The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands — a continuing saga

R.L. Jefferies, R.F. Rockwell, and K.F. Abraham

Abstract: Agriculture has provided a nutritional subsidy to the Anatidae (swans, geese, ducks), which has affected their trophic relationships and the Arctic wetlands where they breed. The Mid-Continent Population of lesser snow geese, which breeds in the Canadian Arctic and which traditionally wintered in the coastal marshes of the Gulf States, now feeds in agricultural landscapes. The geometric growth of this population since 1970 is coincident with increased application of nitrogen to farmland and high crop yields. Widespread availability of agricultural foods allows the birds to meet much of their energy demand for migration and reproduction. Their migration conforms to a stepping stone model linked to land use, but feeding also takes place upon arrival on the Arctic breeding grounds. High bird numbers have dramatically affected coastal marshes of the Canadian Arctic. Foraging has produced alternative stable states characterized by sward destruction and near irreversible changes in soil properties of exposed sediments. Locally, this loss of resilience has adversely affected different groups of organisms, resulting in an apparent trophic cascade. A spring hunt was introduced in 1999 in an attempt to check population growth. The current annual cull is now thought to be higher than the replacement rate. Much of the decline of the Mid-Continent Population is probably linked to shooting, but the harassment of birds that fail to acquire sufficient food for reproduction may contribute. The agricultural food subsidy has led to a mismatch between this avian herbivore and its environment — a consequence of migratory connectivity that links wintering and breeding grounds.

Key words: agricultural crops, lesser snow geese, migratory connectivity, Arctic coastal marshes, grubbing, hypersalinity, the spring hunt.

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Résumé : L'agriculture a fourni un apport alimentaire aux Anatidae (cygnes, oies, canards) qui a affecté leurs relations trophiques avec les terres humides de l'Arctique, où ils se reproduisent. La population de l'intérieur du continent des petites oies blanches, qui niche dans l'Arctique Canadien et qui hivernait traditionnellement dans les marais côtiers des états du golfe, se nourrit maintenant sur les terres agricoles. La croissance géométrique de cette population, depuis 1970, coïncide avec une augmentation de l'application d'azote sur les terres et avec l'accroissement des récoltes. L'abondance et la disponibilité de nourriture agricole permet aux oiseaux de rencontrer une bonne partie de leur besoin en énergie, pour la migration et la reproduction. Leur migration suit un modèle en pied-à-terre, lié à l'utilisation des sols, mais leur nutrition se poursuit lorsque les oiseaux arrivent sur les terrains de reproduction de l'Arctique. Ces grands nombres d'oiseaux ont drastiquement affecté les marais côtiers de l'Arctique canadien. Le broutage a conduit à des états stables alternatifs caractérisés par la destruction des pelouses et des changements irréversibles dans les propriétés pédologiques des sédiments exposés. Localement, cette perte de résilience a affecté négativement différents groupes d'organismes, conduisant à une cascade trophique apparente. En 1999, on a introduit une chasse printanière dans l'espoir de maîtriser la croissance de la population. On pense maintenant que le prélèvement annuel dépasse le taux de remplacement. Une bonne partie du déclin de la population de l'intérieur du continent est probablement liée à la chasse, mais le harassement des oiseaux qui n'arrivent pas à trouver assez de nourriture pour leur reproduction, peut y contribuer. L'apport de nourriture par l'agriculture à conduit à un écart entre l'herbivorie aviaire et son environnement - une conséquence de la continuité migratoire qui relie les terrains d'hivernage et de reproduction.

Mots clés : récoltes, petite oie blanche, connectivité migratoire, marais côtiers arctiques, essartement, hypersalinité, chasse printanière.

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Introduction

The final phase of the rapid global expansion of land devoted to agriculture is likely to occur in the next 50 years (Tilman et al. 2001). Modern agriculture affects ecosystems by providing resources, such as nitrogen (N), that normally limit ecosystem functioning. Since 1960, the annual application rate of N fertilizers at the global scale, excluding the former USSR, has increased approximately eightfold, and it is predicted to increase a further 2.4 times by 2050 (Tilman et al. 2001). The global N cycle has been altered by human activity to such an extent that more N is released annually from anthropogenic sources in terrestrial environments than is fixed by natural processes (Vitousek 1994; Galloway et al. 1995). In spite of this release of nitrogen, plant growth is often limited in terrestrial ecosystems by inadequate N supplies, which lead to a low percentage of N in plant biomass (<2% of the dry weight) (Delwiche 1970; Epstein 1972; White 1993). If the biomass utilized by herbivores is of low nutritional quality, it may be expected to reduce both the vigour and the reproductive success of individuals, resulting in a reduction in herbivore numbers (Sinclair et al. 1985). However, herbivores show considerable selectivity and flexibility in their diets to maximize the nutritional value of their forage intake (Breman and De Wit 1984; Sinclair and Fryxell 1985). This flexibility includes the use of N-enriched pastures and crops as a source of high-quality forage by both wild and domesticated herbivores. The source represents a nutritional subsidy to herbivores when they are feeding in a N-enriched landscape. In addition, ecosystems are open, and herbivores that live elsewhere may also indirectly benefit from the export of N from agricultural systems. As a result, movements of N both within and from these enriched systems are likely to have a profound effect on the maintenance of herbivore populations and the functioning of ecosystems, including those far removed from the agricultural source. One of the best examples of the effects of changes in agricultural practices is the long-term shifts from 1939 to 1992 in the foraging behaviours and abundances of members of the Anatidae (swans, geese, ducks) in the Netherlands, many of which breed in the Arctic (Van Erden et al.1996). Since 1939 different species

have switched to amended grasslands, depending on the fertilizer inputs. As the nutritional quality of the grasslands has improved over the decades, smaller species with higher metabolic rates have been able to take advantage of the improved food source (Van Eerden et al. 1996). Thus, an allochthonous (external) input can modify trophic relationships by providing a resource that is normally limiting within the system.

In this paper we examine the effects of such a subsidy on populations of Arctic breeding geese with particular reference to the Mid-Continent Population of lesser snow geese, based on results from long-term studies that have been conducted since 1968 at La Pérouse Bay, Manitoba, which is on the Arctic–sub-Arctic boundary. The studies provide insights of the ecological effects of agricultural subsidies on herbivore populations and indirectly the Arctic ecosystems in which they breed, and the results are linked to findings from comparable North American and European investigations. The rationale for this review is twofold. Firstly, the increase in numbers of migratory geese that feed in agricultural landscapes in winter has created conservation and management problems in wintering habitats, on the Arctic breeding grounds, and along the migration routes of the birds. Secondly, trophic relationships on the breeding grounds have been altered as a consequence of the top-down effects of increased numbers of geese, which has impacted all groups of organisms.

Status of the Mid-Continent Population of the lesser snow goose and the likely causes for the population increase

Many species of Arctic breeding geese have increased substantially in numbers during the last 40 years (Abraham et al.1996 and references therein). In North America, they include lesser and greater snow geese (*Chen caerulescens caerulescens* and *C. c. atlantica*), Ross's geese (*Chen rossii*), greater white-fronted geese (*Anser albifrons*) and some populations of Canada geese (*Branta canadensis*), all of which forage during the nonbreeding season in agricultural habitats. In contrast, geese that winter in marine habitats, such as brant and emperor geese (*Branta bernicla, Chen canagica*), have shown little or no increase in numbers (Abraham et al. 1996). Nomenclature follows the American Ornithological Union.

The lesser snow goose nests in dense colonies in wetlands and tundra vegetation from Chukotka and Wrangel Island in the Russian Far East to the eastern Canadian Arctic, and the birds winter in the southern United States and northern Mexico (Mowbray et al. 2000). In North America there are three major regional breeding and wintering populations that include birds that breed in Russia. Although in past decades the three major populations (western or Pacific, Central, and Mid-Continent) were reasonably discrete, the geographical expansion of the populations on the wintering grounds, which is linked to the use of agricultural food sources, has begun to blur the boundaries (Dzubin 1974, 1979; Alisauskas 1998). The Mid-Continent Population traditionally winters along the Gulf Coast of Louisiana and Texas and breeds in the Hudson Bay region, Baffin Island, and in the eastern section of the central Canadian Arctic in the vicinity of Queen Maud Gulf (Fig. 1).

Coordinated winter counts have provided an index of growth of the Mid-Continent Population of lesser snow geese since the middle of the last century; prior to this records are incomplete and largely anecdotal. The counts rose from 0.8 million geese in 1969 to 2.7 million in 1994 (~2.4 million in 2001) (data from reports of US Fish and Wildlife Service and Mississippi and Central Flyway Councils compiled by Kruse and Sharp (2002)) (Fig. 2). The single mid-winter count is thought to consistently underestimate the total size of the Mid-Continent Population of lesser snow geese by about half (Dzubin 1974; Dzubin et al. 1975; Kerbes 1975; Boyd et al. 1982). The population in the mid-1990s was most likely between 4.5 million and 6 million birds (Abraham and Jefferies 1997). Surveys on the breeding grounds in the eastern and central Canadian Arctic of this population have indicated a substantial growth at several colonies in recent decades and the establishment of new colonies (Reed et al. 1987; Alisauskas and Boyd 1994; Kerbes 1994; Cooke et al. 1995). For example, at La Pérouse Bay the population has

Fig. 1. Flyway routes and wintering and breeding areas in North America and the Russian Far East for different populations of lesser and greater snow geese. (Prepared by Mark Vrtiska. From Nebraskaland Magazine, October 1990, reproduced with permission of the Nebraska Game and Parks Commission. ©1990, Nebraska Game and Parks Commission.)

Fig. 2. Mid-winter index of the abundance of lesser snow geese between 1950 and 2002 (after Kruse and Sharp 2002).
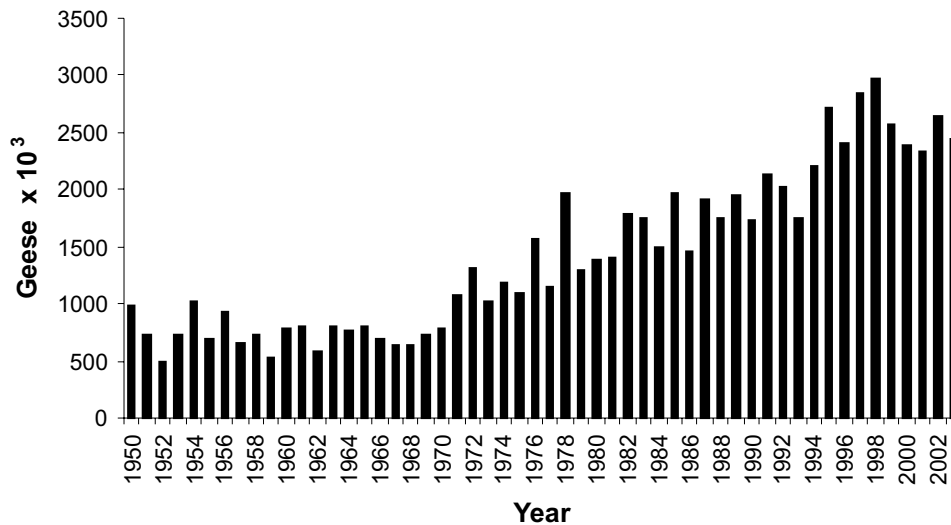
increased from just under 2000 pairs in 1968 to 44 500 pairs in 1997.[2] Increases of other western North American lesser snow goose populations have been slower, but in recent decades they have become similar to that of the Mid-Continent Population (Dzubin 1979; Alisauskas and Boyd 1994).

At least four factors coinciding in time and location appear to have contributed to the observed growth rates of the Mid-Continent Population of lesser snow geese. The first of these is the agricultural food subsidy that is discussed in a separate section. The second is the effect of the presence of refugia from hunting on the migration routes in the United States, most of which were established from the 1930s to the 1970s to protect and restore wetland habitat for breeding and migrating waterfowl (Bellrose 1980). This quickly led to a cessation of the long-distance fall migration of the geese from northern staging areas to Texas (Johnsgard 1974), and from James Bay to Louisiana (Cooch 1955). The refugia functioned as foci for the population, which fed on resources both within reserves and in adjacent agricultural fields, and a disproportionate number of birds used the refugia as a sanctuary from hunting.

The third factor is a decline in the harvest rate. Hunting is the principal cause of mortality of adult geese in recent decades, and the harvest *rate* in the central USA has declined along with hunter numbers in the last 25 years (Owen 1980; Francis et al. 1992; Abraham and Jefferies 1997; Cooke et al. 1999). This decline in harvest rate has occurred, despite no declining trend in the total harvest for the Mississippi and Central flyways and for Canada since 1970: the annual number of birds harvested over the period fluctuated between 300 000 and 700 000 (Cooke et al. 1999; Jefferies et al. 2004*b*). Years of low harvest were often linked to weather-related decreased recruitment on the breeding grounds (Boyd and Madsen 1997; Ganter and Boyd 2000). The harvest from 1970 onwards simply did not rise in proportion with the population growth of the geese, consequently the harvest rate fell, as it was insufficient to contain the population growth.

The escape of the Mid-Continent Population from control by harvesting is related to a more general problem of the control of population dynamics by a fixed-number harvest that creates instability in the population size. Consider a population with a fixed level of reproductive success for which a small natural mortality is increased additively by a fixed number of 1000 individuals that are harvested annually

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[2] K.F. Abraham, R.F. Rockwell, and R.K. Ross. Unpublished aerial survey, 1997.

