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Trophic Interactions in a High Arctic Snow Goose Colony[1]

GILLES GAUTHIER,[2,]* JOËL BÊTY,[3,]* JEAN-FRANÇOIS GIROUX,† AND LINE ROCHEFORT‡

**Département de biologie and Centre d'études nordiques, Université Laval, Québec, Québec, G1K 7P4. Canada*
†Département des sciences biologiques, Université du Québec à Montréal, P.O. Box 8888, Stn Centre-ville,
Montréal, Québec, H3C 3P8, Canada
‡Département de phytologie and Centre d'études nordiques, Université Laval, Québec, Québec, G1K 7P4, Canada

SYNOPSIS. We examined the role of trophic interactions in structuring a high arctic tundra community characterized by a large breeding colony of greater snow geese (*Chen caerulescens atlantica*). According to the exploitation ecosystem hypothesis of Oksanen *et al.* (1981), food chains are controlled by top-down interactions. However, because the arctic primary productivity is low, herbivore populations are too small to support functional predator populations and these communities should thus be dominated by the plant/herbivore trophic-level interaction. Since 1990, we have been monitoring annual abundance and productivity of geese, the impact of goose grazing, predator abundance (mostly arctic foxes, *Alopex lagopus*) and the abundance of lemmings, the other significant herbivore in this community, on Bylot Island, Nunavut, Canada. Goose grazing consistently removed a significant proportion of the standing crop ($\sim$40%) in tundra wetlands every year. Grazing changed plant community composition and reduced the production of grasses and sedges to a low-level equilibrium compared to the situation where the presence of geese had been removed. Lemming cyclic fluctuations were strong and affected fox reproduction. Fox predation on goose eggs was severe and generated marked annual variation in goose productivity. Predation intensity on geese was closely related to the lemming cycle, a consequence of an indirect interaction between lemming and geese via shared predators. We conclude that, contrary to the exploitation ecosystem hypothesis, both the plant/herbivore and predator/prey interactions are significant in this arctic community.

INTRODUCTION

The role of trophic interactions in structuring terrestrial communities has been widely debated. One school of thought advocates that food web structure and dynamics are largely controlled by nutrients and resource availability at the base of food chains, *i.e.*, a ''bottom-up'' regulation (Polis and Strong, 1996; Polis, 1999). Others advocate that food webs are controlled by consumers, *i.e.*, a ''top-down regulation'' (Hairston *et al.*, 1960; Fretwell, 1987). Oksanen *et al.*, (1981) applied the top-down regulation model to food chains of varying length through a primary productivity gradient, the so-called exploitation ecosystem hypothesis (EEH). According to this model, the primary productivity of an ecosystem influences the length of the food chain that it can sustain, and hence determines whether plant-herbivore or predator-prey interactions will drive the system. In very poor environments, primary production will be too low to support viable herbivore populations, and hence plant biomass will be limited by nutrient availability (Oksanen and Oksanen, 2000; Fig. 1). When primary production is sufficient to support herbivore populations but still too low to support viable predator populations dependent upon these herbivores, then the system will be dominated by the plant-herbivore interaction. Under such conditions, herbivores will impose a strong control on plant biomass. Finally, when primary production is high enough to support viable populations of both herbivores and predators, the system should be dominated by the predator-herbivore interaction. Predators should then depress herbivore populations, thus releasing plants from their control by herbivores and enabling them to increase their biomass (Fig. 1).

In moving through a latitudinal gradient of primary productivity, *e.g.*, from Arctic deserts to boreal forests, food chains should increase from 1 to 3 levels (*i.e.*, plants only to plants-herbivores and plants-herbivores-predators), and their control should shift from resources to herbivores and finally to predators (Oksanen, 1992; Crête, 1999; Oksanen and Oksanen, 2000). Testing this model in boreal ecosystems is difficult because communities often have several interacting food chains (*i.e.*, they look more like food webs; Polis, 1999) with many species. In contrast, trophic interactions are easier to study in arctic communities because they have few species and tend to be much simpler. The primary production of tundra ecosystems is relatively low (Gauthier *et al.*, 1996) and below the designated threshold of 700 g/m^2/yr at which functional predators should invade the system (Oksanen and Oksanen, 2000). Therefore, the EEH predicts that tundra food chains should be dominated by the plant-herbivore trophic-level interaction and that the impact of herbivores on plants should be strong (Oksanen, 1983).

We have been studying trophic interactions in a tundra community of the Canadian High Arctic where greater snow geese (*Chen caerulescens atlantica*) are the dominant herbivore. Snow geese are a migratory species that predominantly uses tundra wetlands for

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[2] E-mail: gilles.gauthier@bio.ulaval.ca

[3] Present address: Département de biologie, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec, G5L 3A1, Canada.

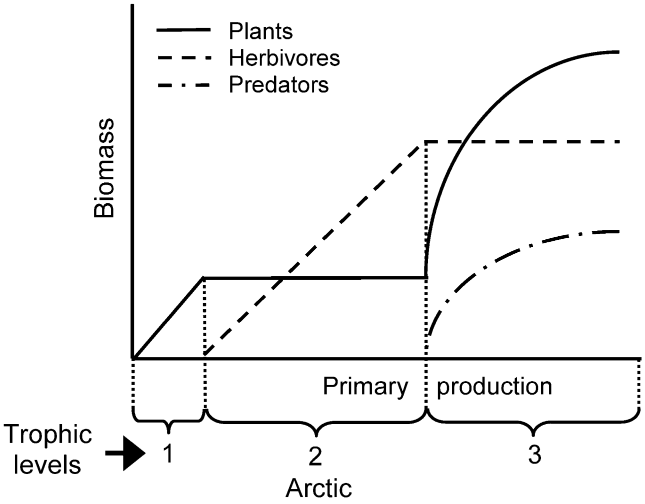

FIG. 1. Change in standing biomass of plants, herbivore, and predators through a gradient of primary productivity as predicted by the exploitation ecosystem hypothesis of Oksanen *et al.* (1981). Numbers refer to the number of trophic levels present. Arctic tundra communities should normally be in the range of two trophic levels.

breeding during the summer (Hughes *et al.*, 1994; Gauthier *et al.*, 1996). Snow goose populations have increased considerably during the second half of the XXth century, in part due to the food subsidy that they receive while feeding in southern agricultural lands during the winter (Reed *et al.*, 1998; Menu *et al.*, 2002). However, despite this population increase, greater snow goose populations breeding in the High Arctic have not exceeded the carrying capacity of their habitat (Massé *et al.*, 2001), unlike those of lesser snow geese (*Chen caerulescens caerulescens*) which breed in the low Arctic (Abraham and Jefferies, 1997; Jano *et al.*, 1998). Our objective was to test two predictions of Oksanen's EEH in the High Arctic tundra: (1) the plant-herbivore interaction should be strong, and (2) the predator-herbivore interaction should be weak because of the low primary productivity of the ecosystem.

