; Thompson and Wallace 1998), the NAO index (NAOI) was consistently more strongly associated with local parameters than the AO index. We therefore used the NAOI in subsequent analyses. When NAOI and local temperatures were correlated, we used them in different statistical models in order to avoid multicollinearity.

We used spectral analyses (Proc SPECTRA; SAS Inst. 2002–2003) to determine if annual breeding productivity followed regular cycles. We used the Fisher Kappa statistic (k) to test the null hypothesis of no cycle. We used simple linear regression analysis to estimate the effect of the annual goose productivity on population dynamics (population growth rate, r). We used annual estimates of spring population size (N_t) to calculate annual growth rate: $r = \ln(N_{t+1}) - \ln(_{N_t})$.

We used multiple linear regression analyses (Proc GLM: SAS Inst. 2002–2003) to examine the effects of various explanatory variables on goose breeding productivity. In the models we included climatic variables calculated for specific time periods (Table 1) and an a priori list of candidate models that was selected based on our predictions regarding the effects of climatic conditions, trophic interactions, density dependence and carry-over effects. We used square terms to investigate potential non-linear effects (NAOI and snow depth variables). Due to sample size constraints and to avoid data mining, we tested for only one interaction (spring climatic conditions and lemming abundance) and all possible combinations of variables were not tested. The Akaike information criterion adjusted for small sample size (AICc) and Akaike weights were used to select the most parsimonious general linear model. The model with the lowest AICc value was considered to be the most parsimonious, and those with differences of < 2 AICc units were considered well supported by the data (Burnham and Anderson 2002). We used model averaging (multimodel inference) to estimate parameters as it reduces bias and increases precision (Burnham and Anderson 2002). The individual contribution of independent variables entered in the most parsimonious model, while controlling for the effect of other variables, was depicted in partial residual plots. Inspection of residuals indicated no violation of the assumptions of normality, homogeneity of variance or independence (time lag of 1 to 7 years: $r < 0.40$, $p > 0.05$; Proc ARIMA: SAS Inst. 2002–2003). Data transformation was not required (even if the response variable was a percentage). We also verified correlations among all variables included in any given model; no correlation was higher than 0.50. All analyses were run in software SAS 9.1 (SAS Inst. 2002–2003).

Results

Relation between local and large-scale climatic variables

Mean spring temperature (20 May to 20 June) recorded on the main breeding site (Bylot Island) was negatively correlated with the spring NAOI (1976 to 2006: Pearson correlation, $r = -0.58$, $p = 0.002$, $n = 30$) but no association was found between local spring snow depth and NAOI ($r = 0.20$, $p = 0.28$, $n = 30$). Although slightly weaker, negative correlations between the NAOI and local mean temperatures during the mid and late summer were also found ($r = -0.42$, $p = 0.02$, $n = 30$ and $r = -0.37$, $p = 0.04$, $n = 30$, respectively). Finally, the fall NAOI was negatively associated with mean fall temperature at Cape Dorset ($r = -0.61$, $p < 0.001$, $n = 30$). Overall, these results indicate that positive NAOI values were associated with cold temperatures on the goose breeding grounds and the northern part of the migration route. Therefore, NAOI values were expected to be negatively related to goose productivity (Table 1).

Annual breeding productivity

Breeding productivity of geese showed very strong annual variation, ranging from 2% in 1999 to 48% in 1993 (average = 24.2%, SD = 12.1, n = 31; Fig. 3c). The annual breeding productivity was significantly related to the annual population growth rate (r) and explained 27% of its variation ($r = -0.102 + 0.007 \times$ proportion of juveniles; $n = 30$, $R^2 = 0.27$, $p = 0.003$). Thus, a 10% increase in productivity raised the population growth rate by 0.07 (95% CI: 0.02–0.11).

The models selected to explain annual variation in breeding productivity are shown in Table 3 (see Table A2 in Appendix 1 for a complete list). The most parsimonious model accounted for 66% of the variation in goose productivity but four other models provided a similar fit to the data ($\Delta AICc < 2$). Below, we separately present the different effects included in the preferred models.

