The Exploitation of Wetland Ecosystems by Herbivores on Bylot Island

Gilles Gauthier  
Département de biologie et Centre d’études nordiques  
Université Laval  
Ste-Foy, Québec  G1K 7P4

Lise Rochefort  
Département de phytologie et Centre d’études nordiques  
Université Laval  
Ste-Foy, Québec  G1K 7P4

Austin Reed  
Canadian Wildlife Service  
1141 route de l’Église, PB 10100  
Ste-Foy, Québec  G1V 4H5

SUMMARY
We examine the interactions between herbivores, plants and climatic factors in arctic wetlands using, as a case study, results of our research on grazing by snow geese on Bylot Island. During the summer, geese are the most important herbivore on the island and consume a high proportion of the annual graminoid production (grasses and sedges). Herbivores can sometimes enhance plant production by increasing the turnover rate of nitrogen, a nutrient which commonly limits growth of arctic plants. However, we found no evidence of positive feedback of grazing on plant growth and, on the contrary, chronic goose grazing tended to decrease production of these ecosystems in the long term. Geese need large quantities of high-quality plants to breed successfully, and negative effects on goose reproduction as a result of lack of food were detected. Herbivore populations are also influenced by climatic factors, either directly or indirectly through effects on plant growth. It is likely that tundra plant-herbivore systems will be strongly affected by future climatic changes.

RÉSUMÉ
Nous examinons les interactions entre les herbivores, les plantes et les facteurs climatiques dans les terres humides arctiques en utilisant nos recherches sur le broutement par les oies des neiges à l'Île Bylot comme étude de cas. Durant l'été, les oies sont les herbivores les plus importants de l'île et elles consomment une forte proportion de la production annuelle de graminoides. Les herbivores peuvent parfois stimuler la production végétale en augmentant le taux de recyclage de l'azote, un nutriment qui limite fréquemment la croissance des plantes arctiques. Cependant, nous n'avons pas trouvé d'évidence de rétroaction positive du broutement sur la croissance des plantes et, au contraire, le broutement chronique par les oies semblait diminuer la production de ces écosystèmes. Les oies ont besoin d'une grande quantité de plantes de haute qualité pour se reproduire avec succès, et des effets dépendants de la densité sur leur succès reproducteur suite à un manque de nourriture ont été détectés. Les populations d'herbivores sont aussi influencées par des facteurs climatiques, soit directement ou indirectement par les effets sur la croissance des plantes. Il est probable que les systèmes plantes/herbivores de la toundra seront fortement affectés par les changements climatiques futurs.

INTRODUCTION
The plant-herbivore interaction is usually the dominant trophic interaction of arctic terrestrial ecosystems. Although predation may be important locally, it is believed that the abundance of arctic herbivores is limited largely by resource availability, i.e., plants (Oksanen et al., 1981; Messier et al., 1988; Jefferies et al. 1992). In contrast, plant productivity and distribution appears to be little affected by herbivores at the landscape level, although herbivores locally may have a high impact on plant communities (Jefferies et al. 1994b). Abiotic factors (water, temperature, nutrients) appear to be more important than herbivory in limiting arctic plants.

In this paper, we examine the nature of the interactions between herbivores, plants and climatic factors in the Arctic. This review focuses on the plant and herbivore communities found on northern Baffin Island. We use research that we have conducted over the past eight years on grazing by snow geese (Chen caerulescens) in the wetlands of Bylot Island as a case study. Nutrient cycling through the herbivore occupies a prominent place in our review as this is thought to be a key process in this system. The role of climatic factors will also be discussed in the context of global warming.
PLANT COMMUNITIES OF NORTHERN BAFFIN ISLAND

Tundra vegetation is extensive in low-elevation areas (<300 m) surrounding Eclipse Sound on Bylot and Baffin islands. At a small scale, the spatial heterogeneity of the vegetation is considerable, mostly in response to the moisture gradient. Because permafrost blocks much of the underground water movement, poorly drained areas readily develop into wetlands. Topography features that contribute to wetland formation include patterned ground (polygons), thermokarst pits, or any depression. Wetlands that do not retain standing water during the summer are commonly covered by a rich and diverse community of mosses. These wetlands develop into fens, i.e., peat-accumulating systems. A lush vascular plant community also occupies these wetlands and is composed mostly of sedges (Carex aquatilis, Eriophorum scheuchzeri, E. angustifo-lium), grasses (Dupontia fisheri and Pleurogonon sabinei), and a few forbs (herbaceous plants) (e.g., Pedicularis spp.; Zoltai et al., 1983; Gauthier et al., 1995). These fens are often called wet sedge or cottongrass meadow because of the abundance of graminoids (grasses and sedges).