STUDY AREA

This study was carried out on the south plain (1,600 km^2) of Bylot Island, Nunavut, Canada (73°N, 80°W) from 1990 to 2002. The breeding population of greater snow geese is estimated at 25,000 pairs (Reed *et al.*, 1998). Most geese nest in colonies over a restricted portion of the island (Bêty *et al.*, 2001) but during brood-rearing they range over all the south plain, concentrating their foraging in wetland habitats (Reed *et al.*, 1992; Massé *et al.*, 2001). Wetlands (mostly polygon-patterned fens) are dominated by sedges such as *Carex aquatilis* var. *stans*, *Eriophorum scheuchzeri*, and *E. angustifolium*, and grasses such as *Dupontia fisheri*, *Pleuropogon sabinei*, and *Arctagrostis latifolia* (Gauthier *et al.*, 1995, 1996). All of these plants are consumed by geese. Polygon fens are also covered by a thick layer of brown mosses that are not eaten by geese.

Two species of lemmings are the only other herbivores that occur in significant numbers on the island. Large mammalian herbivores like muskox (*Ovibos moschatus*) or caribou (*Rangifer tarandus*) are absent or almost absent. The brown lemming (*Lemmus sibiricus*) prefers polygon-patterned fens and feeds primarily on graminoids (grasses and sedges; Negus and Berger, 1998). In contrast, the collared lemming (*Dicrostonyx groenlandicus*) prefers dry upland habitat and feeds mainly on dicotyledonous plants (Negus and Berger, 1998). Predators of both lemmings and geese (mostly of eggs and goslings in the latter case) are, in decreasing order of importance with respect to geese, arctic foxes (*Alopex lagopus*), parasitic jaegers (*Stercorarius parasiticus*), glaucous gulls (*Larus hyperboreus*) and common ravens (*Corvus corax*; Bêty *et al.*, 2001). In addition, snowy owls (*Nyctea scandiaca*), rough-legged hawks (*Buteo lagopus*), and stoats (*Mustela erminea*) are also present and prey on lemmings but not (or very little) on geese.

Our studies were concentrated at 2 sites on the island. Site-1 has a small and variable number of nesting geese but receives a large influx of families moving from Site-2 during the brood-rearing period due to its high density of wetlands. Site-2, located 30 km from Site-1, has the largest concentration of nesting geese on the island but is a minor brood-rearing area (Mainguy, 2003).

METHODS

Plant sampling

Since 1990, we have estimated annual plant production and the intensity of goose grazing in polygon fens at Site-1. We installed 12 new goose exclosures (1 × 1 m; made of chicken wire, 2.5-cm mesh) every year at snow-melt in late June. Plant biomass was sampled in ungrazed and grazed areas (*i.e.*, inside and outside all exclosures) at the end of the growing season in mid-August by removing pieces of turf of 20 × 20 cm. All live above-ground plant biomass was cut, sorted out into sedges (*Eriophorum* or *Carex*) and grasses (mostly *Dupontia fisheri*), dried, and weighed (see Gauthier *et al.*, 1995). Above-ground biomass of vascular plants included all green material and white basal stems buried in mosses. Goose grazing impact is defined as the difference in plant biomass inside and outside exclosures at the end of the summer.

We installed 18 permanent, long-term goose exclosures (4 × 4 m) in polygon fens in 1994. Within each exclosure, a 2 × 2 m area located in one corner was further protected from lemming grazing using a welded wire fence (1.2 cm mesh) 60 cm high and buried 15 cm into the ground. No signs of goose or lemming activity (grazing, feces) were observed in areas where each species had been permanently excluded. Each year for 5 consecutive years, we sampled vascular plants in the exclosure section where only geese were excluded in early August using the same method as for annual exclosures. In addition, a piece of turf 8.5

cm in diameter was extracted from the 20 × 20 cm sample removed inside exclosures and was used to measure moss biomass and production. We defined above-ground biomass (standing crop) of mosses as the loose individual stems of mosses above the network of roots, rhizomes and rhizoids of the organic turf. Primary production was estimated using natural markers (Russell, 1988). Many bryophyte species show visible annual growth segments when growing in dense, vertical growth forms in highly seasonal climates (Clarke *et al.*, 1971; Vitt and Pakarinen, 1977; Longton, 1979). For *Polytrichum* or *Meesia* mosses growing in wetlands of Bylot Island, this results in seasonal differences in leaf size and spacing. Thus, moss biomass above the root system of vascular plants was cut, separated into brown and green portions, dried, and weighed. Before cutting mosses, we collected at least 20 stems of *Polytrichum* sp. and/or *Meesia triquetra*. These stems were pressed, dried, and later used to estimate production.

Goose, lemming and predator monitoring

We have searched annually for greater snow goose nests during laying and early incubation since 1990 at Site-1 and 1994 at Site-2 (see Bêty *et al.*, 2001). Nests were revisited periodically until hatching, and their content as well as any signs of predation was noted at each visit. The lay date is the date that the first egg is laid. A nest was considered successful when at least one egg hatched. Since 1996, nest density has also been determined in a portion of the colony at Site-2 where all nests are systematically positioned with a GPS receiver (see Bêty *et al.*, 2002). We calculated the total number of eggs depredated (ED) as follows:

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

where NMR is the nest mortality rate for the entire nesting period, TCL is the total clutch laid, CSH is the clutch size at hatch in successful nests and ND is the nest density.