Fig. 3. The relationship between population growth rate (lambda) and population size when a fixed number of individuals are harvested. In this population, 1000 individuals are harvested annually and this mortality is additive to a small natural mortality. The system is locally stable when the population size is 2605.
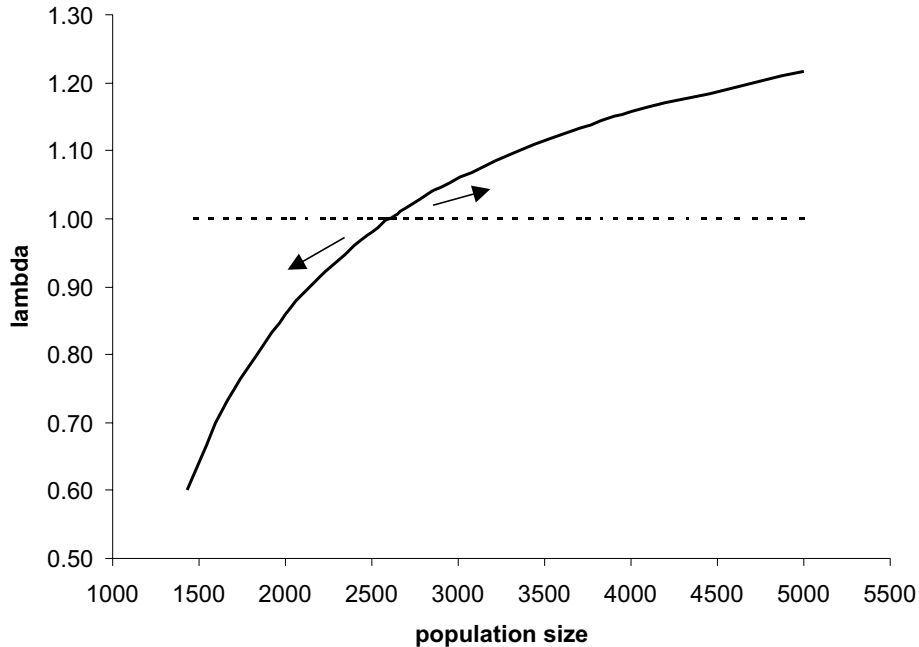
regardless of the size of the population. For such a population, there will exist some population size (N) for which the reproductive success in consort with the overall mortality rate (an additive function of the natural rate plus $1000/N$ – the rate of the fixed number harvest) will lead to a population growth rate of $\lambda = 1.00$ (the replacement rate where there is no net change in the size of the population). In the example depicted in Fig. 3, this population size is 2605. If the population grows very slightly because of some chance event or environmental change, so that the population is now $N + \Phi$, then the portion of the fixed number harvest that makes up the overall mortality ($1000/(N + \Phi)$) will be reduced, as will the overall mortality, and the population's growth rate will exceed $\lambda = 1.00$. The population will start to grow, and the portion that the fixed harvest number contributes to the overall mortality will decline even more, resulting in further population growth. Conversely. if the population declines to $N - \Phi$, the portion that the fixed number harvest contributes to the overall mortality will increase, as will the overall mortality, and hence, the population will decline at an ever increasing rate. The dynamics of a system in which mortality is influenced by a fixed harvest component is inherently unstable. As depicted in Fig. 3, at the point where the line showing the relationship of λ to N intersects the reference line for $\lambda = 1.00$, the system is locally stable. Any departure from that point continues to move the system further from the point, as indicated by the arrows (unless the process is reversed).

Lastly, climatic change and a shift in the nesting location of many of the birds in the Mid-Continent Population may have contributed to the increase in numbers. An anomalous cold area has occurred in the region of Baffin Island and Ungava in recent decades that was most pronounced in April, May, and June, but which affected much of Hudson Bay region and resulted in the persistence of snow and ice (Skinner et al. 1998). In the last decade this climatic anomaly has weakened somewhat. The distribution of breeding lesser snow geese has changed dramatically since the 1940s, when 99% of all Mid-Continent birds bred at sites north of 60°N (Cooch 1958, 1961). This change may be linked

to this climatic anomaly, because by the 1970s 43% bred south of this latitude (Kerbes 1975) where the climate is less severe. Since that time the trend has reversed, so that by 1997, 80% again nested north of 60°N.[3] An example of the recent decline in the percentage of birds nesting in the Low Arctic – sub-Arctic is the present size of the colony at Cape Henrietta Maria, Ontario (cf. Fig. 4).[3] However, as discussed later, the increasing numbers of birds may have exhausted the resource base at these southern sites, forcing birds to nest further north, irrespective of an amelioration of the climatic anomaly. On the west coast of Hudson Bay in the vicinity of the McConnell River the intertidal marshes have been lost (Kerbes et al. 1990) and there has been a decline in the size of the snow goose colony (Kerbes 1983). Significantly, the proportion of blue phase snow geese at Queen Maud Gulf has risen from less than 5% to 17% in recent decades, a proportion similar to that at the McConnell River (Kerbes 1983), suggesting an emigration–immigration event linking the two sites.

There appears to have been a series of years when more favourable conditions prevailed that contributed to above-average reproductive success (Abraham and Jefferies 1997). However, in a number of years (1972, 1978, 1982, 1983, 1992, 1999) late springs associated with the cold anomaly led to reproductive failure, particularly in the northern region of Hudson Bay (Boyd and Madsen 1997; Ganter and Boyd 2000). Hanson et al. (1972) have argued that originally some southern colonies may have established in years with late springs, including the colonies at Cape Henrietta Maria, Ontario, at La Pérouse Bay, and at the McConnell River. In the first of these colonies, for example, the proportion of blue phase birds to white phase birds was similar to that on Baffin Island (75% to 95%), and in addition, Cape Henrietta Maria lies on the migration route of those flocks of Baffin Island geese that follow the west coast of James Bay northwards. Cooch et al. (2001) have shown that at least some of the birds that short-stop and breed in these southern colonies return in subsequent years. Many of these birds may be 2- or 3-year-olds that are breeding for the first time.

Although all the above causes likely have contributed to the increase in the size of the Mid-Continent Population of lesser snow geese, we will provide evidence that the consistent and readily available agricultural food subsidy is the major contributor.

Migration routes of lesser snow geese and foraging behaviour of the Mid-Continent Population

Mid-Continent snow geese commence their southward migration from the Hudson Bay region at the end of August or early September, depending on local conditions, although groups of birds may remain in the Hudson Bay Lowland until late October in favourable years (Mowbray et al. 2000). Band recoveries from birds banded at La Pérouse Bay indicate that the birds migrate through Manitoba and the Dakotas to the Missouri River between Nebraska and Iowa, and then they fly south to the Gulf of Mexico, stopping in Missouri, Arkansas, and northwest Louisiana. They arrive on the coast by 15 November in most years (Bellrose 1980; Mowbray et al. 2000). Spring migration northwards to the breeding grounds begins in February, and most birds arrive on the breeding grounds by mid- to late May. The birds stage at a number of locations en route, such as in agricultural fields adjacent to the Platte River in Nebraska and in similar habitats in southern Manitoba and Saskatchewan. They track the retreating snowline northwards, and large assemblages of geese stage south of the snow line in the Hudson Bay Lowland in May, feeding in those freshwater sedge meadows where the surface layers of sediments are thawed sufficiently to allow birds to forage. Snow geese are voracious foragers, and often high densities of birds will feed in one area. Females forage for up to 12 h/d during spring migration and up to18 h/d on the breeding grounds before nesting when hours of darkness are few (Ganter and Cooke 1996; Mowbray et al. 2000). In salt-and freshwater marshes there are three types of foraging behaviour, namely grubbing, shoot pulling, and grazing, which are strongly linked to seasonal

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[3] K.F. Abraham, R.L. Jefferies, and R.T. Alisauskas. Unpublished data.

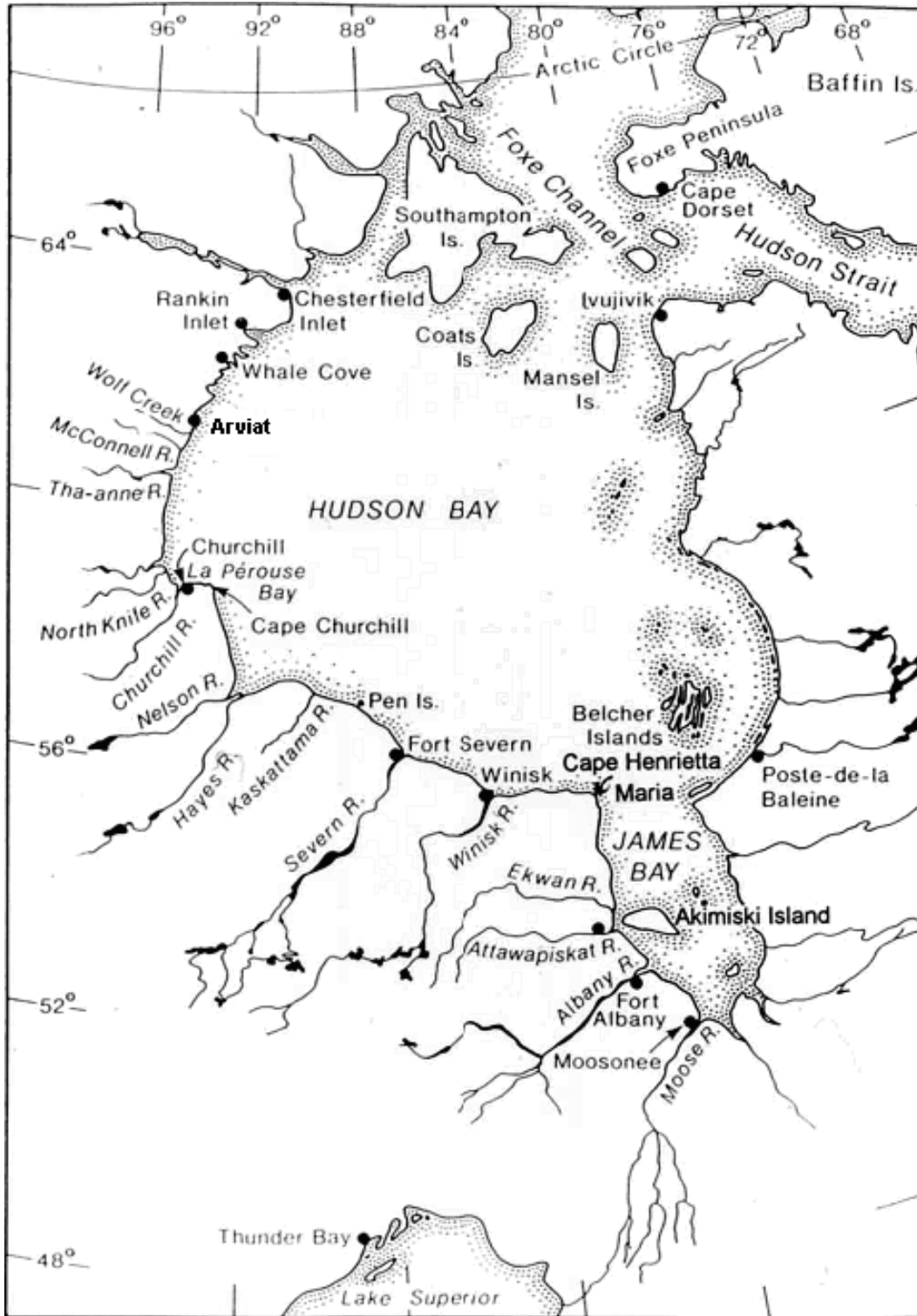**Fig. 4.** Map of Hudson Bay region.

Table 1. Foraging activities of lesser snow geese in the coastal regions of the Hudson Bay Lowland. Most grubbing and shoot-pulling occurs in spring, little takes place in fall.

Activity	Vegetation	Time
Grubbing	Salt-march swards	Spring (Fall)
	Festuca grasslands	Spring (Fall)
Shoot-pulling	Fresh-water sedges	Spring (Fall)
	Lyme-grass	Spring (Fall)
Grazing	Salt-march swards	Summer

changes in the state of vegetation (Table 1) (Abraham and Jefferies 1997). Grubbing (Fig. 5*b*, Fig. 5*d*) occurs primarily in spring in coastal salt marshes immediately after the upper layer of sediment has thawed in the intertidal and supratidal zones, but before the above-ground growth of the prostrate or low-lying salt-marsh grass (*Puccinellia phryganodes*) and sedge (*Carex subspathacea*) has started. This vegetation is the preferred summer forage for family groups of lesser snow geese, which graze on the swards during the post-hatch period. The birds dig in the soft sediment in early spring and remove the roots and rhizomes of these forage species, resulting in exposed sediment with little plant cover. A snow goose can be expected to grub vegetation at a rate of approximately 1 m^2/h at this time of year (Hik 1988). Grubbing also may occur in early autumn, but at a much reduced frequency compared with that in spring. In contrast, shoot-pulling takes place in freshwater marshes, particularly where *Carex aquatilis*, *Eriophorum angustifolium*, and *Dupontia fisheri* are abundant, but formerly it also occurred on beach ridges and gravel bars where *Elymus arenarius* was present (now uncommon because of shoot-pulling) (Ganter et al.1996). Plant nomenclature follows Porsild and Cody (1980). Live shoots, of which the distal portion is marcescent (dead tissue, but still attached) are pulled up by the geese once the ground has thawed, and the living base of the shoot is eaten and the remainder discarded. The base is rich in soluble nitrogen and carbohydrates (Gadallah and Jefferies 1995*a*). Over successive seasons of shoot removal the plants are weakened, resulting in their death and exposure of the underlying moss, peat, or sand (Kotanen and Jefferies 1997).

At the start of the autumn migration about 18% of the diet of lesser snow geese staging in the Hudson Bay Lowland consists of seeds and berries, particularly seeds of *Triglochin maritima* and fruits of blueberry (*Vaccinium* spp.) and other Ericoids (Prevett et al. 1979). On the wintering grounds in the coastal marshes of Texas and Louisiana, subterranean organs of a wide range of species are pulled up and eaten, including alkali grass (*Distichlis spicata*), cord grasses, (*Spartina pectinata* and *S. patens*), Olney bulrush (*Scirpus americanus*), salt-marsh bulrush (*S. robustus*), and cattails (*Typha latifolia* and *T. angustifolia*) (McIlhenny 1932; Lynch et al. 1947; Alisauskas et al. 1988). Lists of plant species that are grazed or grubbed in these marshes are given in Glazener (1946). Lynch et al. (1947) have described the results from this grubbing of below-ground organs by geese (and muskrats), which leads to the development of open-water mudflats ("eatouts") where the geese roost. The damage to the vegetation by geese can be greatly accelerated by livestock grazing of marshes (Bateman et al.1988). Similar eatouts occur in the Atlantic marshes and estuarine marshes in the Gulf of St. Lawrence where greater snow geese (*Chen caerulescens atlantica*) feed on rhizomes of *Spartina alterniflora* (Smith and Odum 1981) or *Scirpus americanus* (or *S. pungens*) (Giroux and Bédard 1987; Giroux et al. 1998). In the Dutch Wadden Sea, greylag geese, *Anser anser*, grub stands of *Spartina* sp. and *Scirpus* sp. (Bakker et al. 1999).