Moist areas with fine soil material also have a rich and diverse vegetative cover, although plant abundance generally decreases along a decreasing soil moisture gradient. Polygon rims, sloping terrain, and hummocky tundra are examples of this habitat. In this paper, we refer to these areas as uplands. Common plants of this habitat include shrubs (Salix spp., Vaccinium uliginosum), forbs (Cassiope tetragona, Oxytropis maydelliana), grasses (Arctagrostis latifolia, Alopecurus alpinus, Poa glauca, Luzula confusa), and some mosses (Zoltai et al., 1983). Finally, exposed areas with dry, gravel soil such as ridges have a very sparse vegetative cover consisting of only a few plant species (e.g., Dryas integrifolia, Saxifraga oppositifolia).

THE HERBIVORE COMMUNITY OF NORTHERN BAFFIN ISLAND

Northern Baffin Island supports six species of vertebrate herbivores. One conspicuous absence is the muskox (Ovibos moschatus). This species has been absent from the area possibly since the last glaciation (Zoltai et al., 1983). The herbivore community of northern Baffin Island is summarized in Table 1. All her-bivores but one, the snow goose, are permanent residents.

Even though geese are present for only part of the year, they are certainly the most abundant herbivore from late May to early September on Bylot Island, and probably over much of northern Baffin Island. This whole area holds large breeding colonies of greater snow geese (subspecies atlantica) and may account for half of the subspecies' total breeding population. Based on censuses conducted on the spring staging ground along the St. Lawrence estuary in Quebec, this population has increased considerably over the past three decades.

The total population expanded from 25,000 birds in 1965 to 669,000 birds in 1996, an average annual rate of increase of 11% (Reed, 1990; unpbl. data). During the period 1983-1993, the breeding population of the south plain of Bylot Island experienced the same increase, 11%-a¹ (Fig. 1). In 1993, the brood-rearing population of Bylot Island was composed of 69,500 adults and 86,500 goslings.

The caribou is the most important mammalian herbivore. Although it is locally abundant over parts of northern

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Abundance</th>
<th>Population Trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caribou</td>
<td>Upland, wetland</td>
<td>Low to moderate</td>
<td>Increasing</td>
</tr>
<tr>
<td>Rangifer tarandus</td>
<td>Dry upland, slopes</td>
<td>Low</td>
<td>Unknown</td>
</tr>
<tr>
<td>Arctic hare</td>
<td>Wetland (polygon fen)</td>
<td>Low (except in peak years)</td>
<td>Populations with irregular cycles</td>
</tr>
<tr>
<td>Lepus arcticus</td>
<td>Dry upland</td>
<td>Low (except in peak years)</td>
<td>Populations with irregular cycles</td>
</tr>
<tr>
<td>Brown lemming</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lemmus sibiricus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collared lemming</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dicrostonyx groenlandicus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greater snow goose</td>
<td>Wetland (polygon fen)</td>
<td>Moderate to high</td>
<td>Increasing</td>
</tr>
<tr>
<td>Chen caerulescens atlantica</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock ptarmigan</td>
<td>Dry upland</td>
<td>Low</td>
<td>Unknown</td>
</tr>
<tr>
<td>Lagopus mutus</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 1 Population size of greater snow goose on the south plain of Bylot Island partitioned by adult breeders and non-breeders, and goslings. Censuses were conducted in late July. Standard error of total estimate is given (from Reed and Chagnon, 1987; Reed et al., 1992; Reed, unpbl. data).
Baffin Island, it is rare on Bylot Island. Caribou were extirpated from the island in 1943 (Zoltai et al., 1983) although over the past few years small numbers have moved back to the island in summer. Caribou migrate seasonally over a large area of Baffin Island and use a variety of habitats, including both wetlands and uplands (Ferguson, 1996).