Families of greater snow geese have been captured annually in early August since 1990 (mostly at Site-1), using mass banding-drives when adults are molting and before young can fly. All captured birds were aged (young of the year or adult), sexed, and marked (see Menu *et al.*, 2001).

An annual index of lemming abundance has been obtained in July at Site-1 since 1993 with snap-trap censuses (except in 1993 when a lemming winter nest survey was used). Trapping was done in two study plots (wet polygon fens and dry upland), except in 1994 (only one plot in polygon fens). In each plot, 50 baited traps were set for 10–11 days (see Bêty *et al.*, 2001). Trapping conducted at Site-2 since 1997 generally has shown a spatial synchrony in the fluctuation of lemming abundance at the regional scale.

Since 1993, we have searched for snowy owl nests. Most owl nests were found by spotting flying owls from a distance during goose nest searches (owls initiate their nests ≥2 weeks earlier than geese). Nests were positioned with a GPS receiver, their contents were noted, and they were revisited to determine their success.

Since 1994, we have searched for and monitored arctic fox dens at both study sites. Dens were visited at least once in June or early July to check for signs of fox presence (*i.e.*, fresh scats, tracks, prey remains or recent digging). Dens with signs of activity were revisited to determine the presence and number of pups. Litter size was defined as the highest number of pups observed at any visit, which must be regarded as a minimum number. New dens have been found every year because the size of the surveyed area has increased during the study, but we are confident that we have located the majority of dens present within the surveyed area each year.

RESULTS

Plant-herbivore interaction

Graminoid plant biomass in annual exclosures at the end of the growing season (a good index of annual production in this community; Gauthier *et al.*, 1995) showed large annual variation, ranging from 22 to 72 g/m^2 (overall mean: 43.3 ± 3.7 [SE]; Fig. 2). Goose grazing reduced standing crop in all years but the magnitude of this impact was variable among years. For instance, in 1993 the reduction in standing crop was 60% whereas it was negligible (14%) in 1999. *Eriophorum* tended to be more heavily grazed than grasses such as *Dupontia*. Despite the increasing trend in the goose population, there was no corresponding increase in grazing impact ($r = -0.35$, $P = 0.26$, n = 12) or decline in plant production ($r = 0.71$, $P = 0.009$, n = 12) over the years. On the contrary, plant production generally increased over time, especially after 1994, a year of very low biomass production (Fig. 2). In 1994, drought conditions prevailed due to an absence of snow cover and lack of precipitation until late summer (G.G., unpublished data). There was nonetheless a close association between the proportion of biomass grazed by geese and the young:adult ratio in our mass captures at the end of the summer (an index of goose density; Fig. 3). Furthermore, the proportion of annual biomass grazed by geese was positively related to lemming abundance (partial $R^2 = 0.32$, $P = 0.02$, n = 10 yr; in this analysis, annual reproductive effort of geese is controlled statistically by using lay date as covariate).

Long-term exclusion of geese from this ecosystem showed that moderate but chronic goose grazing had an effect on plant communities of polygon fens. After 5 years of goose exclusion, *Eriophorum* biomass was 4.2 times higher than at the beginning, whereas the biomass of *Dupontia* had increased 2.7 times (Table 1). During the same period, the biomass in annual exclosures (Fig. 2), which can be used as control for the

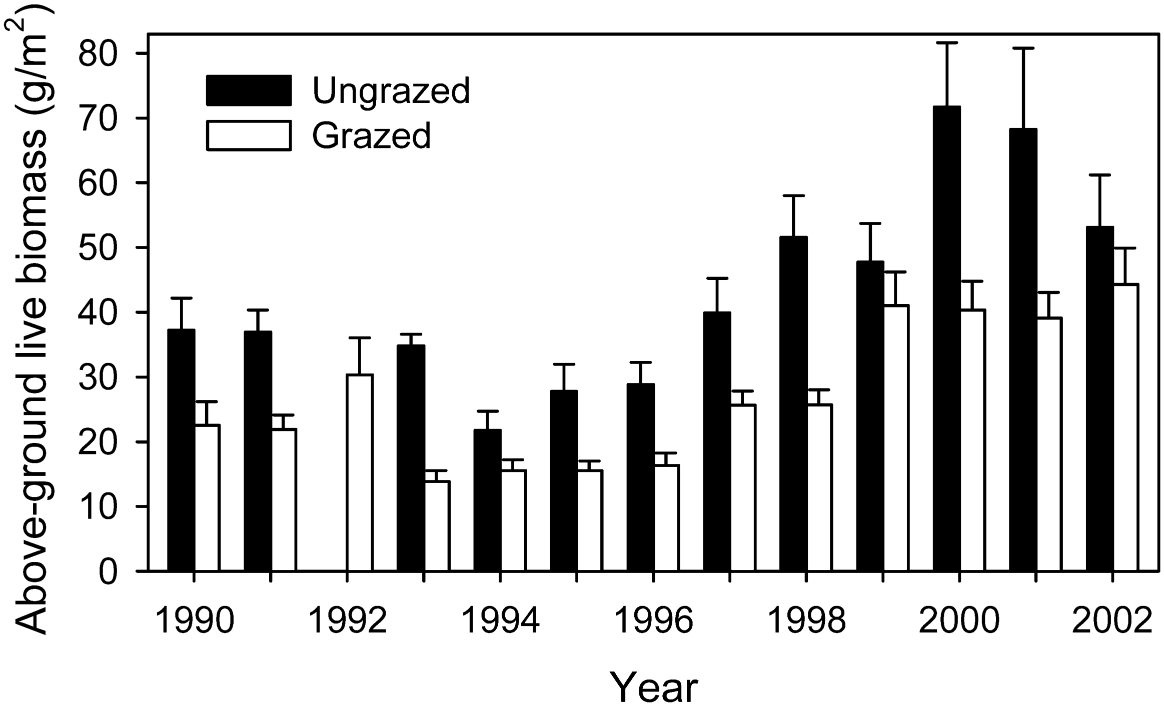

FIG. 2. Fluctuations in annual above-ground live biomass (mean + SE, dry mass) of graminoids at the end of the growth season (mid-August) in polygon fens grazed and ungrazed by snow geese, Bylot Island (2-way ANOVA on log-transformed biomass excluding 1992: year effect: $F_{11,262} = 17.5$, $P < 0.001$; grazing effect: $F_{1,262} = 88.7$, $P < 0.001$; interaction: $F_{11,262} = 1.6$, $P = 0.10$; n = 12 exclosures per year).