Although in the past some lesser snow geese may have flown directly between the breeding grounds on Hudson and James Bay and the Gulf marshes (Cooch 1955), in the last 40 years most birds use stop-

Fig. 5. Effects of grazing on intertidal and supratidal vegetation in coastal areas of the Hudson Bay Lowland: (*a*) intertidal grazing lawn; (*b*) grubbing of intertidal marsh in early spring; (*c*) an exclosed area in the intertidal area that was established in 1982 when a grazing lawn was present. Now it is surrounded by exposed sediment — the outcome of grubbing by lesser snow geese; (*d*) loss of vegetation, death of willows, and exposure of peat in the supratidal marsh as a result of grubbing.

over sites along the migration routes in both spring and autumn, including Lake Manitoba, National Wildlife Refuges in North and South Dakota, Iowa, and Missouri, and sites in Nebraska and Arkansas (Mowbray et al. 2000). Many of these reserves have been established in agricultural landscapes in the last 40 years, coincident with the increase in crop production and the use of fertilizers. This stepping-

stone pattern of migration compared with a direct flight means that birds can "top-up" en route and are less dependent on available energy and nutritional resources immediately upon arrival at either the breeding or wintering grounds. Alisauskas (1988) has suggested that this stepping-stone pattern may have been a behavioural response to the predictable availability of food resources in wildlife refuges and agricultural fields in the last 40 years. As patterns of land use change, we anticipate on-going changes in the geographical location of staging sites and migration routes. The birds are opportunistic and respond to change by exploiting sources of forage that meet their nutritional requirements at different stages of migration. Much of their feeding in nonagricultural landscapes is in early successional habitats that are undergoing rapid change. Sutherland (1998) has reviewed the evidence of changes in migratory patterns of different bird species in recent decades, including those of the lesser snow goose.

The agricultural food subsidy

Agricultural changes and patterns of goose foraging in coastal prairies of the Gulf States

In the 1920s the Mid-Continent Population of lesser snow geese wintered predominately in the Gulf coastal marshes that then stretched from Port Lavaca, Texas, to the Pearl River, Louisiana (McIlhenny 1932: Lynch et al. 1947; Bateman et al. 1988; Miller et al. 1996). Birds were rarely observed in fields more than 13 km inland from the coast, and the tall grass prairies that were contiguous with the coastal marshes did not support wintering populations of geese (McIlhenny 1932). Rice was grown locally in these prairies in Texas as early as 1850, but the crop was not irrigated and was harvested by hand (Hobaugh et al. 1989). Irrigation of rice began in 1891, but it was not until after World War II that rice production became highly mechanized. Fertilizers and pesticides were added to the land that increased the yield and disease resistance of new varieties of rice (Hobaugh et al. 1989). In the 1960s a second crop each year became commercially feasible with the release of varieties of rice that matured in 100 d (Craigmiles 1975). The second crop only required re-flooding of cut stubble and the application of fertilizer and herbicides. By 1989, the area devoted to rice production in the former tall grass prairies was 526 500 ha in Texas and Louisiana and the term "rice prairies" had been introduced to describe the cultivated land devoted to rice production (Hobaugh et al.1989).

Geese began using rice fields in Texas in the 1920s, but it was not until the 1940s that birds started visiting rice fields in Louisiana. In Texas, the fields are close to the brackish coastal marshes, unlike those in Louisiana, which may be 30 km or more from the coastal marshes. However, initially the use of these rice prairies was minimal, and as late as the mid-1950s the birds were feeding and roosting in the coastal marshes (Hobaugh et al. 1989). It was not until the late 1950s and early 1960s that lesser snow geese began to remain in the rice fields overnight and discontinued their flights to the coastal marshes. This change appeared to be in response to landowners flooding fields with pumped water and restricting hunting in these areas, thereby providing a secure roosting sanctuary (Bateman et al.1988).

The intensive feeding in rice stubble from early October until the end of November coincides with the peak availability of rice after the harvesting of the second crop, which is estimated at 140 kg ha^{-1} (range: 73–214 kg ha^{-1}) (Hobaugh 1984). In December, geese switch their diet to soybean crops that are grown in riparian flatlands as well as young green shoots of the weeds of rice and soybean fields that are often ploughed in winter. The diet may be supplemented with weed seeds, especially during cold weather, and in late winter the subterranean organs of these weedy grasses and forbs are eaten (Alisauskas et al. 1988). Some of the tall grass prairie has been converted to livestock pasture in which rye grass is the dominant species. During the 1960s and 1970s, lesser snow geese fed in rye grass pastures in late winter after the goose hunting season closed. This occurred particularly during cold weather that delayed the germination and growth of weedy annuals in rice and soybean fields (Bateman et al. 1988). In recent years the use of these pastures has decreased, partly because of a decline in their availability and partly because the farmers have resorted to hazing practices to reduce goose damage in sensitive areas (Bateman et al. 1988).

In the late 1960s, lesser snow geese began to winter in rice fields in northeast Louisiana, associated with a decline in numbers in coastal areas of this state that started in the late 1950s. In the 1970s, they also started wintering in Arkansas, which produces more rice than any other state, and numbers increased rapidly throughout the 1980s (Widner and Yaich 1990). The birds are restricted to the eastern third of the state in the Mississippi alluvial valley adjacent to the Mississippi River. The Missouri River valley in northeast Missouri, southwest Iowa, northeast Kansas, and southeast Nebraska is a major staging area for migrating snow geese, particularly in spring, but few used it in autumn prior to 1940. However, from that year onwards it has been used increasingly as an autumn stop-over site and a wintering area, and numbers of birds increased dramatically ($20\times$) from the early 1950s to 1971 (Burgess 1980). In these northern states, where rice cultivation is absent or not widely practiced, the birds started to feed on spilled corn and other crops. Estimates of the time spent feeding in different crops as a percentage of the total foraging time are 80% in corn fields, 5% in soybean stubble, 7% in grassland, and 8% in winter wheat or other areas (Alisauskas et al. 1988).

Crop production, fertilizer use, and population growth of geese

Boyd et al. (1982) suggested that the increase in the Mid-Continental Population of lesser snow geese was due to their ability to benefit from changes in agriculture. Increases in numbers of lesser snow geese along the Mississippi and Central Flyways and on their wintering grounds in the southern United States appear to be closely linked to increases in crop production and to changes in agricultural practices (Fig. 6). These figures show the total area of cultivation of corn (maize) and soybean, the total production of these respective crops, and the application of nitrogen fertilizer for the above crops for selected states, together with the winter index of abundance of lesser snow geese along the Mississippi and Central Flyways. The states listed for each crop are those where production and area of cultivation are highest, and they are broadly coincident with the geographical areas of the respective flyway routes and the wintering grounds of birds.

Although the total area of corn production has not increased since the 1950s, a sharp rise in yield took place between 1970 and 1975, associated with the use of high-yielding crop varieties and the increased use of fertilizers. Winter counts of goose numbers were relatively steady between 600 000 and 800 000 from 1965 to 1975; thereafter, numbers progressively increased to about 2 million birds by 1990. The coefficient of determination of lesser snow geese with corn yield gives an r^2 value of 0.89, and the corresponding value between production and total fertilizer use is 0.84. Coefficients of determination (r^2) between total bird counts and yield of rice and wheat are 0.91 and 0.90, respectively, and the corresponding values between yield and fertilizer use for the two crops are 0.91 and 0.80, respectively (Jefferies et al. 2004a). In contrast to cereal crops, spatial and temporal changes in soybean production in the midwestern states are different. Total area of cultivation has increased almost threefold since 1950, although there has been little overall change since 1980. Over the same period, yield increased fivefold, but in the last decade it has declined somewhat. However, the coefficient of determination between the index of abundance of lesser snow geese and soybean yield is weaker ($r^2 = 0.75$). This food source is not eaten as extensively as corn or rice.

Similar changes in agricultural practices in the Netherlands have led to long-term shifts in the abundance of Anatidae as indicated above (Van Eerden 1990; Van Eerden et al. 1996). In particular, the improved quality of grasslands (crude protein, increased digestibility, longer season) has resulted in a higher carrying capacity for the true grazers amongst the avian herbivores. There has been a sixfold increase in N (kg ha^{-1} a^{-1}) applied to permanent grassland in the western Netherlands between 1939 and 1992. During the 1980s the amount of added fertilizer (N) was, on average, 300 kg ha^{-1}a^{-1}, which has extended the growth of the plants for an extra 10 to 30 d (Van Steenbergen 1977; Van Eerden 1990). The timing of the initial use of agricultural crops by different bird species was not the same; it appears to be linked to the body mass of birds (Mattocks 1971; Owen 1971; Poorter 1981; Prop and Vulink

Fig. 6. The relationships between area cultivated, increases in corn and soybean yields, fertilizer use, and goose counts between 1950 and 1990. (From Jefferies et al. 2004*a*, Figure 2, reproduced with permission of University of Chicago Press. ©2004, The University of Chicago Press.)
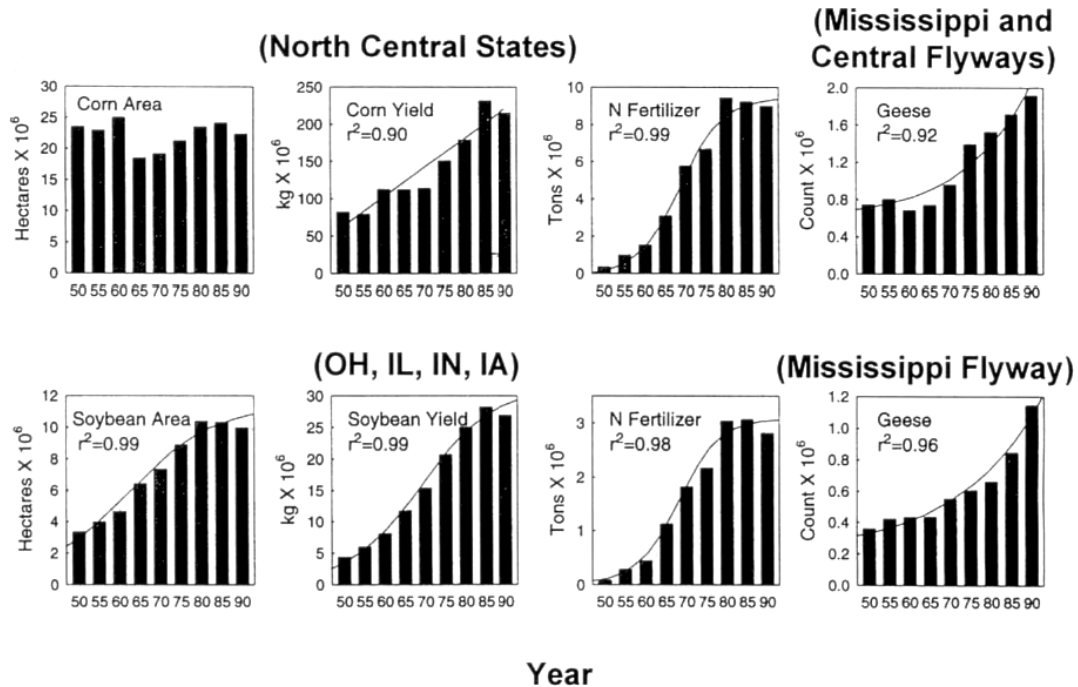
1992; Van Eerden 1984, 1990). With their lower basal metabolic rate, when expressed as Watts per gram of tissue, the larger species can afford to be less choosy with respect to forage quality. In fact, they switched to agricultural crops decades before the steadily improving quality of the pastures enabled the smaller species to take advantage of this new food source (Van Eerden 1984; Van Eerden et al. 1996).

All these examples represent the biomanipulation of populations of the different species at the continental scale.

Energy constraints

Good timing is essential for successful breeding in the seasonal Arctic environment (Klaassen 2002). Drent and Daan (1980) introduced the concept of capital and income breeders that extended the earlier studies of Ryder (1970) and Ankney and MacInnes (1978). Birds in the first group bring resources (capital) acquired on the wintering grounds, or along the migration route, to the breeding grounds that are used in egg production (energy sources and protein). In contrast, income breeders produce eggs from nutrients obtained from the local diet on the breeding grounds. These two types of resource acquisition and investment represent the two extremes of foraging behaviour that meet the dietary demands for reproduction (Bonnet et al. 1998; Meijer and Drent 1999; Klaassen 2002). Originally, the concept was applied at the species level, but more recently it has been applied at the level of the individual, the outcome of phenotypic plasticity in response to environmental conditions. The relationship between body mass of adult females, egg size, and clutch size may influence whether a female is an income or capital breeder. In addition, migratory food stores that are built up in winter and early spring may not provide the required protein and fat composition necessary for egg production, so that a female may be forced to forage selectively at both staging and breeding sites to meet nutritional demands of egg

production (Klaassen 2002). Arctic geese appear to rely on residual body stores following migration to meet at least some of the nutrient and energy requirements of the early stages of breeding (Ryder 1970; Ankney and MacInnes 1978, McLandress and Raveling 1981). Klaassen et al.[4] have detected evidence of a δ^{13}C signature in the down feathers of newly hatched goslings that indicates the presence of some carbon derived from plants with the C_4 type of photosynthesis (e.g., corn–maize) that are absent from the northern breeding grounds. However, it is well known that many Arctic geese forage intensively upon arrival at the breeding grounds in a given year (Budeau et al.1991; Gauthier and Tardiff 1991; Bromley and Jarvis,1993; Ganter and Cooke 1996; Carrière et al. 1999). Both greater and lesser snow geese do not appear to be exclusive capital or income breeders, and considerable annual variation exists in their reliance on post-migratory residual body stores (Choinière and Gauthier 1995, Ganter and Cooke 1996; Klaassen 2002). This variation within a species is influenced by the availability and nutritional quality of the different types of forage at the staging sites and on the breeding grounds, which are dependent on local weather conditions and seasonal phenology in a given year. Meijer and Drent (1999) estimated that, depending on clutch size, between 14% and 55% of egg protein and 46% to 70% of the fat required for egg formation and body metabolism in lesser snow geese are derived from reserves. Using the naturally occurring stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) as a basis, Gauthier et al. (2003) determined that the percentage contribution of endogenous reserves to egg protein and egg lipid was only 22% to 33% and less than 25%, respectively, in greater snow geese from Bylot Island. Females that were in an excellent pre-migratory condition had an earlier laying date than those in a low condition, but clutch size was not related to pre-migratory condition (Bêty et al. 2003). The authors interpret the data as a test of the condition-dependent model of optimal clutch size.