Climatic effects

Spring climatic conditions in the Arctic were the dominant factor affecting breeding productivity of geese (spring NAOI, partial $R^2 = 0.17$; spring snow depth, partial $R^2 = 0.12$). Positive spring NAOI (i.e. low temperature) and high spring snow depth were associated with low breeding productivity (Fig. 3a). Mid-summer local temperature was the other climatic parameter present in the most parsimonious model, explaining 11% of the variation in breeding productivity (Table 3, Fig. 3a). The method used to obtain snow depth and mean temperatures changed part way through the study (Methods) but the slopes of the relationship between these variables and breeding productivity did not differ between the two periods (all $p > 0.75$; Fig. 3). There was little evidence that negative fall NAOI leads to a reduction in breeding productivity (Table 3). As negative fall NAOI values are associated with warmer temperatures along the migratory route, we expected to find the opposite (Table 1). However, this predictor explained a very small proportion of the variation in goose productivity (partial $R^2 = 0.04$).

We found weak evidence for a quadratic effect of spring NAOI on breeding productivity (Table 3; partial $R^2 = 0.03$). Although the effect was in the direction predicted (the slope of the squared term was negative), high spring temperatures (i.e. extremely negative NAOI) observed over the study period did not generate noticeable negative effect on annual goose productivity (Fig. 3). Finally, productivity was apparently not influenced by the amount of precipitation during the incubation and hatching periods. The hypothesis that precipitation reduces nest predation rates and hence increases breeding productivity was therefore not supported at the population level.

Predation pressure effects

No cyclic pattern in goose breeding productivity was detected ($k > 2.08$, $p > 0.39$). However, large annual fluctuations in lemming abundance positively influenced goose productivity and explained 18% of the annual variation (Table 3, Fig. 3b). We found weak evidence for an interaction between spring NAOI and lemming abundance (interaction term included in three of the ten preferred models: $\Delta AICc > 2.31$, Table A2 in Appendix 1). Variation in lemming abundance tended to have a minor effect on goose breeding productivity when spring climatic conditions were unfavourable for reproduction (i.e. cold temperatures; interaction term slope parameter ranging from –4.6 to –6.8, $0.09 < p < 0.19$).

Snowy owl data from the Christmas Bird Count were used to estimate lemming abundance from 1976 to 1992, while trapping was used from 1993 to 2006. Since climatic conditions could also influence owl reproduction and survival, and hence winter counts, this could generate an overestimation of the genuine effect of lemmings on goose productivity. However, because we found similar results when restricting the analyses to the 13-year time series when lemming index was measured directly (lemming abundance, partial $R^2 > 25\%$), we are confident that the observed lemming-goose relationship mostly reflects variation in predation pressure. Moreover, the slope of the relationship between lemming index and goose breeding productivity was not affected by the method used to track rodent oscillations (difference between slopes ± SE = -1.1 ± 3.4).

Carry-over and density-dependent effects

The implementation of spring hunting on the main goose staging site from 1999 to 2006 reduced their breeding productivity by 7% on average, and the carry-over effects caused by this human-induced disturbance was retained in the most parsimonious model (Table 3, Fig. 3d). Finally, despite the strong population increase over the study period (Fig. 3e), we found no evidence of density-dependent effects ($\Delta AICc > 2.7$, $\beta = -2.5$, $SE = 2.7$, $p = 0.38$, partial $R^2 = 0.02$).

Discussion

Greater snow goose breeding productivity is highly variable among years and we showed that it significantly affected the annual population growth rate. Although hunting pressure has considerable impact on a heavily hunted species like snow geese (Menu et al. 2002), it also illustrates the importance of environmentally-induced changes in recruitment on population growth rates in long lived species breeding in harsh and variable environments (Gaillard et al. 1998, Sæther et al. 2004).