long-term exclosures, showed a similar increase for *Dupontia* (2.5 times; Year 1: 13.6 ± 1.8 g/m^2, Year 5: 35.0 ± 6.2 g/m^2; $F_{4,55} = 3.62$, $P = 0.01$) but only a very weak increase for *Eriophorum* (1.9 times; Year 1: 6.6 ± 1.3 g/m^2, Year 5: 12.5 ± 3.7 g/m^2; $F_{4,55} = 2.47$, $P = 0.056$). Hence, after 5 years of goose exclusion, *Eriophorum* had become the dominant plant in exclosures (>50% of biomass), whereas initially it accounted for only 36% of the biomass. Exclusion of geese also resulted in an increase of vascular plant litter, which almost doubled after 3 years (Table 1). Finally, above-ground biomass (standing crop) of mosses in long-term exclosures decreased by almost half after 5 years of goose exclusion, although moss production remained unchanged throughout (average: 120 ± 10 g/m^2).

Predator-herbivore interaction

Lemming abundance showed cyclic variations of large amplitude on Bylot Island. Lemming abundance peaked every 3 to 4 years during the period 1993–2002 (peaks were in 1993, 1996 and 2000) with variations in the lemming abundance index exceeding 60-

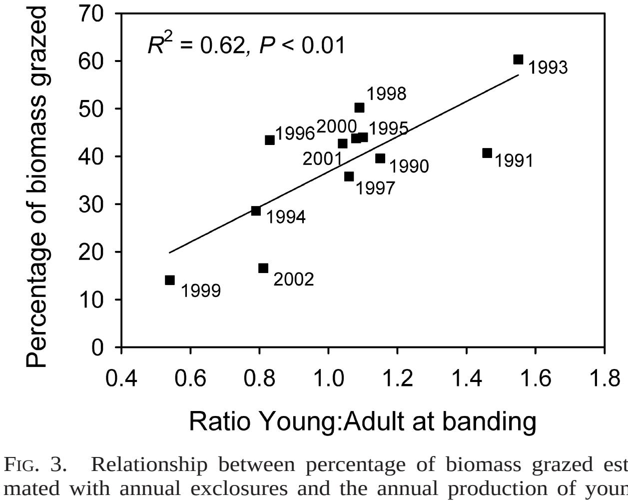

FIG. 3. Relationship between percentage of biomass grazed estimated with annual exclosures and the annual production of young estimated when goose families are captured for banding at the end of the summer, Bylot Island.

TABLE 1. *Above-ground live biomass (dry mass, g/m^2) of vascular plants, litter and mosses in long-term exclosures (n = 18) in early August after goose exclusion, Bylot Island (Year 1 = 1994; Year 5 = 1998). Mean ± SE.**

Year	*Dupontia fisheri*	*Eriophorum scheuchzeri*	Litter	Mosses
1	13.8 ± 1.8 ab	10.9 ± 2.6 a	19.1 ± 3.9 a	—[a]
2	13.4 ± 2.1 a	10.1 ± 2.3 a	29.2 ± 4.0 b	833 ± 84 a
3	18.5 ± 2.6 b	18.1 ± 4.2 b	37.5 ± 6.9 b	559 ± 73 b
4	32.2 ± 4.8 c	34.0 ± 7.9 c	27.0 ± 4.5 ab	468 ± 50 b
5	37.6 ± 6.0 c	46.0 ± 10.5 c	33.4 ± 6.2 b	478 ± 58 b
F[b]	7.7	10.6	4.6	6.6
df	4, 67	4, 67	4, 67	3, 48
P	<0.001	<0.001	0.003	<0.001

[a] No data.

[b] ANOVA for repeated measures. Data were log-transformed to respect normality and homogeneity of variance.

* Values with the same letter within columns do not differ significantly (LS means).

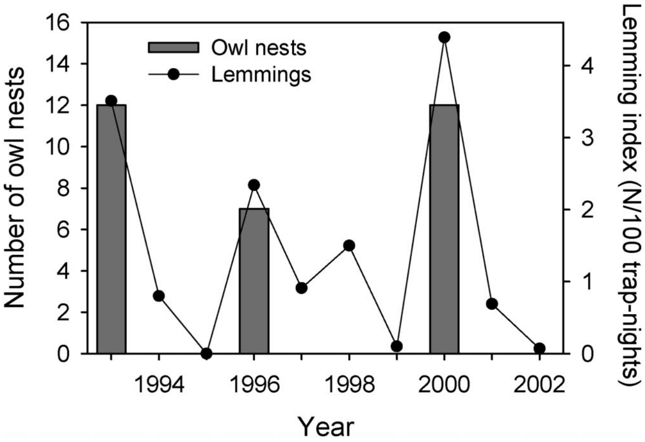

FIG. 4. Fluctuations in annual number of snowy owl nests and lemming abundance on Bylot Island.

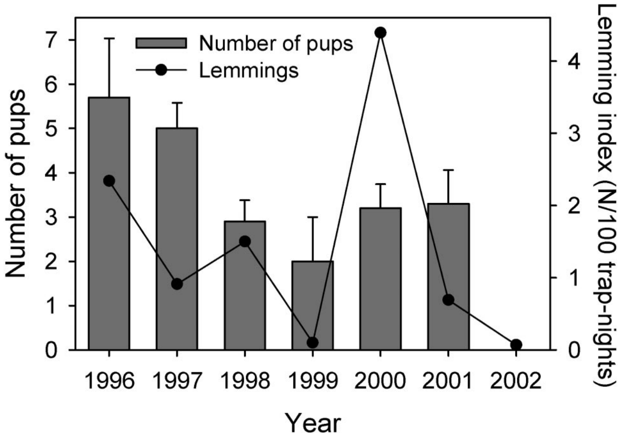

FIG. 5. Fluctuations in annual mean (+ SE) litter size of arctic fox (annual n = 2 to 8) and lemming abundance on Bylot Island. Effect of lemming abundance (high, intermediate, low) on fox litter size: $F_{2,27} = 1.13$, $P = 0.33$.

fold between peak and low years (Fig. 4). It is noteworthy that the decline phase of the cycle was spread over 2 to 3 years and was longer than the increase phase, which occurred over 1 year. Variations in lemming abundance had a considerable effect on many other vertebrate species in this community. Snowy owls were observed nesting only in peak lemming years (Fig. 4). Breeding attempts were never recorded in other years, and in low lemming years owls were rarely seen throughout the summer.