Alisauskas and Ankney (1992) examined habitat use in spring and diets of migrating Mid-Continent adult lesser snow geese. They concluded that in the southern areas of the prairies of the United States in late winter and early spring, the birds primarily forage on a mixture of grasses and seeds that is linked to protein storage. As the birds move further north, there is increasing emphasis on the consumption of carbohydrates at staging sites in southern Manitoba that enhances fat storage. At this stage foods such as spilled corn and the underground organs of aquatic plants, not green vegetation, form the bulk of the diet of the birds, and the rate of fat accumulation per day peaks (Alisauskas 1988, 2002; Alisauskas and Ankney 1992). Lesser snow geese, which nest in the coastal areas of the Hudson Bay Lowland or on Baffin and Southampton Islands, stage in the coastal zones of Hudson and James Bays. In 1983 and 1984, female and male geese utilized between an estimated 77 and 104 g and 120 and 140 g of fat, respectively, on the flights from southern Manitoba to Winisk, Ontario, on the Hudson Bay coast (Alisauskas 1988). Upon arrival in these coastal wetlands, they feed on the shoot bases of sedges and *Senecio congestus*, and on shoots of horsetail (*Equisetum* spp.) (Prevett et al.1985). There is also intensive grubbing of roots and rhizomes of salt-marsh graminoids (Jefferies 1988). The use of different food sources reflects the relative abundances of the various species in different geographical regions of the Hudson Bay Lowland. This feeding also appears to be linked to a second phase of protein storage in the birds (Wypkema and Ankney 1979). Using a period of 35 d (23 May to 27 June), during which time the birds complete nest construction, egg laying and incubation, Wypkema and Ankney (1979) estimated that the protein reserves fall 1 and 2 g/d, respectively, in adult male and female birds. The heavy bout of feeding in the Hudson Bay Lowland and on the breeding grounds allows birds to build up these reserves to sustain this rate of depletion during incubation. Females that do not build up adequate protein are unlikely to breed successfully. Despite the cold weather that often prevails in spring in these coastal wetlands, adults maintained their fat reserves, which appear adequate until hatch when family groups start feeding intensively on new plant growth (Ankney 1977; Ankney and MacInnes 1978; Alisauskas 2002).

In autumn, between the time of moult on the breeding grounds and their departure from staging sites in the coastal wetlands of James Bay in mid-September, adult geese undergo a large increase in

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[4]M. Klaassen, K.F. Abraham, and R.L. Jefferies. Unpublished data.

body weight associated with the build-up of protein and fat reserves that are important for the autumn migration (Wypkema and Ankney 1979). Cooch (1955) provides evidence that historically some birds built up sufficient fat reserves to fly direct from James Bay to Louisiana (a distance of 2700 km). There is also evidence that other birds flew nonstop from the Hudson Bay Lowland in the vicinity of James Bay to Sand Lake, South Dakota, a distance of 1500 km (Wypkema and Ankney 1979), although now most stop in Manitoba. The mean rate of fat utilization for a flight speed of 40 km/h to South Dakota was calculated as 5.65 g/h. Based on the mean fat reserves of birds leaving James Bay, the theoretical flight ranges are 2189 km for adult males, 1977 km for adult females, 1849 km for juvenile males, and 1792 km for juvenile females, which are more than sufficient for the flight of 1250 km (Wypkema and Ankney 1979). The increases in fat reserves of birds in these coastal wetlands, therefore, appear to be very important for the successful completion of the first stage of the southerly migration. On the wintering grounds in Texas peak fat reserves appear to occur in birds in November with low values detected in February (Hobaugh 1985), but this difference may reflect differences among geese feeding in different habitats rather than seasonal changes (Alisauskas 1988). Ankney (1982) described the annual cycle of body weight in lesser snow geese and suggested that the low mass during winter minimized the foraging requirements of the birds. Alisauskas et al. (1988) estimated the energy requirements of adult geese in winter based on a diet of marsh plants (mostly subterranean organs), rice (primarily green shoots), and corn (grain). They estimated the maintenance energy requirement for a 2 kg bird as 167 kcal per bird per day. The birds would need to consume 88.2, 82.7, and 67.6 g (dry weight), respectively, of marsh plants, rice, and corn to meet this demand. These amounts provide 7.1, 22.3, and 8.5 g of protein, all of which are above the estimated maintenance requirement of crude protein per day. However, it is unknown whether the amino acid composition of these different foods is balanced (Alisauskas et al. 1988). The pattern of the acquisition of protein reserves in the greater snow goose during the spring migration is generally similar to that of the lesser snow goose, but there are some differences with respect to fat deposition (Gauthier et al. 1984, 1992). During the spring migration, greater snow geese store fat more rapidly at the beginning rather than late in migration, in contrast to lesser snow geese (Gauthier et al. 1992). At least half the fat reserves accumulated in spring are used during migration, and the birds feed intensively on waste corn and the rhizomes of *Scirpus* sp. at staging sites along the shores of the St. Lawrence Estuary, which increases body fat. Greater snow geese fly approximately 2900 km over the unsettled boreal forest from the St.Lawrence staging sites to Bylot Island, whereas the comparable distance in the case of lesser snow geese is only about 1200 km, hence the need for "topping-up" on arrival at the breeding grounds in the former species. The daily food intake by female geese on the breeding grounds is high: the birds do not have sufficient fat reserves at the onset of incubation to sustain a complete fast during this period (Boismenu et al. 1992). The diet of birds at the breeding grounds on Bylot Island, Nunavut, is similar to that of lesser snow geese during the spring staging in the coastal marshes of James Bay (Bédard and Gauthier 1989; Prevett et al.1985). Some of the plant species, such as *Equisetum* spp., have a high protein content (Gauthier 1993). Prop et al. (1984) also have reported feeding by incubating barnacle geese (*Branta leucopsis*) on the northern breeding grounds. Likewise, white-fronted geese (*Anser albifrons frontalis*) and Canada geese (*Branta canadensis hutchinsii*) feed heavily in coastal marshes on the Kent Peninsula, N.W.T., prior to egg laying (Carrière et al.1999). In all these examples the birds make long-haul flights over unsettled landscapes.

An apparent trophic cascade and the loss of Arctic coastal vegetation

Theoretical constructs

The geometric increase in the Mid-Continent Population of lesser snow geese is estimated to have been between 5% and 7% per year in recent decades (Cooke et al. 1995; Abraham et al. 1996). The population size in late autumn of 1997 (including the young of the year) was in excess of 5 million and possibly as high as 7 million. The breeding colony at La Pérouse Bay on the Cape Churchill Peninsula, 30 km east of Churchill, Manitoba, has increased from about 1300 pairs in 1967 to an estimated 44 500
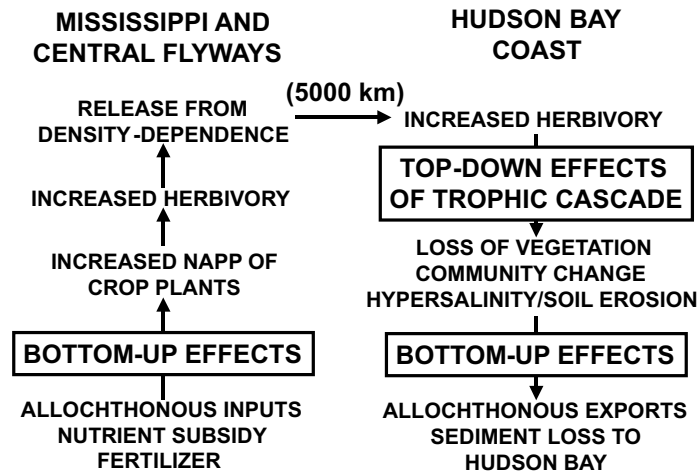
pairs in 1997 (Cooke et al. 1995),[2] and the geographical extent of the colony has increased substantially, similar to other colonies within the coastal zone of the Hudson Bay Lowland (Abraham and Jefferies 1997). Such a large increase in numbers may be expected to have a substantial effect on these coastal lowlands, particularly in the vicinity of breeding colonies. The colony at La Pérouse Bay and its impact on the local vegetation, soils, and other animal species have been studied intensively since 1968 when Cooke and his colleagues started their detailed investigations on the population structure of the colony (Cooke et al. 1995). The results from this long-term study provide considerable evidence of the effects of increasing numbers of birds on these salt- and freshwater wetlands and the plethora of interactions between the geese and their forage species. The findings can be placed in a series of linked theoretical constructs, which are described below.

Patch models have been developed that examine the interactions between consumers (geese) and prey (plants) that are characterized by scale differences in the use of space by both groups (de Roos et al.1998; Richards and de Roos 2001). Prey occupy patches at the local scale and there is a low rate of migration of prey between patches, whereas consumers are homogeneously distributed over the entire area and thus exert a global influence as a result of their broad scale foraging behaviour that extends from the local to the global level. It is possible to incorporate into the models a high number of consumers, which can occur when mobile, widely dispersed individuals flock to a local area where the density of prey patches is high. Such a situation describes the increasing numbers of snow geese seeking decreasingly available patches of preferred forage in the intertidal and freshwater marshes at La Pérouse Bay. The outcome of the models indicates that multiple equilibria can occur, but an equilibriium with a large number of barren patches (exposed sediment or peat) devoid of higher plants is stable and gives rise to an alternative stable state (cf. Holling 1973; Noy-Meir 1975; May 1977, Westoby et al. 1989). The stable state can result from abrupt and rapid changes in vegetation and soils, which are effectively irreversible and which are controlled by positive feedbacks (Maruyama 1963; DeAngelis et al. 1986; Oksanen 1990). Small changes to plant–soil systems indirectly caused by herbivores foraging at saturated densities (high goose numbers) may initiate positive feedbacks, which lead to irreversible catastrophic shifts in vegetative states, the outcome of which is loss of vegetation, a disruption of plant–soil interactions, and irreversible changes in soil properties (Van de Koppel et al.1997; Van de Koppel et al. 2001). The geese are the catalyst of change, which is mediated via the plant–soil system and involves both biotic and abiotic processes.

Two major constraints on the growth of herbivore populations are resource limitation and predation. Where a simple trophic ladder exists consisting of primary producers, consumers, and predators, if the population growth rate of predators declines, consumer numbers (herbivores) are predicted to increase dramatically, resulting in a true trophic cascade characterized by a sustained reduction in the biomass of the primary producers and changes in the species assemblages of communities (Paine 1969; Power 1992; Strong 1992; Polis and Strong 1996). The same effect on primary producers may occur if consumers increase in number as a result of an allochthonous external food subsidy, without a concomitant increase in predation (Polis 1999). Because there is not a sustained reduction in predator numbers that triggers the onset of the changes here, this is not a "true" trophic cascade, and we have used the term "apparent trophic cascade" to describe the effects of a burgeoning population of snow geese on vegetation and soils in Arctic wetlands, but especially the coastal marshes of the Hudson Bay Lowland. The consumer has increased in numbers in response to an agricultural subsidy triggered by the bottom-up effect of the application of fertilizers to increase crop yields (Fig. 3). The top-down impact of the consumer on the primary producer occurs 3000 to 5000 km away on the breeding grounds in the coastal regions of the Hudson Bay Lowland and at other nesting sites in the Arctic. Events in temperate biomes may indirectly impact Arctic environments via their effects on migratory species. This migratory connectivity (Webster et al. 2002) links temperate and Arctic biomes (Fig. 7).

The lack of a sustained response of predators to increased numbers of consumers implies that there are constraints on the growth of predator populations that are not completely understood. Unfortunately,

Fig. 7. Summary flow diagram of major changes associated with allochthonous inputs in relation to the wintering and breeding areas and migration routes of the Mid-Continent population of lesser snow geese (From Jefferies et al. 2004*b*, reproduced with permission of the Society of Integrative and Comparative Biology. ©2004, Allen Press Inc., Lawrence, Kansas, USA.)

MISSISSIPPI AND CENTRAL FLYWAYS   **HUDSON BAY COAST**

(5000 km)

RELEASE FROM DENSITY-DEPENDENCE → INCREASED HERBIVORY

↑

INCREASED HERBIVORY

↑

INCREASED NAPP OF CROP PLANTS

BOTTOM-UP EFFECTS

↑

ALLOCHTHONOUS INPUTS NUTRIENT SUBSIDY FERTILIZER

TOP-DOWN EFFECTS OF TROPHIC CASCADE

↓

LOSS OF VEGETATION COMMUNITY CHANGE HYPERSALINITY/SOIL EROSION

↓

BOTTOM-UP EFFECTS

↓

ALLOCHTHONOUS EXPORTS SEDIMENT LOSS TO HUDSON BAY

there has been no systematic monitoring of predator numbers over the years at La Pérouse Bay or at other goose nesting areas. The primary predators of eggs and goslings at breeding colonies in the Hudson Bay Lowland are herring gulls (*Larus argentatus*), parasitic jaegers (*Stercorarius parasiticus*), ravens (*Corvus corax*), and Arctic foxes (*Alopex lagopus*). Whole clutch loss occurs at varying rates (mean 8%, Cooke et al. 1995). The entire brood may be taken soon after hatch by herring gulls hunting in groups (mean 8.5%, Cooke et al. 1995). Survival rates of goslings are lower when goslings are small and dependent on parental care (Williams et al. 1993). In recent years polar bears (*Ursus maritimus*) and Arctic fox have become important predators of both adults and goslings during the post-hatch moult period in the inter- and supratidal zones of La Pérouse Bay. The predation by bears appears to be local as far as we can determine, although it has been observed at other colonies (e.g., Akimiski Island, Nunavut), and it has led to a near total loss of goslings of family groups that persistently forage in the immediate vicinity of the bay in the post-hatch period. Foxes and wolves, which are nomadic predators but not migratory on a scale matching geese, cannot act as a top-down regulator of their summer prey, which is migratory and unavailable from late August to late May. Neither species is able to maintain a sustained increase in numbers in response to the high goose numbers in summer, when winter conditions limit food availability.