Our approach, which relied on mechanisms identified in small-scale studies, provides evidence for the strong influence of climate, indirect trophic interactions and non-lethal carry-over effects on the population breeding productivity of a key High-Arctic herbivore. While the effects of climatic conditions most likely reflect bottom–up processes (through food availability), indirect trophic interactions with small rodents reflect top–down processes via shared predators. Estimating

Table 3. (a) Variables, sign of the effect, number of estimated parameters (k), deviance, ΔAICc, Akaike weights and proportion of variation explained by the five most parsimonious candidate models relating environmental factors to annual breeding productivity (% of juveniles in the fall population between 1976 and 2006) in greater snow geese. (b) Model-averaged parameter estimate and unconditional standard error (SE).

(a) Selected models

Variables	k	Deviance	Δ AICc	ωi	R^2
-NAO_sp, –snow, +temp_ms, +lem, –hunt	7	115.7	0.00	0.15	0.66
-NAO_sp, –snow, +temp_ms, +lem, –hunt, +NAO_f	8	112.4	0.48	0.12	0.69
-NAO_sp, –snow, +temp_ms, +lem	6	120.5	1.32	0.08	0.60
-NAO_sp, –snow, +temp_ms, +lem, –hunt, –NAO^2_sp	8	113.4	1.44	0.07	0.68
-NAO_sp, –snow, +lem	5	124.1	1.84	0.06	0.55
Null	2	147.8	17.42	0.00	0.00

(b) Parameter	NAO_sp	NAO^2_sp	NAO_f	snow	temp_ms	lem	hunt	Intercept
β	–9.7*	–5.9	5.0	–0.46*	5.0*	5.8*	–7.0*	–3.2
SE	3.1	4.4	3.0	0.18	2.2	1.7	3.4	15.8

* = $p < 0.05$; NAO_sp = spring NAOI, snow = spring snow depth, temp_ms = mean temperature mid-summer, lem = lemming abundance, hunt = spring conservation hunt (1 = with; 0 = without), NAO_f = fall NAOI.