Lemming cycles also had a strong effect on arctic foxes breeding activity. The proportion of dens with breeding activity was similar during years of peak and intermediate lemming abundance (16.7% and 19.0%, respectively), but was drastically reduced during the low phase of the lemming cycle (1.9%; lemming effect: $\chi^2 = 15.5$, df = 2, $P < 0.001$, logistic regression; total n = 228 for the period 1996–2002). The minimum number of pups per litter did not vary significantly with the phase of the lemming cycle, but nonetheless tended to be smallest during the low phase (Fig. 5).

Goose nesting success was related to lemming abundance (Fig. 6), being highest in peak lemming years and poorest in low lemming years. In geese, nest predation is the main cause of breeding failure (Tremblay *et al.*, 1997; Bêty *et al.*, 2001). However, the association between lemming abundance and nesting success was weaker for geese nesting at high density than those at low density (Fig. 6). In peak lemming years, many geese nesting at low density nest in association with snowy owl, which provides protection from egg predators and contributes to the high nesting success of geese in those years (Bêty *et al.*, 2001). However, even when excluding nests under owl protection, Bêty *et al.* (2001) showed that the association between nesting success and lemming abundance remained significant for geese nesting at low density.

The proportion of goose nests destroyed by predators may not always be a good measure of the absolute predation pressure in this system because goose nest density can differ markedly between years. The total number of goose eggs depredated (*i.e.,* total response of predators) is thus a better index of predator pressure (Bêty *et al.,* 2002). The total response of predators on goose eggs at the high-density site showed a 3-fold variation and was closely associated with the phase of the lemming cycle (Fig. 7). On average, predators consumed 42 ± 24 (SD) % of the estimated annual egg production at the goose colony, but this value was much higher in low lemming years (70% on average in 1999 and 2002), 2 or 3 years after the peak.

DISCUSSION

We found that goose grazing had a large effect on plant communities in polygon fens of Bylot Island as they reduced primary production and maintained a certain species composition. Our results thus provide support for the prediction of the EEH that plant-herbivore interactions should be strong in Arctic communities and that herbivores should reduce plant biomass (Oksanen *et al.*, 1981; Oksanen, 1990; Oksanen and Oksanen, 2000). However, egg predation also had a large impact on geese and this effect was highly variable according to the abundance of another prey, lemmings. Therefore, in contradiction to another prediction of the EEH (Oksanen, 1992; Oksanen and Oksanen, 2000), our results also provide evidence for strong predator-herbivore interactions in this community.

Plant-herbivore interaction

Vascular plant production in polygon fens of Bylot Island was quite variable but nonetheless similar to other Arctic tundra sites (Gauthier *et al.*, 1996). Vascular plant production was lowest in 1994, probably because it was a drought year. This year also followed a year of very high grazing impact due to a record density of broods in 1993 (see Fig. 3). The increase in production in subsequent years may represent the recovery of plants from these stresses, which may take several years in the Arctic. For instance, Beaulieu *et*

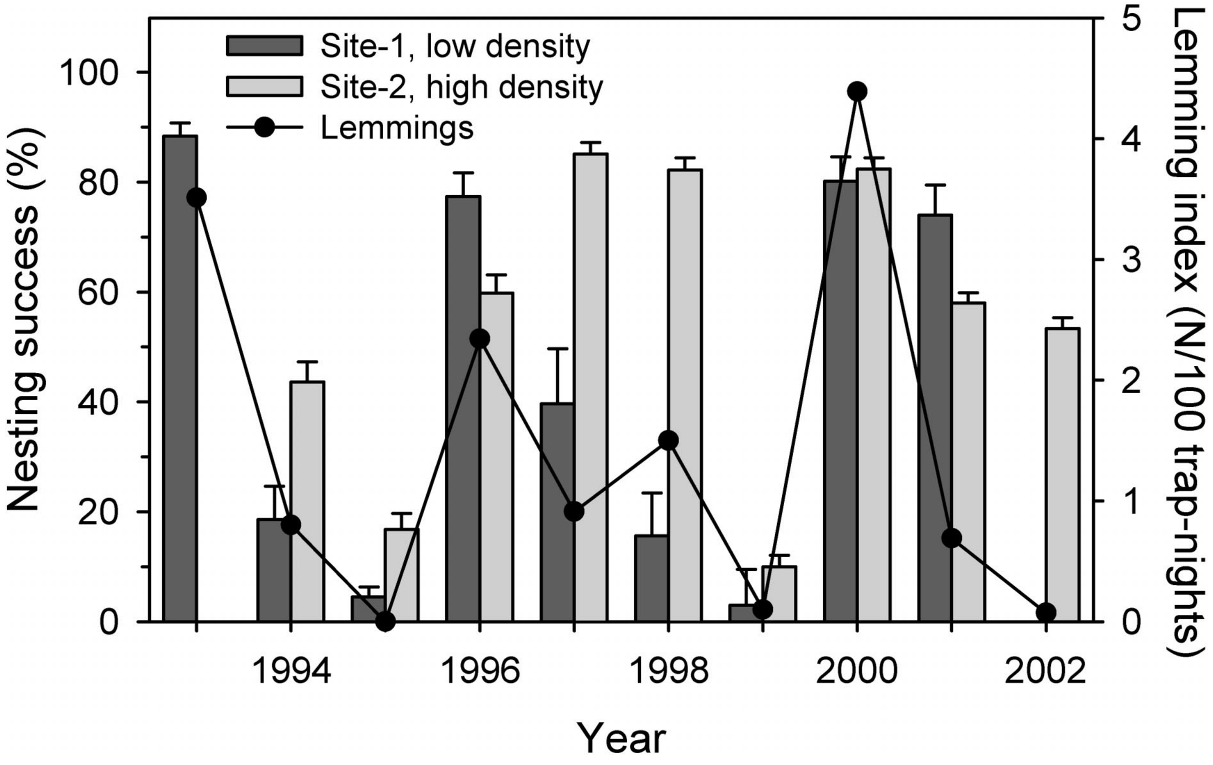

FIG. 6. Fluctuations in annual goose nesting success at two study sites (Site-1, low nesting density, n = 688; Site-2, high nesting density, n = 2,236) and lemming abundance on Bylot Island. Association between mean annual nesting success and lemming abundance: Site-1, *r* = 0.77, *P* = 0.015, df = 9; Site-2, *r* = 0.62, *P* = 0.075, df = 8.