The increased use of agricultural lands for wintering and for spring and fall migration is a potential route for increased exposure and intake of pesticides, fungicides, and herbicides, which could reach levels in eggs that may lead to increased rates of gross developmental abnormalities amongst embryos and near-hatch goslings. The baseline rate of gross external abnormalities amongst lesser snow geese at La Pérouse Bay is 3.937×10^{-4} per egg (95% confidence limits: 1.7053×10^{-4} to 6.507×10^{-4}) (Rockwell et al. 2003*a*). The mean is near the upper end of the range of rates reported for similar deformities in a range of species in minimally or uncontaminated habitats. However, the relative distribution of defects of the beak are inconsistent with the rates of spontaneous abnormalities of the beak (Romanoff 1972). If this higher frequency of beak defects persists or increases, then it is likely that contaminants, most probably insecticides, acting as type 1 teratogens are responsible (Rockwell et al. 2003*a*).

Table 2. Types of foraging on coastal species that are heavily utilized by lesser snow geese on the Cape Churchill Peninsula.

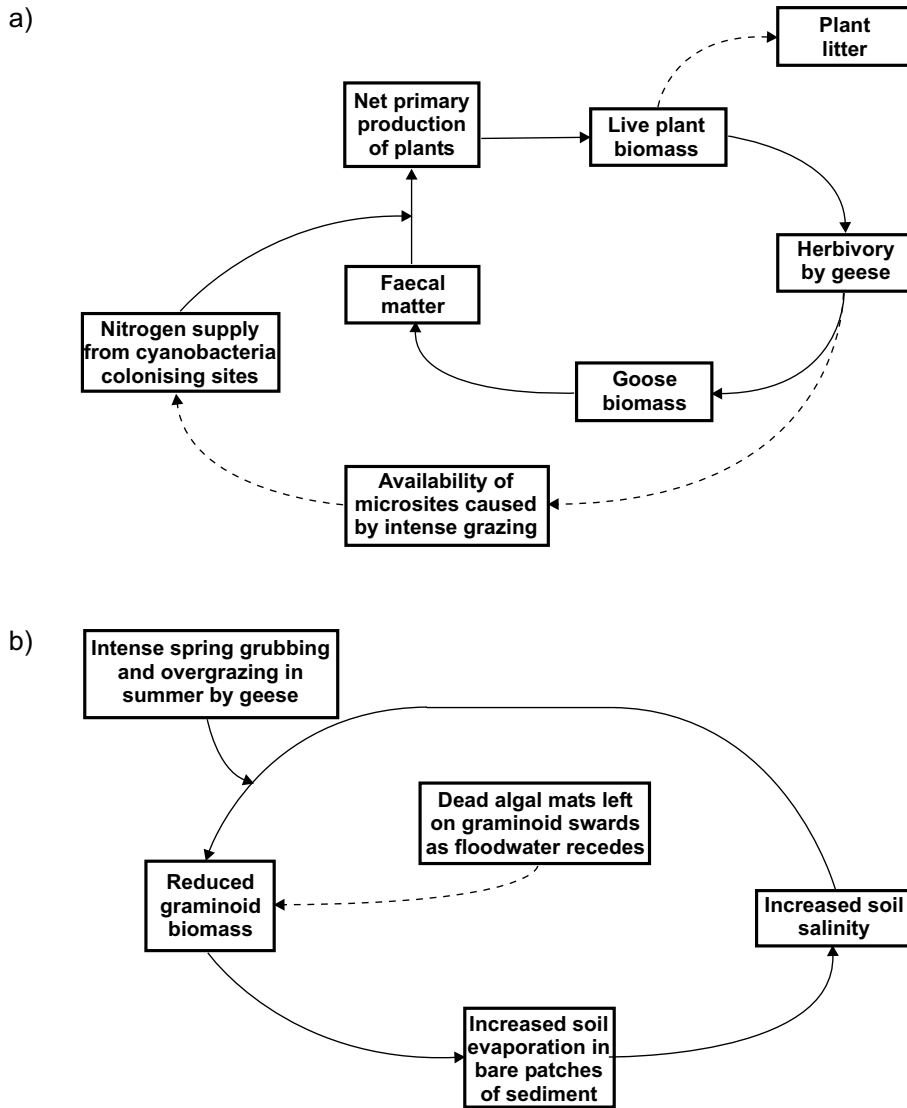|	Grazed	Grubbed	Shoot-pulled
Salt-marsh monocotyledons			
Puccinellia phryganodes	√	√	—
Carex subspathacea	√	√	—
Festuca rubra	√	√	—
Calamagrostis deschampsioides	√	√	—
Triglochin maritima	√	√	—
Triglochin palustris	√	√	—
Salt-marsh dicotyledons			
Plantago maritima	√	√	—
Potentilla egedii	√	√	—
Chysanthemum arcticum	√	√	—
Stellaria humifusa	√	√	—
Senecio congestus	—	—	√
Fresh-water marsh monocotyedons			
Carex aquatilis	√	—	√
Eriophorum angustifolium	√	—	√
Other *Carex* species	√	—	√

Plant–herbivore interactions: the tale of two positive feedbacks that occur either in summer or spring

The interactions between snow geese and their preferred forage species are inherently unstable and are sensitive to goose numbers and the intensity and type of foraging. The foraging geese initiate two positive feedbacks, depending on their numbers and the time of year (Fig. 8) (Jefferies et al. 1985; Srivastava and Jefferies 1996). In the intertidal salt marshes of the Hudson Bay Lowland when the density of geese is low and swards are intact and not damaged (see below), grazing during the post-hatch period in summer can result in increased above-ground primary production of the intertidal graminoid species in grazed swards compared with that in ungrazed swards, as well as increased N content of the leaves (Cargill and Jefferies 1984b; Hik and Jefferies 1990). The second positive feedback occurs in spring and results in the destruction of the salt-marsh grazing lawns (sensu McNaughton 1984) and exposure of intertidal sediment. It is dependent on the presence of high densities of geese that grub the salt-marsh swards where the ground is thawed, which results in loss of vegetation and soil degradation (Jefferies 1988). Hence, the outcome of the feedback is sensitive to numbers of geese, the type and intensity of foraging, and the extent and quality of the graminoid swards. The increasing area of exposed sediment acts as a negative feedback to stop the positive feedback. The types of foraging by lesser snow geese on the different coastal species are shown in Table 2.

The first positive feedback: over-compensatory growth of forage plants during the post-hatch period in summer in response to low densities of grazing geese

The preferred prostrate forage species on low-lying Arctic shores, including the inter- and supratidal salt marshes at La Pérouse Bay, are an asexual triploid, stoloniferous grass, *Puccinellia phryganodes,* and a rhizomatous sedge, *Carex subspathacea.* The latter flowers and fruits very infrequently, especially when grazed (Jefferies 1988). In North America, only the sterile triploid form of the grass is present, hence seed set is absent (Dore and McNeil 1980; Jefferies and Gottlieb 1983). The dominant forage

Fig. 8. Positive feedbacks between lesser snow geese and their forage plants in intertidal marshes in the Hudson Bay Lowland: (*a*) feedback at low goose densities leading to increased primary production of forage plants within the season, (*b*) positive feedback at high densities of lesser snow geese resulting in destruction of intertidal grazing lawns (after Bazely and Jefferies 1996).

a)

```
                                          ┌──────────┐
                                          │  Plant   │
                                          │  litter  │
                                          └──────────┘
   ┌────────────┐        ┌────────────┐
   │ Net primary│        │ Live plant │
   │ production │───────▶│  biomass   │
   │ of plants  │        └────────────┘
   └────────────┘               │
         ▲                       ▼
         │                ┌────────────┐
   ┌────────────┐         │ Herbivory  │
   │  Faecal    │         │  by geese  │
   │  matter    │         └────────────┘
   └────────────┘               │
   ┌──────────────┐      ┌────────────┐
   │ Nitrogen     │      │   Goose    │
   │ supply from  │◀─────│  biomass   │
   │ cyanobacteria│      └────────────┘
   │ colonising   │
   │ sites        │
   └──────────────┘
         ▲   ┌────────────────────┐
         │   │ Availability of    │
         └───│ microsites caused  │
             │ by intense grazing │
             └────────────────────┘
```

b)

```
   ┌──────────────────────┐
   │ Intense spring       │
   │ grubbing and         │
   │ overgrazing in       │
   │ summer by geese      │
   └──────────────────────┘
            │                    ┌──────────────────┐
            ▼                    │ Dead algal mats  │
   ┌──────────────┐             │ left on graminoid │
   │  Reduced     │◀╌╌╌╌╌╌╌╌╌╌╌╌│ swards as         │
   │  graminoid   │             │ floodwater recedes│
   │  biomass     │             └──────────────────┘
   └──────────────┘                    ┌──────────────┐
            │                          │ Increased    │
            ▼                          │ soil         │
   ┌──────────────┐                   │ salinity     │
   │ Increased    │                    └──────────────┘
   │ soil         │
   │ evaporation  │───────────────────────┘
   │ in bare      │
   │ patches of   │
   │ sediment     │
   └──────────────┘
```

species in the adjacent freshwater sedge meadows is *Carex aquatilis*, which can grow to a height of 50 cm or more and increasingly has become an important food plant with the loss of salt-marsh vegetation (Kotanen and Jefferies 1997).

During the late 1970s and early 1980s, the breeding colony of lesser snow geese at La Pérouse Bay removed up to 90% of the net above-ground primary production (NAPP) when family groups grazed intertidal swards in summer during the post-hatch period from mid-June to mid-August (Cargill and Jefferies 1984*b*). Goslings increased in weight from c. 80 g at hatch to about 1500 g at fledging (Cooke et al. 1995). In the absence of grazing, growth of the salt-marsh swards is nitrogen-limited

(Cargill and Jefferies 1984*a*). A low to moderate grazing intensity, as occurred in the decade mentioned above, increases both soil nitrogen availability for plants and NAPP via the first of the positive feedback mechanisms (Figs. 5*a* and 8*a*).The increase in NAPP by the end of the season is about 50% that of ungrazed swards (Cargill and Jefferies 1984*b*; Hik and Jefferies 1990). Within a season, flow of soil N is increased by a rapid recycling of this element from goose faeces (Bazely and Jefferies 1985; Ruess et al. 1989). Passage of food through the gut is fast (60–90 min) and adult geese defaecate, on average, once every 4 to 5 min. Much of the soluble nitrogen moves from faeces to the soil within 48 h of deposition (Kotanen 2002). When experimental additions of fresh goose droppings are added to swards, there is a subsequent increase in NAPP compared with that in control plots (Bazely and Jefferies 1985). Thus, goose grazing initiates a positive feedback, in which increased growth of salt-marsh swards is driven by improved N availability derived from faecal inputs. When captive goslings graze plots of these graminoids for different lengths of time, there is a subsequent increase in NAPP, depending on the length of the grazing period (Hik and Jefferies 1990). The results of this experimental study using captive goslings strongly supports the herbivore-optimization models of Dyer (1975) and McNaughton (1983*a*), one outcome of which is that plants show over-compensatory growth in response to herbivory. However, similar studies using captive goslings in Alaska indicate no effect on biomass or the N content of tissues of *Carex ramenskii* and *Triglochin maritima* (Zacheis et al. 2002*a*). They suggest that the low density of foraging geese may have contributed to the apparent lack of response. Nevertheless, even light grazing during the spring migration altered the species composition of plant communities and affected forage availability in the salt marshes of Cook Inlet, Alaska (Zacheis et al. 2001).

The growth habit of the two low-lying graminoid forage species (*Puccinellia phryganodes* and *Carex subspathacea)* at La Pérouse Bay enables an increase in NAPP to occur within the season in response to defoliation and the addition of N. In both species there is a very rapid turnover of leaves (Kotanen and Jefferies 1987; Bazely and Jefferies 1989*a*). Most leaves (<1 cm) are grazed, but regrowth occurs because the basal meristem remains intact in clipped leaves. The geese are not normally able to graze the prostrate or low-lying shoots of these species because they are too close to the ground for their bills to access shoots. *Puccinellia phryganodes* is stoloniferous, hence there is considerable axillary shoot development, particularly in grazed swards. Ungrazed or partially grazed leaves of this grass live approximately 24 to 35 (45) d, and new juvenile leaves, which have a high N content, develop at intervals of about 12 d from mid-June until early August. In grazed swards leaf births per axillary shoot are higher than those in ungrazed swards (Bazely and Jefferies 1989*a*). The life expectancies of partially grazed or ungrazed leaves of *Carex subspathacea* in grazed swards are between 33 and 35 d, in contrast to expectancies of 45 to 47 d for leaves from ungrazed swards (Kotanen and Jefferies 1987). Lastly, most of the root/rhizome systems of both species is located in the top 3 cm of sediment, which allows easy access to soluble nitrogen derived from faeces. In early spring, the upper layer of the soil warms rapidly, which encourages early growth of these forage species. Air temperatures may be less than 5 °C, but soil surface temperatures reach 15 °C under high irradiance at summer solstice (Bazely and Jefferies 1989*b*; Wilson and Jefferies 1996).

Intense grazing also maintains open swards with bare microsites that are colonized by nitrogen-fixing cyanobacteria, particularly early in the season (Bazely and Jefferies 1989*b*). Results from nutrient budgets of the system indicate that inputs of nitrogen from fixation balance nitrogen incorporated in the body mass of the geese when swards are intact (not grubbed) (Wilson and Jefferies 1996; Walker et al. 2003). Recently, we have established that the availability of soluble soil organic N relative to inorganic N is high, particularly in summer (Henry and Jefferies 2002). Much of the soluble organic N in soils consists of amino acids. The different amino acids present are similar (but not identical) to the soluble amino-acid signature of faeces. Based on studies using the stable isotopes of carbon and nitrogen, *Puccinellia phryganodes* can absorb amino acids intact from the soil despite competition from soil microorganisms. The free amino acids may contribute substantially to the total N uptake in this grass (and therefore plant growth) in summer when supplies of inorganic N in soils are low because of

uptake by plants and microorganisms. Hence, amino acids derived from the geese appear to facilitate plant growth at a time of nitrogen shortage when demands for forage are high (Henry and Jefferies 2003*a*, 2003*b*). In similar studies in Alaska, Zacheis et al. (2002*b*) have found no effect of the presence of geese on organic N availability in soils beneath grazed salt-marsh swards. However, higher rates of net N mineralization were detected in these soils, which were probably the outcome of geese trampling plant litter into the sediment and nitrogen fixation by cyanobacteria on the soil surface.