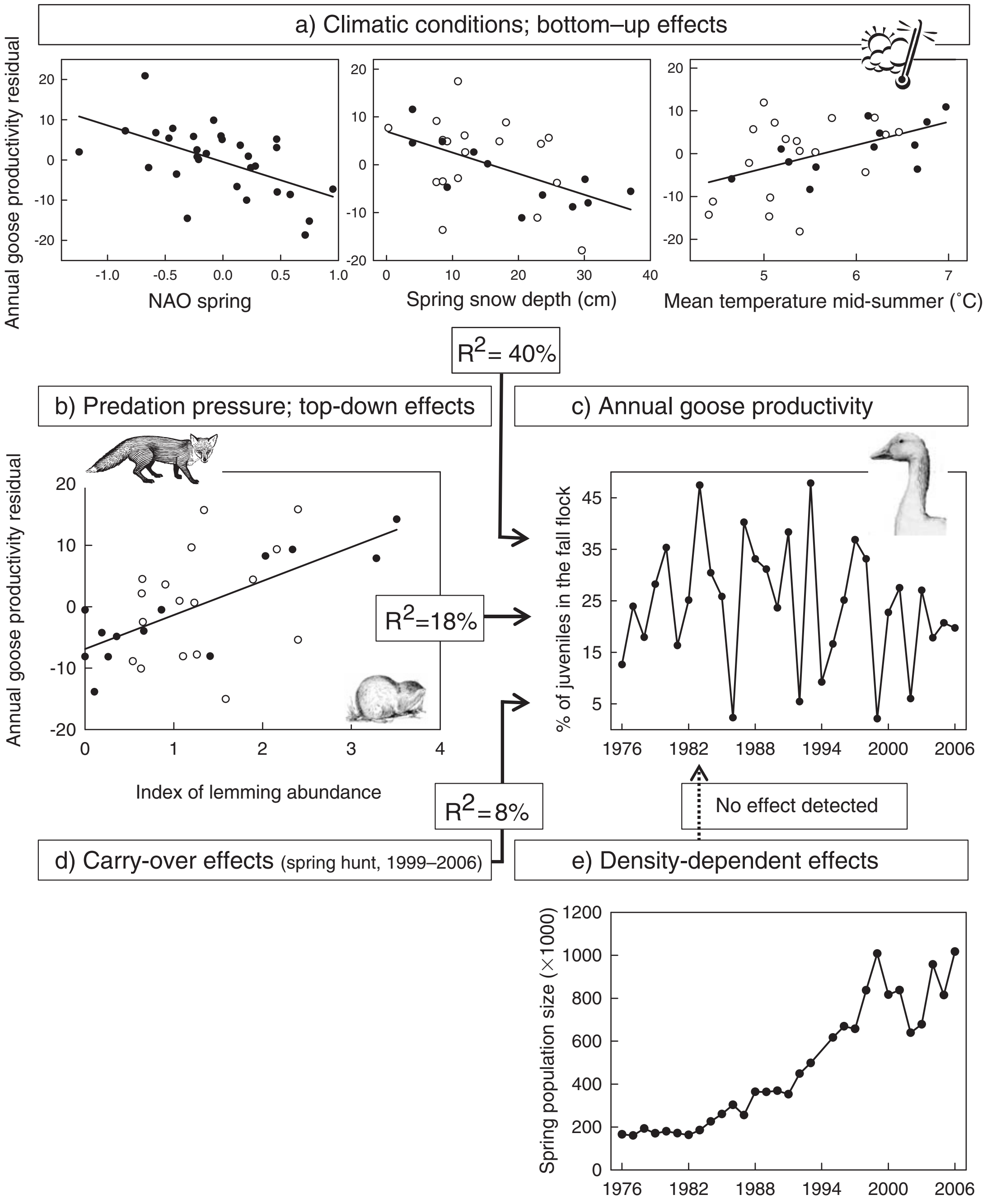

Figure 3. Relationships between residual values of greater snow goose annual breeding productivity (% of juveniles in fall flock) and variables included in the most parsimonious model (Table 3). Lemming abundance index corresponds to pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights. Population size variation is also shown, although not selected in the model. The method used for collecting some environmental data changed part way through the study and the two periods are illustrated by different symbols (open = 1976–1992/1993, and filled = 1993/1994–2006; Methods).

the relative importance of different ecological factors is difficult to perform at the population level, especially when predictors are of varying quality. Our data nonetheless indicate that climatic conditions, encountered slightly prior to or at the start of the goose breeding season, were the main factors determining the maximum potential breeding output and that fluctuations in rodent abundance indirectly influenced the proportion of the goose productivity consumed by predators during the summer. In fact, extreme spring weather conditions were always associated with major breeding failures (< 5% of juveniles: 1986, 1992 and 1999) but this was not always true in years of lemming population crashes.

Annual productivity and climatic conditions: bottom–up processes

The reduced breeding productivity in years with low temperatures and deep snow is consistent with previous findings indicating that spring climatic conditions are the main factors affecting arctic-breeding geese (Alisauskas 2002, Dickey et al. 2008). Greater snow goose females must acquire most of the nutrients required for egg formation on their breeding grounds (Gauthier et al. 2003). They also tend to reduce their clutch size or may not even attempt to breed in years with poor spring climatic conditions as an adaptive response to seasonally declining survival prospects of offspring (Bêty et al. 2003, Reed et al. 2004). Temperature and snow influences the phenology and growth of Arctic plants (Aerts et al. 2006), and snow cover can further affect the accessibility of feeding sites for pre-breeding birds (Gauthier 1993). Thus, the effect of these parameters on nutrient acquisition rates of pre-breeding individuals is likely a key mechanism linking climate to goose population productivity.