al. (1996) showed that goose grazing reduces accumulation of soluble carbohydrates in graminoid rhizomes, upon which regrowth and vegetative reproduction depend in subsequent years. High plant production in recent years may also have been favored by warm summers in 1998, 2000 and 2001 (G.G., unpublished data).

Each year, geese removed a significant amount of plant biomass in polygon fens. The large annual variation in the amount of plant consumed by geese can be explained by variations in the size of the ''local'' goose population. The reproductive effort of geese is strongly affected by climatic events at the onset of laying (Bêty *et al.*, 2003; Reed *et al.*, 2004). When the reproductive effort is low due to late snow-melt, the production of young is reduced, resulting in a low young:adult ratio at the end of the summer. Most non-breeders and early failed-breeders also leave Bylot Island to molt elsewhere during the summer (Reed *et al.*, 2003), further reducing the summer density of geese in years of low reproductive effort or high predation intensity (see below). Thus, large annual variation in the size of the local population may explain why we see no increasing trend in grazing impact over the last 13 years despite the increase in the size of the total population (Reed *et al.*, 1998).

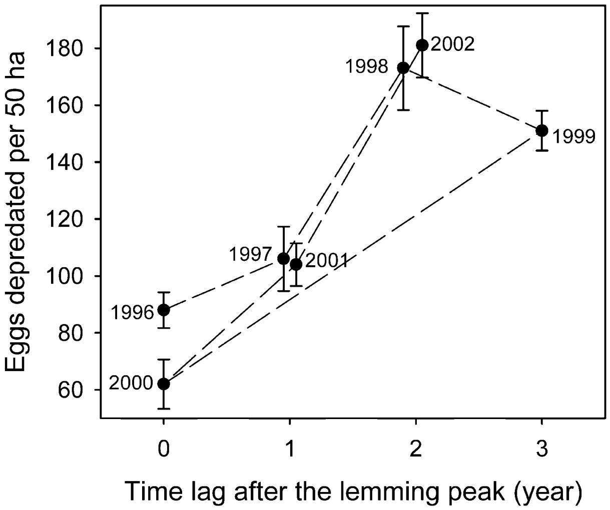

FIG. 7. Fluctuations in annual mean (+ SE) number of goose eggs depredated (total response of predators) with respect to the phase of the lemming population cycle on Bylot Island.

Permanent exclusion of geese from polygon fens nonetheless showed that goose grazing decreases vascular plant production, at least for *Eriophorum*. The reduction in *Eriophorum* production leads to a shift in specific composition with a dominance of graminoids like *Dupontia fisheri* in areas chronically grazed by geese. The reduction in moss biomass in areas where geese had been permanently excluded is believed to be an indirect effect resulting from increased shading due to the increase in vascular plant production and accumulation of dead litter (Graglia *et al.*, 2001). We therefore suggest that high goose abundance leads to a low-level production equilibrium between the herbivore and vascular plants in this ecosystem. However, the system appears stable as shown by the absence of long-term decline in plant production in annual exclosures. In other arctic areas such as the west coast of Hudson Bay, goose grazing can severely impact salt-marsh plant communities when it becomes too intense, and results in vegetation loss over large expanses (Srivastava and Jefferies, 1996; Kotanen and Jefferies, 1997; Jano *et al.*, 1998; Jefferies and Rockwell, 2002). No similar damage has been reported on Bylot Island because the goose population is still below the carrying capacity of the ecosystem (Gauthier *et al.*, 1995; Massé *et al.*, 2001). Moreover, goose-plant interaction may also be inherently more stable in freshwater wetlands than in salt-marshes (Gauthier *et al.*, 2004).

On Bylot Island, we have yet to quantitatively assess the impact of lemmings on plants. In Fennoscandia, the impact of grazing by Norwegian lemmings (*Lemmus lemmus*) in years of peak abundance is severe (Moen *et al.*, 1993; Virtanen *et al.*, 1997). Brown lemmings (an ecological equivalent of Norwegian lemmings) are also common in polygon fens on Bylot Island. However, visual comparison of long-term exclosures where both lemmings and geese are excluded revealed no obvious difference with exclosures where only geese were excluded, even in lemming peak years (G. Gauthier, personal observation). Moreover, we found no reduction in vascular plant production in years following lemming peaks of 1996 and 2000 (see Fig. 2) as would be expected if lemmings had overgrazed the vegetation (the decrease that occurred after the lemming peak in 1993 is confounded with other factors; see above). Although these preliminary observations are by no means sufficient, they nonetheless provide no compelling evidence that lemmings have a large impact on plant biomass on Bylot Island.

Predator-herbivore interaction

Arctic fox is the most important egg predator on Bylot Island, accounting for 45% to >90% of all goose eggs depredated in a given year (Bêty *et al.*, 2002). The impact of predation on goose productivity is variable but in some years (*e.g.*, 1999) it may result in an almost complete failure of nesting geese. The impact of fox predation on geese results from a complex interaction between geese, foxes, lemmings, and to a lesser extent snowy owls (Bêty *et al.*, 2001, 2002; Wilson and Bromley, 2001). Lemmings are the main prey of arctic foxes (Macpherson, 1969; Angerbjörn *et al.*, 1999; Elmhagen *et al.*, 2000) and our results show that fox reproduction is strongly affected by lemming abundance. Fox litter size tended to decrease and fox breeding activity almost completely stopped in low lemming years, as reported elsewhere (Tannerfeldt and Angerbjörn, 1998).