The second positive feedback: loss of vegetation as a result of spring grubbing by geese at high densities

Late spring thaws in some years during the last 20 years in the Hudson Bay region, coincident with the increasing goose population, have resulted in large numbers of staging geese at La Pérouse Bay during the pre- and early nesting period (Jefferies 1988; Skinner et al. 1998), in addition to the local breeding population. At this time, the birds grub in ground that has thawed for the roots and rhizomes of their preferred salt-marsh graminoids, which initiates the second positive feedback process (Fig. 8*b*). This has led to the destruction of the intertidal salt-marsh swards and the death of willow bushes in the supratidal marsh, the latter largely from the effects of hypersalinity (Jefferies 1988; Kerbes et al. 1990; Iacobelli and Jefferies 1991; Srivastava and Jefferies 1995, 1996). Grubbing acts as a trigger that results in near-irreversible changes in sediment properties in the intertidal and supratidal marshes, including the development of hypersalinity in summer, compaction of sediment, decrease in infiltration rate, loss of soil nitrogen and organic matter, and the depletion of the soil seed bank (Iacobelli and Jefferies 1991; Srivastava and Jefferies 1996; Chang et al. 2001; McLaren 2003). On occasions, the salinity of the soil solution can reach 120 g/L of solutes in mid-summer, almost $3 \times$ the salinity of seawater and $9 \times$ the salinity of inshore water along the north coast of Cape Churchill[5] (Iacobelli and Jefferies 1991). The loss of a seed bank is associated with a decline in seed viability, an absence of a seed rain, and erosion of the thin veneer of organic matter (ca. 5.0 cm in depth) that lies above the underlying mineral sediment (Chang et al. 2001). Once most of the vegetation has been lost as a result of grubbing, increased evaporation from the exposed sediment occurs, which draws inorganic salts to the surface by capillary action from the underlying marine clays. These were deposited from the time when the region was beneath the Tyrell Sea from the early to the late Holocene (i.e., the land has since risen above the sea as a result of isostatic uplift; cf. Hansell et al. 1983). The salts give rise to the hypersalinity that develops in summer, and this, together with the other adverse changes in soil properties mentioned above, kills any remaining vegetation. In spring when the salinity is lower, extensive biocrusts composed of a community of cyanobacteria, diatoms, and mites develop on exposed soil surfaces in the intertidal zone where the thin organic layer still remains. The community is transitory, it rapidly dries out in summer as aridity and hypersalinity develop, and either it remains as a salt-encrusted hardened layer or it may be blown away with the remaining soil organic matter exposing the underlying mineral sediments (Fig. 5*c*). In the foremarsh at the seaward edge of the intertidal marsh at La Pérouse Bay, newly established patches of *P. phryganodes* are rapidly grubbed by staging geese and the local breeding population, which severely limits long-term establishment of vegetation in this zone. In summary, the second feedback is composed of coupled biotic and abiotic components. The biotic effect (grubbing) acts as a trigger for the abiotic effect (subsequent changes in soil properties).

Patch dynamics and loss of vegetation

The hostile soil conditions depress the clonal growth of the two salt-marsh graminoids and the ability of individuals to establish from vegetative fragments (seed set does not occur in *Puccinellia phryganodes* and is a rare event in *Carex subspathacea*) (Chou et al. 1992; Srivastava and Jefferies

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[5]R.L. Jefferies. Unpublished data.

1995, 1996; McLaren 2003). Experimental studies indicate that if the diameter of patches of exposed soil exceeds 20 cm, re-colonization of the sediment by inward clonal growth of *P. phryganodes* from an adjacent intact sward or from plant fragments that root in the sediment is very slow, because of deleterious changes in soil properties (McLaren 2003). In addition, developing shoots of these graminoids in early summer do not penetrate the hardened thick algal crust below which anaerobic conditions often develop. Whether anoxia or mechanical impedance or both restrict plant growth is unknown. As a result, it is very difficult to re-establish tillers of *Puccinellia phryganodes* in these consolidated, degraded soils without at first amending the soil with mulch and fertilizer (Handa and Jefferies 2000).

Patches of ungrazed or lightly grazed vegetation vary greatly in size and can be contiguous, but over time patches of intact vegetation become smaller and smaller as the effects of spring grubbing and the subsequent abiotic processes reduce their area. Hence, both the mean and variance in patch size decline over time. In the intertidal zone and to a lesser extent the supratidal marsh, the highly fragmented vegetative mosaic is ultimately lost, which leaves an alternative stable state of exposed hypersaline sediment in which re-establishment of vegetation is long term (>20 years) (Hik et al. 1992; Handa et al. 2002; Jefferies and Rockwell 2002). A fully parameterized model with alternate stable states simulating N flows within the intertidal system at La Pérouse Bay in response to goose herbivory (Walker et al. 2003) indicates that grubbing limits the input of N from fixation and the system collapses. A small increase in the overwinter survival rate of the geese (one result from the agricultural food subsidy) and the resultant increase in grubbing are sufficient to bring about the collapse of the system.

Re-establishment of vegetation in unamended intertidal soils requires the availability of unconsolidated soft sediment in which fragments of *Puccinellia phryganodes* or *Carex subspathacea* (generated by goose foraging) can root and colonize (Chou et al. 1992). Sites of this type are uncommon and depend upon erosion of consolidated sediments and their re-deposition at sites that are usually in river channels or seaward of existing sediments (Handa et al. 2002).

Small melt ponds (<4 m in diameter) are present in the inter- and supratidal marshes at La Pérouse Bay in spring, some of which are formed initially when geese grub and create a depression in which melt water collects (Jefferies et al. 1979). The accumulated water frequently floods graminoid swards adjacent to the depression, and the input of faecal matter into the warm, shallow water (~20 °C; air temperature <5 °C) may lead to extensive algal growth. As the water level falls in late spring, the decaying algal mat is stranded on the graminoid vegetation. The anoxic conditions beneath the mat kill the underlying plants and exposed sediment appears by mid-summer.

Loss of the remaining small patches of vegetation (<10 m^2) creates a homogeneous landscape at a larger scale, as a result of the coalescence of areas of exposed sediment in the intertidal zone. This can be detected with the use of LANDSAT imagery (Fig. 9), not just at La Pérouse Bay, but elsewhere around the shores of the Hudson Bay Lowland where the effects of grubbing by staging geese are associated with the presence of nesting geese[6] (Jano et al. 1998). The outcome of these processes is that an ecological sere (the early successional vegetated intertidal zone) has been lost, similar to the process of desertification in the Sahel (cf. Graetz 1991). An abrupt transition is created from exposed tidal flats to freshwater sedge meadows or willow and heathland communities, where formerly salt-marsh communities existed seaward of the transition.

The remote-sensing imagery also shows the effect of shoot-pulling in freshwater sedge meadows inland from the salt marshes. Where the surface layer of peat has thawed the geese are able to pull up shoots of sedges and consume the basal portion. This type of foraging is particularly prevalent where there are colonies of nesting geese and melt water is available. The water thaws the basal portion of the plant and the surrounding soil surface. The annual loss of shoots in spring weakens the plants, which die, exposing a moss layer or the underlying peat. If these dry out in summer, the result is the death of mosses and a loss of basal cover of vegetation. Oxidation processes, together with wind and water

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[6]A.P. Jano. Unplublished data.

Fig. 9. Satellite image of vegetation changes at La Pérouse Bay from 1973–1993. Red refers to areas that have lost vegetation over the period, green indicates no net change and blue indicates water (Image prepared by Andrew Jano, Ontario Ministry of Natural Resources. From Jano et al. 1998, reproduced with permission of the British Ecological Society. ©1998, Blackwell Publishing, Oxford.)
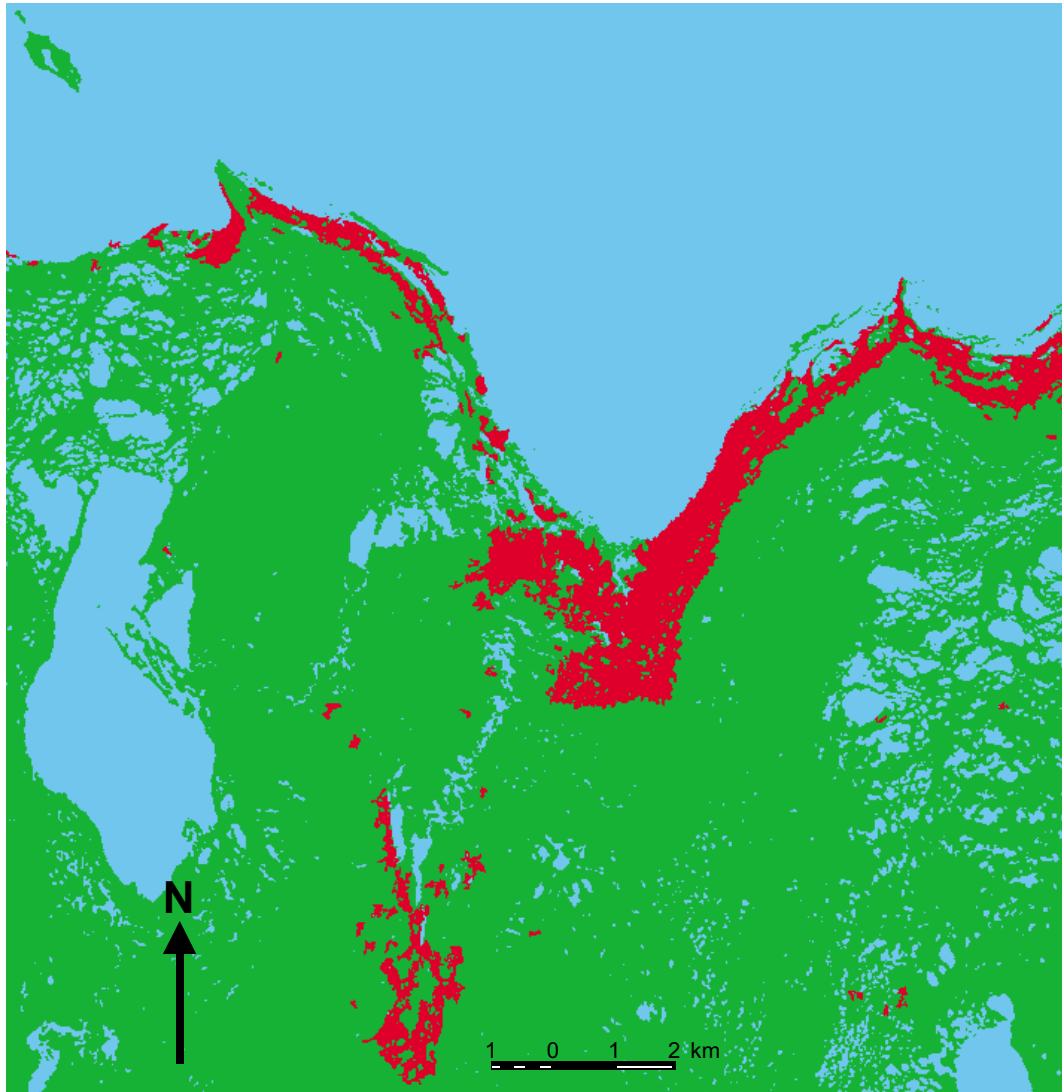
erosion, result in the loss of peaty material and exposure of the underlying mineral base, which may be calcareous marl, glacial gravels, or marine clay. Extensive areas of peatland have either been lost or are denuded of vegetation on the west coast of Hudson Bay in the vicinity of Arviat (Eskimo Point) (Kerbes et al.1990). Likewise, loss of sedges in shallow ponds leads to the break-up and decomposition of the sedge tussocks (Kotanen and Jefferies 1997). Organic debris is suspended in the water column and the sediment surface is very unstable, as wind action is continually re-working the organic material. Under these conditions no re-establishment occurs. With further loss of vegetation anticipated, these degraded

peatlands should become even more evident on the remote-sensing images, as the geese continue to forage in these freshwater sedge meadows.

An apparent trophic cascade

It is important to stress that the effect of the consumer on these coastal ecosystems is not confined solely to changes in vegetation and soils of the inter- and supratidal marshes and the adjacent freshwater sedge meadows. In addition to the above habitats, beach ridges and riverine marshes are adversely affected, leading to a loss of vegetation and changes in plant species abundances.[7] The long-term decline in forage availability has impacted directly the different fitness components of the goose population (Cooke et al. 1995; Cooch et al. 2001). From 1973 to 1992 there was a long-term decline in clutch size from approximately 4.25 to 3.4 (adjusted for laying date). Food availability on migration and locally is the likely prime proximate mechanism influencing clutch size (Cooke et al. 1995). Mean annual body mass and tarsus and culmen length of pre-fledging goslings declined significantly by approximately 16%, 4%, and 2%, respectively in cohorts hatching between 1976 and 1988, resulting in a similar decrease in the size of locally hatched adults (Cooch et al. 1991). Goslings reared by the same individual adult female tracked over several years were smaller in size in later years, suggesting that the general decline reflected a non-genetic change in gosling growth rates during the fledging period (Cooch et al. 1991). The decrease was not dependent on mean hatch date, egg or hatch mass, or post-hatch weather. The probability of total brood loss between hatching and fledging has increased from 10% during the early 1970s to 20 to 40% during the late 1980s (Cooke et al. 1995), and in all likelihood it has increased further in the 1990s. The mean annual survival of young banded just before fledging declined from 0.60 to about 0.30 over the period 1970 to 1987 (Francis et al. 1992), but unfortunately data are unavailable for the 1990s. Most surviving females return to their natal colony, and it is assumed that the cohort-specific return rate to the colony is proportional to the immature survival rate (Cooke et al. 1995). Thus, there is a cost to philopatry with respect to clutch size, survival, and body mass of goslings if the female returns to the original brood-rearing area in subsequent seasons. In dramatic contrast with the decreased survival of immature birds, adult survival rate has increased commensurate with the increase in the size of the population, the agricultural food subsidy in winter, and a decline in the rate of deaths attributable to hunting before 1999 (Francis 1999; Cooke et al. 1999; Cooch et al. 2001).