There are marked geographic and taxonomic biases in the literature on the effects of the NAO on terrestrial ecosystems as the majority of studies have been conducted in Europe (Sæther et al. 2004) or on mammals (Stenseth et al. 1999). Our study on a key herbivore breeding in the Canadian High-Arctic is one of the first to demonstrate how NAO influences populations of North American birds. Our results also illustrate that NAO (commonly viewed as a winter phenomenon) can be a good predictor of spring environmental conditions encountered by wildlife (see Mysterud et al. 2008 for an example in northern Europe). Indeed, local temperatures measured at the main goose breeding site better predicted breeding productivity than climatic oscillations during mid-summer only (when total sea level pressure variability explained by the NAOI reaches its minimum). Overall, NAOI seems to adequately integrate local climatic conditions that affect geese during the most critical phases of their breeding cycle (i.e. pre-laying and laying), and likely represents conditions met by geese over a large part of their breeding range.

Annual productivity and rodent cycles: top–down processes

Our results indicate that variations in predation pressure on goose eggs and young due to predators shared with lemmings were strong enough to affect the breeding productivity at the population level. Similar effects have been found in populations of several arctic-nesting waders and Siberian goose species, where breeding output typically follow three-year cycles (Summers and Underhill 1987, Blomqvist et al. 2002). Although previous studies did not investigate the relative importance of several environmental factors using a rigorous mechanistic-based approach and longterm dataset, they nonetheless provide good evidence that predation is a key driver of breeding performance in these populations. Unlike most smaller tundra birds, greater snow geese are large enough to successfully defend their eggs and goslings against their primary nest predator, the arctic fox (Bêty et al. 2001). They also nest in colonies where birds can benefit from a predator dilution effect during the laying period (Bêty et al. 2001), a critical phase during which nests are left mostly unattended. Thus, differences in body size and relative vulnerability to mammalian predators likely explain part of the disparity with other tundra bird species in the strength of the association between breeding productivity and rodent cycles. Accordingly, breeding productivity of northern birds that are mainly susceptible to avian predators, such as cliff-nesting species, appears mostly driven by bottom–up, climate-induced effects (Hatch and Hatch 1989).

Although the cause of lemming oscillations is still debated, they likely result from both bottom–up and top–down processes (Ims and Fuglei 2005). Winter climatic conditions may also have strong impact on their population dynamics and several lines of evidence now point to climate forcing as the general underlying cause of the recent collapsing of northern rodent population cycles in many areas (Ims et al. 2008). Given that the seasonal characteristics of lemming population dynamics are dependent on a thick and dry snow pack (Ims and Fuglei 2005), we may expect that the relationship between lemmings and Arctic bird populations will change significantly if winters become, as predicted (Callaghan et al. 2004), considerably warmer and more variable.

Carry-over effects

Incorporating non-lethal carry-over effects in population models of migratory birds may be important for predicting population dynamics (Norris and Taylor 2006) and our study provides a rare empirical test based on a large-scale manipulation. The body reserves accumulated by geese on spring staging areas are an essential fuel source for the northward migration and contribute to their breeding success (Alisauskas 2002, Bêty et al. 2003). As expected, the unplanned manipulation (spring hunt) showed that a reduction in pre-migration body condition caused a substantial decrease in population breeding productivity. This result also corroborates previous models suggesting that about half of the reduction in population growth rate due to spring hunt was a consequence of a reduction in fecundity, the remainder being due to increased mortality (Gauthier and Reed 2007). Quantifying carry-over effects experimentally in migrating species has proven to be a very challenging task (Studds and Marra 2005). Such estimates are nonetheless essential to better predict the fitness consequences of environmental changes, density dependence effects or human-induced disturbance along the migratory route (Klaassen et al. 2006).

Density dependence

Although it is widely accepted, density dependence effects have rarely been demonstrated at the population level in migratory birds (Newton 1998). Despite a six-fold increase in population size over three decades, we found no evidence of such effects on greater snow goose breeding productivity. While recent declines in body size and condition of juveniles has been attributed to increasing intra-specific competition on the breeding grounds (Reed and Plante 1997), it appears that density-dependent effects have not yet significantly affected population dynamic (Menu et al. 2002). This may not be surprising considering that the Bylot Island breeding population (main colony) was approximately at 46% of the estimated carrying capacity of the wetlands in 1996 (Massé et al. 2001). Expansion of birds into new colonies may also limit detection of density dependence effects on recruitment