Two species of lemmings occur on northern Baffin Island, each species preferring slightly different habitats (Table 1). In most years, lemmings occur at low density. However, their populations undergo cyclic fluctuations, periodically increasing to very high density for a short period, typically one year. Difference in lemming abundance between the high and low phases of the cycle can be more than one order of magnitude. Population cycles of lemmings in the high Arctic appear to be longer and more erratic than the regular 3-4 year cycle commonly observed in the low Arctic (Fuller et al., 1975; Krebs et al., 1995; Gauthier, unpubl. data). Reasons for this are unclear, but may be related to the shorter growing season of higher latitudes, which allows fewer breeding cycles per year (Jeffries et al., 1992). The last two species of herbivores, the arctic hare and rock ptarmigan, are present in low numbers in the area (Zoltai et al., 1983).

Many herbivore species depend either mostly (snow geese, brown lemmings) or partly (caribou) on wetland graminoids for their food (Table 1). Yet, wetlands occupy only a small proportion of the tundra around Eclipse Sound. In our 70 km² study area on Bylot Island, wetlands (ponds and wet meadows) occupy only 23% of the land area even though the site includes some of the most extensive wetland complexes on the island (Hughes et al., 1994). This stresses the importance of this habitat for arctic herbivores.

NITROGEN CYCLING BY HERBIVORES

In the Arctic, nutrient availability is often deficient and limits plant growth (Babb and Whitfield, 1977; Ulrich and Gersper, 1978; Jeffries et al., 1994b). Fertilization experiments have shown that nitrogen is often the most limiting nutrient for tundra plants (McKendrick et al., 1978; Cargill and Jeffries, 1984a; Shaver and Chapin, 1995). At Bylot Island, growth of wetland graminoids was enhanced by addition of nitrogen, either alone or in combination with phosphorus, but not by phosphorus added alone (Pineau et al., unpubl. data).

Soil nitrogen for plant growth usually comes from three sources: microbial decomposition, fixation of aerial nitrogen by bacteria, and from precipitation. In the Arctic, turnover of nutrients is slow because the cold temperature considerably slows microbial decomposition of litter in the soil (Nadelhoffer et al., 1992), by far the most important source of soil nitrogen (Chapin and Bledsoe, 1992). Herbivores may play a key role in increasing the turnover rate of nitrogen in the Arctic: fecal material contains a high proportion of soluble nitrogen that can be readily absorbed by plants, and hence enriches the soil (Bazely and Jeffries, 1985). Thus, the passage of plants through the gut of an herbivore can replace the rate-limiting process of soil microbial decomposition. A speeding up of nitrogen recycling through the herbivore can, therefore, have the same effect as fertilization and enhances the primary production of forage species.

Enhanced primary production following grazing — a process referred to by botanists as overcompensation — has been observed in coastal salt marshes of Hudson Bay grazed by lesser snow geese (Chen caerulescens caerulescens; Cargill and Jeffenes, 1984b; Hik and Jeffries, 1990; Jeffries et al., 1992). Jeffries and co-workers have shown that the positive response of graminoids (Puccinellia phryganodes and Carex subspathacea) to grazing in this ecosystem is largely a consequence of an increase in the availability of nitrogen to plants via the deposition of feces by the herbivore (Bazely and Jeffries, 1985; Hik and Jeffries, 1990). A second, positive effect of the herbivore on nitrogen recycling is that, by preventing the accumulation of litter on the ground, it promotes the colonization of bare sediments in grazed swaths by nitrogen-fixing cyanobacteria (Bazely and Jeffries, 1989).

Overcompensation in response to herbivory has been reported in only a few arctic plant–herbivore systems. Several conditions must be met to obtain such response, including a rapid turnover of nutrients in the rooting zone, continuous and rapid regrowth of the plants, presence of basal meristems, intensive grazing without destruction of meristems and rapid return of fecal nitrogen to the soil (see Jeffries et al., 1994b for a complete list of characteristics). In contrast to the situation prevailing in the coastal marshes of Hudson Bay, we have failed to detect any evidence of overcompensation in graminoid plants grazed by snow geese in wet meadows on Bylot Island (Gauthier et al., 1995). In this ecosystem, the presence of goose feces does not seem to have any fertilization effect on the plants (Beaulieu et al., 1996), even though fertilization experiments showed that lack of nitrogen is limiting plant growth.