During the last decade, the breeding population at La Pérouse Bay has become widely dispersed on the Cape Churchill Peninsula, both during the nesting phase and the post-hatch period, but few data are available on the reproductive success of birds in these newly occupied alternative habitats. In years with early springs, such as 1977 and 2001, melt water drains from the coastal sedge meadows before nesting commences and geese nest on the strings (raised ridges that are a feature of sub-Arctic mires). In the event of global warming, this nesting pattern may be expected to become more prevalent. In the last 20 years the snow goose population has expanded geographically during the post-hatch period, and small family groups have become widely scattered throughout the northern section of the Peninsula where they forage primarily on freshwater sedges. This creates a doughnut effect, marked by a resource loss and an absence of snow geese in the originally occupied core area of La Pérouse Bay (occupied for >40 years). The few goslings that remain with parents at La Pérouse Bay during the post-hatch period only weigh about 850 g in early August (1200 g is the expected weight at that time), and they do not survive to undertake the autumnal migration.[8] Since the late 1980s, those birds that nested at La Pérouse Bay itself mostly used the relatively intact salt and freshwater marshes on the east coast of the Cape Churchill Peninsula during the brood-rearing phase. Family groups with young goslings have been observed in successive years moving from the vicinity of La Pérouse Bay to these marshes. The body mass of goslings from these marshes, as distinct from those remaining at La Pérouse Bay in years

[7] K.F. Abraham, R.L. Jefferies, and R.F. Rockwell. Unpublished data.
[8] R.F. Rockwell. Unpublished data.

during the 1990s, has stayed high, and it is similar to the mean weight of goslings at the latter site in the 1970s (Cooch et al. 1993). Recently, however, on-going destructive foraging has depleted even these alternative resource bases, so that salt-marsh vegetation, in particular, has been lost from most sites on the Peninsula. Geese no longer nest in any numbers at La Pérouse Bay, and in 2000 and 2001 Ross's geese and Canada geese often outnumbered snow geese and their families on the degraded intertidal flats during the post-hatch period (Pezzanite 2003). The same changes occurred earlier on the west coast of Hudson Bay[9] (Kerbes et al.1990).

Goslings are only dependent on the availability of the easily digestible and accessible (as measured in bites per minute) N-rich leaves of salt-marsh plants in the damaged intertidal marshes (or brackish-water plants, such as *Dupontia fisheri*) during the first 14 d of life (Gadallah and Jefferies 1995*b*); thereafter, their gut is sufficiently developed for them to utilize other forage species, including freshwater sedges. Hence, although the local populations of snow geese traditionally did not forage extensively in these freshwater marshes, they have quickly adjusted to the loss of intertidal vegetation and modified their foraging behaviour, thereby escaping density dependence. Recently, Ngai (2003) has established that in contrast to the salt marshes, which are nitrogen limited, the adjacent freshwater sedge meadows are phosphorus limited. In addition, many meadows are mesotrophic, in which the availability of calcium is lower than that in salt-marsh soils, and this is reflected in the calcium concentration in the vegetation (Ngai 2003). It is possible that the decline in gosling weight during recent decades is not just a reflection of a deteriorating resource base linked to destructive foraging but also a consequence of a smaller structural size. Increasingly inadequate intakes of phosphorus and calcium as the birds are forced to forage more in freshwater sedge meadows may contribute to a decline in skeletal mass.

Loss of vegetation and the deterioration in the condition of coastal habitats have affected other taxa besides flowering plants and geese. As mentioned earlier, hypersalinity destroys willow bushes in grubbed areas in the supratidal marsh and only the woody skeletons remain. Vegetation loss in the supratidal marsh begins when the graminoid ground cover beneath near continuous stands of low willow bushes is grubbed by snow and Canada geese in spring. The small patches (4 m^2) of exposed surface sediment become hypersaline, and the shallow-rooted willow bushes in the vicinity of the patches die. When this happens the stands of willow shrubs become smaller in area, which is reflected in a decline in the mean length of a stand along linear transects. Initially, the exposed patches of sediment are irregularly distributed and the variance associated with the stand mean length is high. As goose grubbing continues over several years, the remaining stands decrease in area and their mean length further declines. With subsequent decreases in area, the stands tend to become similar in size, characterized by a low variance of their mean length. The reverse pattern of change occurs with respect to the exposed patches, which increase in area over time, coalesce, and their mean length and variance increase. The changes may occur gradually or abruptly, depending on the extent of grubbing, prevailing weather conditions, and the proximity of bushes to exposed patches. Savannah sparrows (*Passerculus sandwichensis*) nest at the base of live willows where there is ample grass for nest construction and concealment. The 63% decline in vegetative cover in this habitat over the last 25 years coincides with a decline of 77% in the number of nesting pairs of this local population that is linked to processes associated with the destructive foraging by geese (Rockwell et al. 2003*b*). Other passerines, such as blackpoll warblers (*Dendroica striata*), American tree sparrows (*Spizella arborea*), and Lapland longspurs (*Calcarius lapponicus*), may be similarly affected by changes to their preferred habitats brought about by goose foraging.

The changes have led both to a sharp decline in the abundance of soil invertebrate species and a loss of some species in the supratidal marsh, particularly spiders and beetles that are an important food source for passerines and shorebirds (Milakovic and Jefferies 2003). The same trend is evident in midge (Chironomidae) populations that occur in shallow vernal ponds in this marsh. Brackish ponds in the undamaged salt marsh contained five species from five genera, while only the large-bodied

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[9]A.B. Didiuk. Unpublished data.

Cricotopus sp., most likely *ornatus*, was represented in the hypersaline ponds in the degraded marsh (Milakovic et al. 2001). However, the biomass per unit area did not change. This loss of species of aquatic invertebrates, together with the habitat changes, is also likely to affect populations of shorebirds. Declines in the nesting densities of semipalmated sandpipers (*Calidris pusilla*) and other shorebirds have occurred, although nesting densities of semipalmated plovers (*Charadrius semipalmatus*) and horned larks (*Eremophila alpestris*) have increased in open, degraded areas where little vegetation remains.[7] One of the causes for the declines in numbers of semipalmated sandpipers and red-necked phalaropes (*Phalaropus lobatus*) may be the loss of breeding habitat (low shrubs interspersed with graminoid vegetation and small ponds at La Pérouse Bay), as a result of goose grubbing. Recently, the population status of shorebirds nesting in the vicinity of Churchill, which is 25 km from La Pérouse Bay, has been assessed (Jehl and Lin 2001). The relative abundance of most species appears to have been stable from the 1930s to the 1960s, but since then considerable changes in the population status of the different species have occurred, which may be linked to the effect of goose grubbing at their study sites.

Overall, the field data indicate large-scale changes in the species composition and abundances of different taxa in response to the top-down effect of the geese on these coastal ecosystems. Although initially the effects are local, over time damaged areas coalesce to produce an alternative stable state at the meso-scale level.

Comparisons of the feedback mechanisms and the apparent trophic cascade in other systems

Intrinsic mechanisms that operate at the level of individual plants and (or) extrinsic mechanisms that involve processes at the ecosystem level have been proposed to account for an increase in net primary production of forage plants at moderate intensities of herbivory (McNaughton 1983*a*, 1983*b*). These include photosynthetic compensation, reallocation of resources for growth, changes in morphology and in rates of leaf turnover, and fertilization by faeces and urine. Circumstantial evidence in support of this prediction of an increase in primary production has come primarily from the responses of terrestrial graminoid communities (McNaughton 1976, 1979; Prins et al. 1980; Cargill and Jefferies 1984*b*) and aquatic and coral communities (Ogden and Lobel 1978; Bjorndahl 1980; Bergquist and Carpenter 1986; Carpenter 1986) to herbivory. The general applicability of these results to the primary production of grazed swards remains controversial (Belsky 1986, 1987; Crawley 1987). Not all plants have the ability to respond to herbivory as rapidly or effectively as *Puccinellia phryganodes.* Swards of two turf-forming grasses common in the upper marsh at La Pérouse Bay, *Calamagrostis deschampsioides* and *Festuca rubra,* do not show increases in growth within the season when grazed (Zellmer et al. 1993). On Bylot Island where a colony of greater snow geese breed, Gauthier et al. (1995) and Beaulieu et al. (1996) found that current levels of grazing by geese had no effect on the production of freshwater wetland plants. Brant geese in Alaska are unable to benefit from any potential increase in plant productivity following early season grazing, because the plant response is too slow (Person et al. 1998). Mulder (1999) has written an extensive review on the growth responses of Arctic plants to herbivory. Brown and Allen (1989) have pointed out that terms such as over- or under-compensatory growth are uninformative unless the timing of the vegetative response is known. The time over which the response is measured will bear directly on the scale (physiological, individual, population, and community levels). In the case of the study on *P. phryganodes* (Hik and Jefferies 1990), the grazer influences the growth of the forage grass at all of these scales. Knowledge of plant morphology and phenology, the grazing regime, and the effects of fertilization from faeces and nitrogen fixation are essential to predict the outcome of grazing on swards. The positive feedback demonstrates the plurality of the effects of grazing on plants involving responses from the level of the individual to that of the ecosystem (Hik and Jefferies 1990).

The second feedback leads to vegetation loss and a deterioration of soil properties. Spring and early autumn grubbing occur every year, although the latter is much less evident in most years. As the population of birds has increased, the spatial scale over which this destructive foraging occurs has also increased, with little likelihood of re-establishment of vegetation in grubbed areas in the foreseeable

future. The creation of patches of exposed sediment results in a spatial mosaic of intact swards and exposed sediment. However, with on-going foraging by birds each year, remaining areas of intact vegetation, in turn, have been depleted, and the patches of exposed sediment have coalesced to give extensive areas of sediment devoid of vegetation (Jefferies and Rockwell 2002). These changes in inter- and supratidal marshes have occurred at numerous sites along the coast of the Hudson Bay Lowland (Abraham and Jefferies 1997). A similar interpretation is applicable to those freshwater marshes where shoot-pulling has occurred. The amount of shoot-pulling differs between years, depending on conditions at the time of arrival of geese in spring. When goose numbers were low, the spatial scale of the destruction was limited, patches of grubbed – shoot-pulled vegetation were small, and the vegetation re-established by clonal growth.[10] Hence, these destructive effects are closely coupled to the density of birds and spring weather conditions.

Similar effects of grubbing and shoot-pulling on a large spatial scale can be detected elsewhere in the Arctic, particularly at Karrak Lake, south of Queen Maud Gulf, Nunavut, where both lesser snow geese and Ross's geese nest.[11] The tundra is characterized by mosses growing in saturated ground around hummocks that are vegetated with sedges, willow, and forbs. Dry and heath tundra plant communities are also present, in which Ericaceous plants are well represented together with sedges and *Dryas integrifolia.* Over 20 years, vegetation cover declined in relation to the duration of nesting in a given area. Lichens and *Cassiope tetragona* were particularly affected by trampling, foraging, and nest construction demands. The oldest areas of the goose colony had the lowest and most variable estimates of vegetation diversity and the largest proportion of damaged habitat and exposed peat. Mosses and *Senecio congestus* (a ruderal species of disturbed habitats, common also at La Pérouse Bay in damaged areas) were more abundant in areas where the geese had been nesting for at least 11 years. Considerable exposure of peat has occurred on the west side of Karrak Lake as a result of the activities of the geese, which is evident on the LANDSAT image for 1989.[11] Another large area where there has been considerable damage is on the west coast of Hudson Bay from the McConnell River northwards to the Maguse River (Kerbes et al. 1990). The loss of intertidal marsh vegetation appears to have occurred much earlier (before 1970) in the vicinity of the McConnell River, where a large nesting colony of snow geese developed since the 1940s. Similar to events at La Pérouse Bay, the original colony moved outward to occupy more inland sites in the coastal region while vacating the original occupied area (MacInnes and Kerbes 1987). Ross's geese are now the most abundant species in the immediate coastal strip (Didiuk et al. 2001), a situation that is increasingly occurring on the intertidal flats at La Pérouse Bay (Pezzanite 2003) where Ross's geese outnumber snow geese for most of the post-hatch period. In this west Hudson Bay region, a distance (N–S) of over 150 km, most of the intertidal vegetation has been lost and exposed peatlands characterize much of the coastal hinterland, particularly north of the McConnell River[9] (Kerbes et al. 1990; Abraham and Jefferies 1997). Similar changes have occurred along the Hudson and James Bay coasts of Ontario in low-lying areas and on Akimiski Island (Nunuvut) in James Bay (Abraham and Jefferies 1997; O 2003).

Collectively, the evidence from all these sites provides an overwhelming case that where large numbers of lesser snow geese occur regularly at high densities (> 1000 nests km^{-2}) in Arctic–sub-Arctic wetlands or tundra sites for much of the snow-free season, top-down effects of the consumer will directly and indirectly impact vegetation and soils, leading to the occurrence of an alternate state. Traditionally, bottom-up forces have been thought to control the development of salt-marsh ecosystems and primary productivity (Valiela and Teal 1974; Weigert and Pomeroy 1981). The established paradigm developed in the 1960s was that detritivores utilize most primary production as necromass and direct herbivory of salt-marsh vegetation is inconsequential (Smalley 1960; Teal 1962). The apparent trophic cascade described above and the recent studies of Silliman and Bertness (2002), in which they describe a

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[10]R.L. Jefferies and A. Jensen. Unpublished data.
[11]R.T. Alisauskas, J.W. Charlwood, D.K. Kellett, and G. Samelius. Unpublished data.

trophic cascade that regulates salt-marsh primary production on the south-east coast of the United States, indicate that this paradigm may require substantial revision as further examples emerge of top-down control of primary production in coastal habitats (Bertness et al. 2004).

Similar effects of increased numbers of animals on plant assemblages that bring about fragmentation of vegetation in the Arctic and sub-Arctic are evident in studies of caribou (Manseau et al. 1996) and geometrid moths (Tenow 1996; Bylund 1999). The latter defoliate and kill mountain birch over large areas of Scandinavia. The fertilization caused by decomposing birch roots and insect fras often leads to vegetation change. Dwarf birch shrubs are replaced by grasses and to a lesser extent herbs. It takes on the order of 100 years for the open birch forest to re-establish (Bylund 1999). Likewise, in Norway heavy grazing by reindeer has led to the replacement of dwarf shrubs by grasses (Olofsson et al. 2001). Similar changes, together with soil erosion, are taking place in western Siberia, where numbers of reindeer have increased substantially in recent years (Vilchek 1997).