(Pettifor et al. 1998) and populations with highly restricted availability of suitable nesting habitat can be more susceptible to such negative feedback (Ebbinge et al. 2002). On the other hand, increasing food availability on the staging areas occurred at the same time as the population grew during the study period (Gauthier et al. 2005). This may have generated positive effects (i.e. better pre-breeding body condition) that compensated for potential negative density-dependent effects on the breeding grounds. Increasing densities on the breeding grounds may also have generated positive effects on goose productivity, as nest predation rate is inversely density dependent (Bêty et al. 2002). It is customary to regress annual productivity against population size of the same year to look for possible density dependence in reproduction. However, we must be cautious in our conclusions because our study is not experimental and local density can be related in a non-linear way to population size. This may result in a failure to detect density dependence effects.

Predicting the relative importance of environmental factors

There is extensive literature demonstrating the effects of both bottom–up and top–down processes on bird populations but no clear rules for predicting them. Moreover, although a shortage of (food) resources or predation can have a large effect on breeding birds at the local scale, they do not necessarily generate strong annual variation in breeding productivity at the population level. Indeed, some mechanisms may have a strong impact locally, but if they are not spatially synchronous, will not affect the overall (large scale) dynamics of a population. Alternatively, other factors may have a weaker effect locally, but if they act synchronously on a large scale, can affect overall species dynamics. For instance, predation pressure could be relatively constant or fluctuations in predation rate could be less spatially synchronised in populations with extensive breeding ranges (van Impe 1996, Blomqvist et al. 2002). In such cases, top–down processes could generate much lower variation in recruitment rate compared to bottom–up (climate-induced) effects operating at a large spatial scale. Detailed studies conducted at few spatially restricted breeding sites can help to identify mechanisms linking local environmental parameters to animal populations but may fail to identify the relative importance of factors driving large scale dynamics. Identifying the scale at which environmental factors operate relative to the extent of the breeding range should help in predicting the key factors that generate oscillations in population productivity.

Finally, as suggested for mammalian populations (Sinclair 2003), we propose that variation in the strength of top–down effects among Arctic birds could be driven by a few key factors such as adult body size (relative to mammalian predators), breeding range, nesting strategy (e.g. colonial, dispersed or cliff nesters), and alternative prey availability and characteristics (e.g. resident, migratory or cyclic).

Conclusion

Detailed data sets allowing the integration of key environmental factors, like those used in this study, remain scarce. By applying a mechanistic-based approach to such a data set, we were able to illustrate that density-dependent effects on the breeding productivity of a key Arctic herbivore were apparently negligible relative to those of climate, indirect trophic interactions and non-lethal carry-over effects. Population models based on previously identified mechanisms will likely allow us to go one step further in our capacity to identify the relative importance of bottom-up and top-down processes, and the potential impacts of global warming on Arctic wildlife and ecosystem functioning.

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Appendix 1

Table A1. Relationships between climatic variables measured at the Bylot Island weather station (Y) and at the Environment Canada weather station of Pond Inlet (X) from 1995 to 2006 according to the different time periods of the goose breeding cycle. Overlapping snow depth data from Bylot Island and Pond Inlet were not available.

Variable	Period	Equation	n	R^2	p
Mean daily temperature	spring	$Y = 0.71 X + 0.16$	11	0.79	<0.001
	early summer	$Y = 1.07 X - 1.12$	12	0.88	<0.001
	mid summer	$Y = 0.53 X + 2.47$	12	0.67	0.001
	late summer	$Y = 1.10 X - 0.89$	11	0.93	<0.001
Cumulative precipitation	early summer	$Y = 0.72 X + 18.37$	12	0.42	<0.001

Table A2. Variables, sign of the effect, number of estimated parameter (k), Deviance, ΔAICc, Akaike weights and proportion of variation explained by candidate models relating various factors to annual greater snow goose breeding productivity (% of juveniles in the fall population between 1976 and 2006).