This is a surprising result because many of the conditions enumerated by Jeffries et al. (1994b) are met on Bylot Island. One important difference, however, with coastal marshes of Hudson Bay is the presence of a thick layer of moss in the wet meadows used by snow geese on Bylot Island. We have hypothesized that most nutrients leaching from goose feces are absorbed by mosses rather than graminoids because mosses have a higher ion exchange capacity than vascular plants (Clymo, 1963; Graigie and Maass, 1966; Gilme et al., 1982). Preliminary results from fertilization experiments show that mosses respond positively to nitrogen addition at lower concentration than graminoids (Pineau et al., unpubl. data). This suggests that mosses act like a sponge, soaking up most of the nutrients released from feces. It thus appears that nitrogen cycling in this ecosystem is more complex and involves three levels (graminoids, mosses and herbivore) rather than only two. More information is needed, however, to better understand the nature of this interaction.

PLANT PRODUCTION AND THE IMPACT OF GOOSE GRAZING ON BYLOT ISLAND

Compared to other arctic ecosystems, primary production of wetlands is high, partly because of the high availability of water (Webber, 1978). However, compared to temperate biomes, production of arctic wetlands is modest. Average annual above-ground primary production of graminoids in arctic wetlands ranges from 20-100 g·m⁻² (Table 2). Although high arctic sites tend to have the lowest production values, there is considerable variability among plant communities and years at the same site. Climatic factors (timing of snow-melt, precipitation, temperature) are most likely involved in annual variation in production. Production data from Bylot Island tend to be at the lower end of the range for wet arctic graminoid communities. It is not known whether this reflects site-specific differ-
in net primary production or is a consequence of the intense, chronic grazing by geese on Bylot Island.

When grazing is too intense, damage to the plants may occur. Damage due to overgrazing by geese has already been reported in coastal salt-marsh habitats along west Hudson Bay (Kerbes et al., 1990; Jeffries et al., 1994a). We have been monitoring the impact of goose grazing at our study area on Bylot Island since 1990. Grazing significantly reduced the above-ground biomass of graminoids at the end of the season. In preferred feeding areas, we estimated that geese consumed from 65-100% of the annual above-ground production of Eriophorum, and from 30-78% for Dupontia (Gauthier et al., 1995). Despite this intense grazing pressure, plants were able to grow back some of the lost foliage, although the production of Dupontia was slightly reduced in grazed areas. Accumulation of soluble carbohydrates in rhizomes was also lower in grazed than in ungrazed plants (Beaulieu et al. 1996). As below-ground reserves are important to sustain production of new tillers in arctic graminoids (Mattheis et al. 1976), chronic grazing eventually could lead to a decrease in both tiller density and overall production.

Preliminary results from the monitoring of long-term goose exclosures showed that, indeed, both the production and composition of the community may be affected by geese. After 5 years of goose exclusion, the peak biomass of Eriophorum, the preferred food plant of geese, was 3 times higher than in sites protected from goose grazing only in the current year (23 g m⁻² versus 8 g m⁻², respectively; Gauthier and Rochefort, unpubl. data), and the number of tillers was twice as high (2048 tillers m⁻² versus 1081 tillers m⁻²). Although Eriophorum was less abundant than Dupontia in the first year of goose exclusion (37% of total graminoid biomass), it had become the dominant species 5 years later (55% of biomass). The shoot-pulling habit of geese is another factor that may contribute to the decrease in tiller numbers in grazed areas. In early spring and late summer, geese often excavate basal stems and rhizomes of graminoids (Gauthier, 1993), thereby killing individual shoots. These results suggest that chronic, intense grazing by geese may lead to a low-level production equilibrium between the herbivore and the plants. Response of the community to the absence of goose grazing needs to be evaluated over a longer period than 5 years, and at the landscape level (i.e., over the whole tundra of Bylot Island).