At moderate lemming abundance, only 50% of prey attacks by foxes foraging in the goose colony were directed at goose nests, the rest being directed at lemmings; however, in low lemming years 100% of attacks by foxes were directed at goose nests (Bêty *et al.*, 2002). This prey switch partially explains the association between lemming abundance and goose nesting success. This association was stronger for geese nesting at low density (Site-1) than those at high density (Site-2), suggesting that fox predation had a greater impact on geese nesting at low density in low lemming years. Inversely density-dependent predation rate is common in predators and explains why predation often has the largest impact on small populations (Messier and Crête, 1985; Patterson and Messier, 2000). In colonial birds nesting at high density, predator swamping also contributes to reduce predation rate.

The cause of periodic multiannual density fluctuations in northern populations of voles and lemmings is still controversial. Recent evidence nonetheless indicates that these cyclic oscillations may result mostly from trophic interactions: either an interaction between rodents and their predators, or between rodents and their food (Korpimäki and Norrdahl, 1998; Stenseth, 1999; Klemola *et al.*, 2000; Turchin *et al.*, 2000). In voles, there is growing evidence that predator-prey interactions may cause population cycles but Turchin *et al.* (2000) suggested that food depletion due to overgrazing (*i.e.*, plant-herbivore interaction) was responsible for lemming population cycles in Fennoscandia, in accordance to Oksanen's EEH (see also Turchin and Batzli, 2001). However, as indicated above, we have no evidence of damage to the vegetation by lemmings in years of peak abundance on Bylot Island. On the other hand, there is a rich community of specialist and generalist predators (arctic foxes, stoats, snowy owls, rough-legged hawks, gulls, jaegers and ravens), all of which feed on lemmings (Fitzgerald, 1981; Korpimäki and Krebs, 1996). Recently, Gilg *et al.* (2003) provided strong evidence that predator-prey interactions were the cause of lemming population cycles in Greenland.

Trophic interactions in Arctic communities

In tundra ecosystems where annual primary productivity is below 700 g/m^2, ''efficient carnivores are predicted to be absent except as temporary visitors exploiting herbivore outbreaks'' (Oksanen, 1992, p. 15). On Bylot Island, combined annual production of mosses and vascular plants is about 165 g/m^2. Yet, our results suggest that plant-herbivore and predator-herbivore interactions are both significant in this community. Oksanen and Oksanen (2000) suggested that arctic foxes were merely scavengers, and thus of little importance in affecting herbivore populations in the Arctic. It is true that foxes often move to sea-ice during the winter to exploit seal carcasses killed by polar bears (*Ursus maritimus*), especially in low lemming years (Angerbjörn *et al.*, 1994; Roth, 2002). Nonetheless, in many areas foxes have been shown to be lemming specialists for most of the year and their population dynamic strongly depends upon lemmings