Selected models Variables	k	Deviance	Δ AICc	ω_i	R^2
–NAO_sp, –snow, +temp_ms, +lem, -hunt	7	115.7	0.00	0.15	0.66
–NAO_sp, –snow, +temp_ms, +lem, –hunt, +NAO_f	8	112.4	0.48	0.12	0.69
–NAO_sp, –snow, +temp_ms, +lem	6	120.5	1.32	0.08	0.60
–NAO_sp, –snow, +temp_ms, +lem, –hunt, -NAO^2_sp	8	113.4	1.44	0.07	0.68
–NAO_sp, –snow, +lem	5	124.1	1.84	0.06	0.55
–NAO_sp, –snow, +temp_ms, +lem, –hunt, +NAO_f, –NAO_sp*lem	9	110.1	2.31	0.05	0.72
–NAO_sp, –snow, +temp_ms, +lem, –hunt, –NAO_sp*lem	8	114.3	2.38	0.05	0.67
–NAO_sp, –snow, +temp_ms, +lem, -hunt, +NAO_f, –rain	9	110.3	2.49	0.04	0.71
–NAO_sp, –snow, +temp_ms, +lem, +NAO_f, –NAO_sp*lem	8	114.6	2.66	0.04	0.67
–NAO_sp, –snow, +temp_ms, +lem, –hunt, –pop	8	114.7	2.72	0.04	0.67
–NAO_sp, –snow, +temp_ms, +lem, –hunt, +temp_ls	8	114.9	2.93	0.03	0.67
–NAO_sp, –snow, +lem, –hunt	6	122.1	2.97	0.03	0.57
–NAO_sp, –snow, +temp_ms, +lem, –hunt, +NAO_f, –NAO^2_sp	9	111.0	3.21	0.03	0.71
–NAO_sp, –snow, +lem, –NAO_sp*lem	6	122.6	3.48	0.03	0.57
–NAO_sp, –snow, +lem, –pop	6	122.8	3.68	0.02	0.56
–NAO_sp, –snow, +temp_ms, +temp_f, +lem, –hunt	8	115.7	3.74	0.02	0.66
–NAO_sp, –snow, +temp_ms, +lem, –hunt, –snow^2	8	115.7	3.75	0.02	0.66
–NAO_sp, –snow, +temp_ms, +lem, –hunt, –NAO_ls	8	115.7	3.76	0.02	0.66
–NAO_sp, +temp_ms, +lem, –hunt	6	123.2	4.03	0.02	0.56
–NAO_sp, +lem, –NAO_sp*lem	5	126.6	4.31	0.02	0.51
–NAO_sp, +lem	4	129.8	4.60	0.02	0.45
+temp_sp, –snow, +temp_ms, +lem, –hunt	7	121.2	5.48	0.01	0.59
+temp_sp, –snow, +temp_ms, +lem, –hunt, +NAO_f	8	117.5	5.54	0.01	0.64
-snow, +temp_ms, +lem, –hunt	6	125.6	6.42	0.01	0.52
-NAO_sp, –snow, +temp_ms, –hunt	6	126.3	7.13	0.00	0.51
-NAO_sp, –snow, +lem, –hunt, –NAO_ms, +NAO_f	8	119.9	7.95	0.00	0.61
-NAO_sp	3	135.8	7.97	0.00	0.33
+lem	3	143.1	15.26	0.00	0.14
+temp_sp	3	143.4	15.50	0.00	0.14
-NAO_sp, –snow, +temp_ms, +temp_ls, +NAO_f, –rain	8	128.3	16.39	0.00	0.48
Null	2	147.8	17.42	0.00	0.00

temp_sp = mean temperature in spring, NAO_sp = spring NAOI, snow = spring snow depth, temp_ms = mean temperature in mid-summer, rain = cumulative precipitations, NAO_ms = mid-summer NAOI, temp_ls = mean temperature late summer, NAO_ls = late summer NAOI, temp_f = temperature in fall, NAO_f = fall NAOI, lem = index of lemming abundance, hunt = spring conservation hunt (1 = with; 0 = without), pop = spring population size.