THE ROLE OF FOOD IN SNOW GOOSE REPRODUCTION

Because the breeding cycle of geese is relatively long compared to the short arctic summer, all activities are compressed in time in order for the goslings to fledge before the end of the summer. One of the most important reproductive decisions facing snow geese is when to start breeding. Even though breeding is highly synchronized among individuals (90% of the clutches hatch within 1 week; Lindholm et al., 1994), the timing of hatching is critical for the growth and subsequent survival of goslings. A difference of as little as 4-6 days between early and late-hatched goslings may have major consequences on their growth.

Timing of hatching affects gosling growth for two reasons. First, geese have a low digestive efficiency (they cannot digest plant fibre and therefore absorb only about one-third of the plant material that they ingest) and need large quantities of high-quality forage. When plant quality decreases, their digestive system is unable to compensate by increasing food intake; hence, rate of nutrient assimilation decreases (Sedinger and Raveling, 1988; Manseau and Gauthier, 1993; Piedboeuf, 1996). Food addition experiments have confirmed that gosling growth is sensitive to slight variations in food quality (Lindholm et al., 1994). During summer, there is a seasonal decline in plant quality (decrease in nitrogen, increase in fibre) which starts at the time goslings hatch (Manseau and Gauthier, 1993). Hence, late-hatched goslings have a slower growth rate than early-hatched ones because they miss the period when plant quality is highest (Lindholm et al., 1994; Lepage and Gauthier, unpubl. data).

Food depletion in preferred feeding areas by early-hatched goslings is a second reason for the slower growth rate of
late-hatched goslings: by the time they hatch, the most nutritive species (Enipephorus) or plant parts (leaf tips) are already partly consumed (Gauthier et al., 1995). Even though plant regrowth after grazing is of higher quality (more nitrogen) than ungrazed plants, this is probably not sufficient to compensate for the decrease in biomass (Piedadeuf, 1996). Seasonal movements of broods from pond margins and wet meadows dominated by Dupontia/Enipephorus to drier upland areas (Hughes et al., 1994; Gauthier, pers. obs.) also suggest that less forage is available for geese in wetland habitats later in the season.

About 10 days after fledging, goslings must start a migration of 3000 km to southern Quebec even though their growth is not entirely completed and they have little fat reserves to meet the energy demand of the migration (Lesage, 1995). Goslings that grow more slowly will fledge later in the season or will be smaller at fledging, and are likely to experience higher mortality during the fall migration (Owen and Black, 1989; Cooch and Cooke, 1991; Cooch et al., 1993; Menu et al., unpubl. data). This could be a density-dependent regulation factor in this population: as population density increases, gosling growth will be depressed through increased competition for high-quality food, and mortality during fall migration will increase. We have already detected evidence of density-dependent effects on gosling growth. Over the past 20 years, birds shot at Cap Tourmente in Quebec have shown a significant decline in body size (Reed and Plante, in press). Since 1991, we have also detected a negative trend in body mass of goslings at fledging on Bylot Island (Lepage et al., unpubl. data).

CLIMATIC EVENTS

Climatic effects on herbivore populations can be either direct and/or indirect through their influence on plant growth. Timing of snow-melt in spring is probably one of the most important direct climatic effects on goose populations. Although there are considerable pressures for the birds to lay their eggs as early as possible in spring to maximize gosling growth, and hence their reproductive success, snow cover often prevents geese from doing so. Date of nest initiation by geese is correlated with both snow-melt date and average temperature in late May and early June (Lepage et al., 1996). Snow-melt affects goose nesting in two ways. First, snow-free areas in relatively dry sites must be available for the geese to initiate their nest. Second, suitable feeding areas must also be available to geese before and during laying. Because egg-laying is energetically costly for geese, they need to feed intensively during this period to acquire enough nutrients to form the eggs (Gauthier and Tardif, 1991; Choinière and Gauthier, 1995). Even though geese are flexible in their choice of feeding areas and nesting sites in spring (Gauthier, 1993; Lepage et al., 1996), late snow-melt will delay nesting and reduce reproductive success.

Episodic climatic events can also have a major impact on the population dynamics of arctic animals, as shown by the variation in annual production of young in greater snow geese. Since 1973, the proportion of young in the fall flock has been monitored when they pass through southern Quebec in migration. The production of young shows considerable annual variation with periodic breeding failure observed (when the proportion of young is < 10%) in 1974, 1986 and 1992 (Fig. 2). These three summers were characterized by extreme weather conditions in the Arctic: snow-melt was severely delayed because of high winter precipitation and cold spring temperatures (Heyland, 1974; Lepage et al., 1996; Reed unpubl. data). Most geese did not even attempt to breed in these years, presumably because not enough time was available to complete their breeding cycle when the snow finally melted. These periodic breeding failures could increase in the future if global warming increases the frequency of these climatic anomalies.