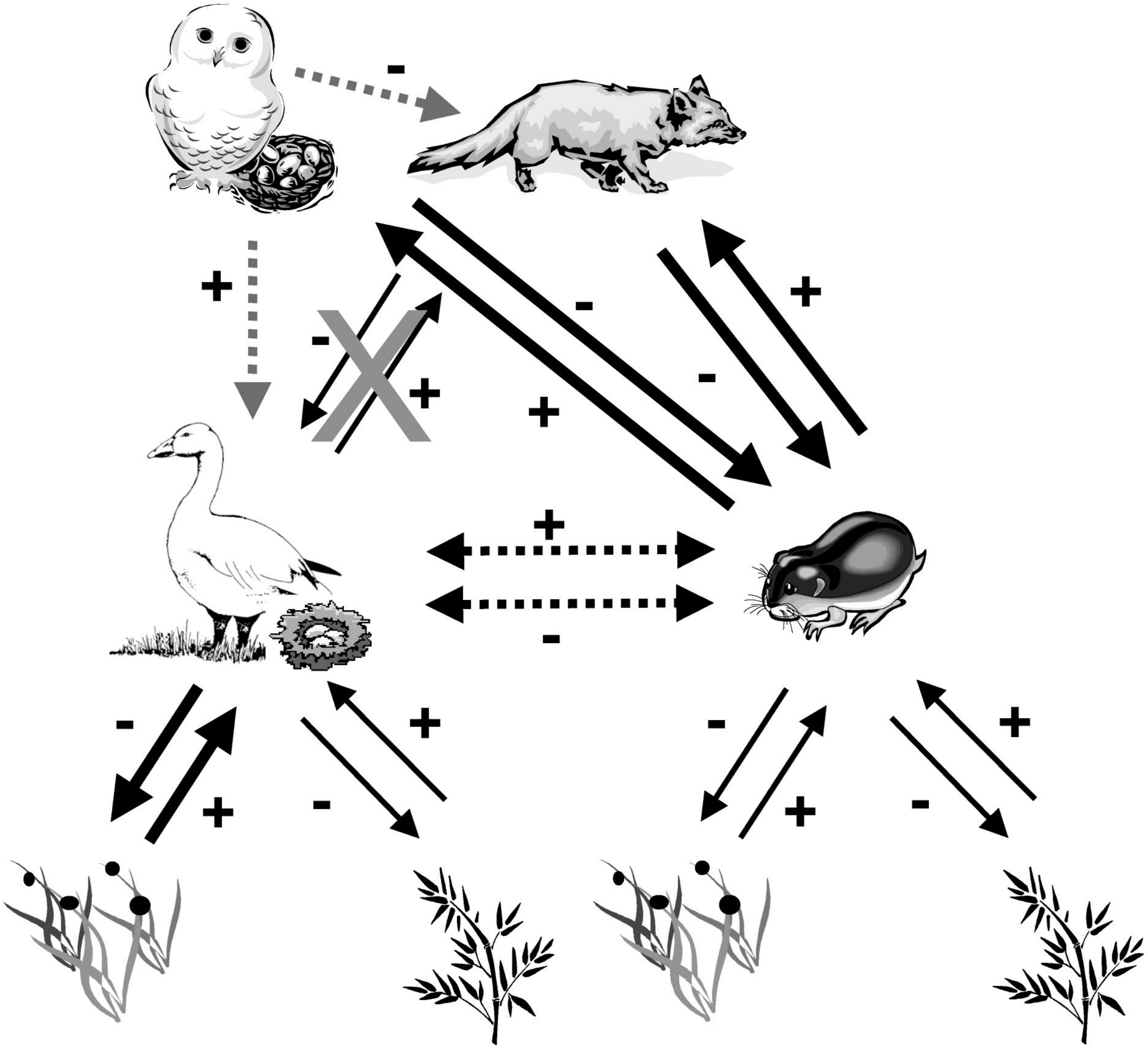

FIG. 8. Simplified schematic representation of direct (full line) and indirect (stippled line) interactions between predators (arctic fox and snowy owl), herbivores (snow goose and lemming) and plants on Bylot Island. The strength of the interaction is proportional to line thickness and intermittent interactions are shown in gray. The ''X'' on goose-fox interaction indicates that this interaction is partly suppressed when snow geese nest in association with snowy owls in peak lemming years.

(Macpherson, 1969; Tannerfeldt and Angerbjörn, 1998; Angerbjörn *et al.*, 1999; Elmhagen *et al.*, 2000).

Our results suggest that the strongest trophic interactions on Bylot Island are between geese and wetland plants (plant-herbivore) and between lemmings and predators (predator-herbivore; Fig. 8). The strength of the interaction between geese and predators like foxes is variable but is definitely strong in low lemming years. Strong indirect interactions thus occur between geese and lemmings due to shared predators (Bêty *et al.*, 2002; see also Wilson and Bromley, 2001), and there is some indication that this indirect interaction cascades down to plants. Indeed, the positive association between the proportion of biomass grazed by geese and lemming abundance suggests the occurrence of some form of ''trophic cascade,'' *i.e.*, when lemming numbers are low, predation rate on geese is high, which reduces the size of the local goose population, and hence the grazing impact. Strictly speaking, trophic cascades are defined as a sustained perturbation occurring at higher level of a food chain that cascades down to lower trophic levels, *e.g.*, a reduction in vegetation biomass due to a dramatic increase in herbivores when predator control is removed (Bazely and Jefferies, 1996). The positive association between lemming abundance and goose grazing impact nonetheless suggests that a similar mechanism may be operating in the short-term. Our results therefore show that ''functional'' predators can indeed be present in the tundra. The goose-predator interaction is further complicated by the presence of nesting snowy owls in peak lemming years. Owls will suppress the predator-goose interaction for geese nesting in association with owls, and this will benefit geese (Fig. 8). Though locally important, this interaction is probably of little significance at the population level due to the low density of owls in relation to geese (Bêty *et al.*, 2001). Preliminary evidence suggests that the lemming-plant interaction is weak on Bylot Island although more work is needed.

Because geese are migratory and are thus present in the Arctic for only three months of the year unlike foxes and lemmings, it could be argued that our work overemphasizes the significance of predation on eggs and goslings in this community. However, food-caching behavior of foxes is common in situation of high food abundance. Samelius and Alisauskas (2000) reported that a single fox foraging in a dense goose colony could cache more than 1,000 eggs in a season. This behavior could considerably extend the period of the year that foxes benefit from geese and could even be essential during critical periods. Bantle and Alisauskas (1998) reported the use of cache eggs by foxes in fall and winter, and Stickney (1991) observed foxes eating cache eggs in early spring, well before the start of egg laying by birds. The role of food caching behavior in fox ecology clearly deserves more studies.

The presence of an abundant alternative prey like geese may contribute to the breeding success, and even winter survival of foxes. In the long term, this could lead to negative indirect interaction between geese and lemmings, *i.e.*, the presence of geese may help to maintain higher fox populations than it would be possible if only lemmings were present, especially in the low phase of the cycle (Bêty *et al.*, 2002). A higher average fox population size will have a negative impact on geese (as shown here) but could also have a negative impact on lemmings. We therefore hypothesize that presence of geese in this system may enhance the regulatory power of foxes on lemmings by allowing higher fox populations to subsist (especially during the low phase of the lemming cycle) than it would be otherwise possible.

The terrestrial community of Bylot Island benefits from allochthonous energy input such as the winter foraging of foxes in the marine ecosystem and the winter and spring feeding of snow geese on southern farmlands. Recent high goose populations at some arctic sites may be a consequence of the food subsidy obtained while feeding on farmlands during the winter (Abraham and Jefferies, 1997; Menu *et al.*, 2002; Jefferies *et al.*, 2004). Without this anthropogenic influence, goose populations could possibly be lower, and thus predator-prey interactions weaker than reported here. However, given that the snow goose population is still below the carrying capacity of the tundra on Bylot Island (Massé *et al.*, 2001), it is uncertain how current numbers compare to population levels before the influence of man. Some could nonetheless question the relevance of such open systems to test the EEH and argue that this island is a special case. However, the presence of large populations of migratory birds such as geese is widespread in the tundra during the summer. In many parts of the Arctic, terrestrial predators also greatly benefit from the presence of colonies of seabirds that feed at sea (Prestrud, 1992; Angerbjörn *et al.*, 1994; Birkhead and Nettleship, 1995). Therefore, the occurrence of allochthonous subsidies between separate or even distant ecosystems may be the rule rather than the exception (Polis and Strong, 1996; Polis *et al.*, 1997; Jefferies, 2000). We thus suggest that by focusing strictly on closed systems, the EEH may provide an incomplete view of the reality of food web dynamics in arctic terrestrial ecosystems.

CONCLUSION

We conclude that, contrary to the exploitation ecosystem hypothesis, both the plant/herbivore (wetland plants/geese) and the predator/prey (foxes/lemmings and foxes/geese) interactions are significant in the arctic community of Bylot Island. This may be partly due to allochthonous subsidies between spatially separated ecosystems. Future work should be aimed at quantifying more precisely the energy input provided by allochthonous sources to arctic terrestrial ecosystems and to determine how essential these are for the maintenance of strong predator-prey interactions in such ecosystems.

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