Another example of a direct effect is the influence of climatic conditions on the thermoregulatory costs of growing goslings. The amount of energy expended by goslings for thermoregulating, a major component of their internal energy budget, is sensitive to variations in temperature, wind speed, and solar radiation (Fortin, 1995). Increased cost of thermoregulation will decrease energy available for growth, and hence may affect gosling survival.

An interesting example of indirect climatic effect on an arctic herbivore population is provided by the snow goose population of west Hudson Bay. The cooling trend recently observed over southern Baffin Island (Findlay and Deutch-Stapf, 1991; Allard et al., 1995) has delayed snow melt at the very large snow goose colonies located on Southampton Island and the Great Plain of the Koudjouaq. This has forced birds nesting in these areas to prolong their staging along west Hudson Bay in spring where they feed by grubbing for rhizomes, thereby destroying salt-marsh plants (Jefferies et al., 1994a). This destruction has had an adverse effect on the local population of snow geese that nest and raise their goslings in the salt marshes of west Hudson Bay.

Late snow melt, flooding, drought or cold temperature are all climatic events that can negatively affect growth of tundra plants during the summer, and hence indirectly influence herbivore populations. Because the hatch of goslings on Bylot Island must coincide with the po-

---

Figure 2  Proportion of juveniles in the fall flock of greater snow geese along the St. Lawrence estuary. Filled dots are years of breeding failure (when proportion of juveniles is < 10%, from Gauvin and Reed, 1987; Reed unpubl. data).
riod of maximum plant quality in order for them to achieve optimal growth, any reduction or delay in plant growth will have an impact on osplings.

CONCLUSION
From the previous discussion, it is clear that population dynamics of arctic herbivores, and geese in particular, are strongly influenced by their food supply. The nature of the interaction between herbivores and plants is affected by the behaviour and physiology of the herbivore, the intensity of grazing, the role of the herbivore in cycling nitrogen, and the growth characteristics of plants. All these processes are modulated by both the overall climatic conditions as well as by episodic events. In the context of global warming, it is difficult to anticipate the effects of predicted climatic changes on these populations since climate acts at many different levels, including soil microbial processes, plant growth, and the herbivores themselves.

The effect of climatic changes on tundra grazing systems was discussed by Jefferies et al. (1992). Predicted increase in temperature may enhance the production of arctic plants. However, modifications to the water regime are more complex and could have both positive and negative impacts on plants as increased winter precipitation will delay snow-melt and the onset of plant growth in spring, but increased summer precipitation could enhance it. Changes in plant production through global warming will affect herbivores. Direct effects on animals could also be positive or negative: higher temperatures may reduce thermoregulatory costs of osplings but late snow-melt will delay nesting by geese. Because tundra plant–herbivore systems are tightly coupled with climate, it is likely that they will be affected by future climatic changes and that they will in turn respond to these changes.

ACKNOWLEDGEMENTS
The goose research on Bylot Island was supported by the Natural Sciences and Engineering Research Council of Canada, the Arctic Goose Joint Venture (Environment Canada), the Fonds pour la Formation de chercheurs et d’aide à la recherche of the Quebec Government, Ducks Unlimited (Canada), Polar Continental Shelf Project, and the Department of Indian Affairs and Northern Development of Canada. We thank the Pond Inlet Hunters and Trappers Association for their support, and Bob Jefferies and Bill Montvevecchi for their comments on this paper.

REFERENCES
Allard, M., Wang, B., and Pilon, J., 1995, Recent cooling along the southern shore of Hudson Strait, Quebec, Canada, documented from permafrost temperature measurements: Arctic and Alpine Research, v. 27, p. 157-166.
Heyland, J. D., 1974, Preliminary report on studies of greater snow geese on Bylot Island, May 26 to June 20, 1974: unpublished manuscript. Québec Fish and Wildlife Service, Québec, Canada.


Accepted as revised 18 November 1996.