Anthropogenic-induced effects that constrain the population growth of Arctic breeding geese

Although agricultural subsidies in both North America and Europe provide reliable food resources for migrating and wintering geese, there are other anthropogenic effects that act to constrain the population growth of these birds. Most effects are recent and are incompletely studied, and the long-term consequences on the target species and the plant and animal assemblages on the Arctic breeding grounds are unclear.

One constraint is the introduction of a spring hunt of populations of greater and lesser snow geese in North America (cf. Ankney 1996 for a wider discussion of the control of goose numbers). The Migratory Birds Convention of 1916, which was signed jointly by the Governments of Britain (for Canada) and the United States, restricts the non-aboriginal hunting of lesser snow geese to autumn and early winter. In contrast, the aboriginal people of Canada have long practiced the harvesting of waterfowl in both autumn and spring, and the spring harvest of adult birds and eggs is particularly significant because it represents the first reliable source of abundant fresh food after the long winter months. In response to the increase in the Mid-Continent Population of snow geese and the damage to vegetation and soils in northern latitudes, including the deleterious changes at La Pérouse Bay, the U.S. Fish and Wildlife Service and the Canadian Wildlife Service have permitted a spring hunt to take place since 1999 and 2001, respectively. A similar hunt of greater snow geese was introduced in Québec in response to vegetation damage in wintering and staging habitats. These changes in the hunting regulations were an attempt by these agencies to reduce the size of the goose population and to allow the vegetation to recover from the adverse effects of intense foraging in northern habitats. Assessments of the effectiveness of the hunt are being made with respect to a reduction in the size of the population and the re-establishment of vegetation in breeding colonies at Arctic sites. The overall objective of these wildlife agencies is to maintain the population growth of the geese at a level below the replacement rate (λ) of 1 (Rockwell et al. 1997).

Individual snow geese have a mean life-expectancy of about 7 years, and the birds usually do not breed until they are two or more years of age. Rockwell et al. (1997) showed in their model of the projected impacts of reductions in survival and fecundity that adult survival had the greatest impact on the growth rate. The collection of eggs, or the shooting of a young immature bird, has a much smaller impact on population growth than the culling of an adult female goose (Rockwell et al. 1997). The harvest rate necessary to achieve a reduction in population size, so that the replacement rate is less than one, has generated considerable debate because of uncertainty over current population values (cf. Cooke et al. 1999; Rockwell and Ankney 1999). However, the output from the model shows that when the population is reduced by a fixed number (1.41 million) each year for 5 years, the annual growth rate falls from 0.94 in 1999 to 0.71 in 2005, and the total migratory population in fall declines from an estimated 8.33 million to 3 million (Rockwell and Ankney 1999). If this level of harvesting can

be sustained and the current unpublished estimates of population sizes, survival, and fecundity in the different populations are correct, the planned reduction of the target population of 50% or more may be achieved in a few years. It is significant that the number of birds harvested has increased from 0.6 million in 1998 to 1.4 million in 2001 (U.S. Fish and Wildlife Reports). The decline in the winter count of the Mid-Continent population since 1999 (Fig. 1) may be the outcome of this increase in the harvest rate, and at the last count (2001) the replacement rate had fallen below one. However, there are many uncertainties at this stage, particularly with regard to appropriate values for the different demographic parameters, including immigration rates. Individual colonies may still be increasing in numbers, as is happening at Queen Maud Gulf (Alisauskas, personal communication). The migration routes for this colony also include the western section of the continent (e.g., New Mexico and California) where there is no spring hunt. The uncertainties of migration patterns emphasize the need for robust surveys of goose population sizes conducted at the regional scale.

Another effect of the spring hunt is the increased harassment of birds at staging sites in southern Canada and the United States. Mainguy et al. (2002) have examined the reproductive success of radio-collared greater snow geese before and after the introduction of the spring hunt. Although these marked birds were not shot, there was a dramatic decline in reproductive output after the introduction of the spring hunt in 1999. Most marked birds failed to breed, and all other factors, such as the weather, were comparable between the two periods (Mainguy et al. 2002). A number of explanations of the decline are possible, but one, in particular, that requires further study is that the harassment limits the ability of the birds to acquire fat and protein at staging sites on agricultural land (Bélanger and Bédard 1989; Mosbech and Glahner 1991; Madsen and Fox 1995; Madsen 1998; Mainguy et al. 2002). Survival of adult birds and the energy demands of migration take priority, and there appear to be insufficient accumulation of reserves for successful reproduction in spite of the availability of food resources (Mainguy et al. 2002). Adult female geese ($n = 34$) that were shot on arrival contained less abdominal fat than birds collected before the introduction of the spring hunt, and egg laying in the colony on Bylot Island has been delayed 1 week since 1999 compared with that in the previous 4 years (Mainguy et al. 2002). By 2002, the spring hunt had led to a decline in population numbers of the greater snow goose to below the original target number. In this species the remedial action has been successful and population numbers have fallen in short order since 1999. Since the introduction of the spring hunt, large numbers of failed breeders of the lesser snow goose also have been observed at La Pérouse Bay.[8] Whether this also is linked to harassment associated with the spring hunt is uncertain, because the observations occurred in a year of late spring thaw. In the case of the greater snow goose and that of the pink-footed goose (*Anser brachyrynchus*) described below, the birds stage at well-established sites of limited area that represent a geographical bottleneck. The high densities of birds are particularly vulnerable to disturbance at this time. In contrast, migrating flocks of lesser snow geese are widely dispersed across the agricultural landscape and are less vulnerable, especially north of the USA–Canada border where hunter numbers are low. The harassment of geese on the northward spring migration is not confined to snow geese. Madsen (2001) and Drent et al. (2003) have reported that the harassment of pink-footed geese by farmers on the island of Vesthålen off the Norwegian coast affects the accumulation of abdominal fat by the birds at this staging site and leads to low reproductive output. The birds feed on pasture grasses in amended grasslands, and the amount of accumulated fat can be estimated based on the size and shape of the abdomen. This abdominal index provides a good measure of the likely reproductive success of marked females. Ringed birds with a low index in spring return in autumn without goslings.

There is intriguing evidence that migrating geese in the coastal area of Helgeland in Norway may be unable to acquire sufficient amounts of high-quality protein derived from agricultural sources (*Phleum* and *Poa* grasses) compared with that available in semi-natural vegetation (salt-marsh grasses such as *Puccinellia maritima* and *Festuca rubra*) (Prop and Black 1998). The authors reported that barnacle geese *(Branta leucopsis)* accumulated insufficient amounts of protein per day when feeding in agricultural fields at this staging site in Norway, which adversely affected their reproductive success. In

contrast, the rate of protein acquisition was much higher in non-agricultural habitats. Of particular interest is the heavy use by migrating geese of coastal wetlands (and to a lesser extent freshwater marshes) immediately before migration and at staging sites en route to the northern breeding grounds. In the Netherlands, barnacle geese start their spring migration when the salt-marsh vegetation, on which they forage, is no longer capable of providing adequate N to maintain a positive daily gain in storage protein (R. Drent, personal communication). Not only does the use of these marshes appear broadly coincident in time with the first flush of spring growth of forage plants that are nitrogen-rich at that stage (cf. the green wave hypothesis (Owen (1980)), but also salt- and brackish-marsh plants may be expected to contain substantial amounts of soluble amino acids and sugars that serve as compatible osmotic solutes under saline conditions (Flowers and Yeo 1992). Amino acids and quaternary ammonium compounds that are abundant in tissues of these plants are proline and glycinebetaine, respectively, but there is a wide spectrum of soluble amino acids in these leaf tissues, including the sulphur amino acids. Hence, developing leaves contain high amounts of both proteinaceous and soluble organic N per unit dry weight resulting in a high intake of N per bite of tissue. As the residence time of forage within the gut of these Arctic geese is the order of 1 h or less, much of the proteinaceous N may be only partially digested, and consequently the birds may rely on halophytic and brackish-water plants to meet their N requirements. Even though agricultural plants do contain high amounts of protein, their amino-acid composition may be deficient in key amino acids for goose nutrition, resulting in inadequate rates of protein storage and reproductive failure, as noted by Prop and Black (1998). In addition, the N content of maturing leaves per unit mass declines, which is reflected in an increase in the C/N ratio of the tissue, so that the intake of N per bite falls (cf. Breman and De Wit 1983).

Although the reduction in numbers of geese can be expected to limit (but not stop) further damage of Arctic coastal vegetation, a striking temporal asymmetry exists between any reduction in the goose population and the recovery of damaged vegetation and degraded soils. Permanent plots at La Pérouse Bay that were exclosed after the vegetation was originally lost as a result of grubbing have remained devoid of vegetation for over 20 years.[4] Much of this is a consequence of the irreversible changes in soil characteristics in intertidal areas described earlier, particularly the development of hypersalinity, soil compaction, and loss of soil nitrogen (McLaren 2003). Erosion of these consolidated sediments and the deposition of unconsolidated soft sediment elsewhere, in which plants can establish from vegetative fragments or from seed, is the most likely trajectory for re-vegetation in intertidal flats. Indeed, this is already occurring in a few localities at La Pérouse Bay, but if large new swards are to develop, the present intensity of goose foraging cannot be maintained. With the ever-present geese, most areas of intertidal flats are likely to remain as exposed sediment. Removal of geese may allow some areas to re-vegetate, but the irreversible changes in soil properties severely limit colonization. The time scale for erosion and deposition of sediment followed by vegetative development is the order of decades, which is far longer than that required to reduce the Mid-Continent Population of snow geese to 3 million birds at current or projected harvest levels. The likely outcome of the destructive forms of foraging on freshwater wetlands, inland from the coast, is increased shrub development. At sites where the upper organic-rich veneer already has been lost, exposing glacial gravels or clay, re-establishment of the original vegetation will not occur. Willow shrub communities are likely to develop on these gravels in response to isostatic uplift, increased elevation, and drainage. Low willow and birch shrubs also may replace former stands of *Carex aquatalis* in sedge meadows that have been partially degraded.

Conclusions

The allochthonous inputs from agricultural sources that provide readily available food resources during the non-breeding season have led to long-term changes in the behaviour of Arctic breeding geese and their trophic relationships. Historically, the Mid-Continent Population of lesser snow geese wintered in the salt marshes of the Gulf States where density-dependent processes, particularly resource availability, apparently regulated bird numbers. The increasing use of agricultural food sources and

continuing dispersion of an expanding population have acted to release the population from the effects of winter density dependence. Similarly, the freshwater marshes of the Hudson Bay Lowland are extensive, and they provide almost unlimited supplies of forage during brood rearing in summer, in spite of the vegetation being less nutritious and accessible (bites per minute) compared with salt-marsh plants.

The changes that have occurred in the foraging behaviour and the distribution of lesser snow geese, in their selection of alternative migration routes and staging sites, and in the changes they have initiated in Arctic coastal wetlands, indicate a very dynamic and fluid scenario. The consequences of these changes are still unfolding, and the outcomes are far from clear. Additional changes in the populations and in habitats frequented by the geese may be anticipated in response to on-going alterations in agricultural and conservation practices and to increased warming trends in the Arctic. Similar changes are occurring in western Europe where migrating Arctic geese are establishing new routes and in some cases are breeding in wintering or southern staging areas. Populations of barnacle geese have started breeding on Gotland and in Estonia where they feed in coastal hay meadows (Larsson and Van der Jeugd 1998; Ganter et al.1999). Recently, a small number of barnacle geese have bred on the Island of Schiermonnikoog off the Dutch coast, which is a traditional winter and spring habitat of the birds (R. Drent, personal communication). These developments are similar to the growth of the Mid-Continent Population of lesser snow geese and the establishment of new breeding sites. Collectively, these changes indicate that most species of Arctic geese adjusted rapidly to modern agriculture, and that in the case of the lesser snow goose and barnacle goose, breeding females are not as philopatric to the site where they hatched, as was originally thought.

Although the evidence is largely anecdotal, before the development of modern agriculture and the widespread use of fertilizers and high-yielding varieties of crops, Arctic breeding geese flew either directly between their breeding and wintering sites or else staged at relatively few sites enroute. This pattern has been replaced by a stepping stone model in which birds stage at sites within a relatively short distance of each other. This is particularly evident in agricultural zones within the southern sections of the migration routes, as the birds do not stage on a regular basis in the boreal forest regions of North America and Europe as far as is known. As mentioned above, the agricultural food provides a predictable and reliable resource, but in spite of this the birds also frequently feed in wetlands adjacent to croplands. Because the birds do not feed exclusively on agricultural foods it may be that semi-natural vegetation provides resources that cannot be obtained in sufficient quantities from weeds of croplands or grain. The most likely missing sources are proteins or soluble organic N that are able to meet the specific amino acid requirements of the birds. In addition, there is widespread foraging by geese on vegetation in Arctic and sub-Arctic coastal areas in the final stages of the spring migration, which also is probably linked to protein acquisition. Once again, a stepping stone model describes this movement northwards as the birds follow the retreating snowline in a series of stop-overs. These flexible tactics enable birds to acquire adequate resources for reproduction, in contrast to birds that migrate to traditional breeding grounds, where resources may be inadequate early in the season (because of weather conditions) to allow early breeding. These breeding sites may not be sustainable in the long term as population numbers increase, because of declining resource availability early in the season (weather and grubbing) and during the post-hatch period (intense grazing).

The loss of vegetation and the irreversible changes in soil conditions in coastal marshes of the Hudson Bay Lowland associated with goose foraging are consistent with the above assertion of lack of sustainability. The increased numbers of geese produce a top-down cascade of direct and indirect effects on these coastal marshes that are a great distance from the source of the original agricultural subsidy — a consequence of "migratory connectivity" (cf. Webster et al. 2002). The catastrophic shift in ecosystem functioning as a result of the biotic exploitation has led to the formation of an alternative stable state of exposed sediment. The coastal marshes on the fringes of La Pérouse Bay have ceased to support a breeding colony of lesser snow geese, except for scattered groups. During the post-hatch period lesser snow geese have been replaced by families of Canada and Ross's geese, which have

different shaped bills compared with snow geese, enabling them to exploit graminoids of very short stature (< 0.5 cm). Lesser snow geese have started to forage at other coastal and inland sites on the Cape Churchill Peninsula, thereby escaping density-dependent effects operating at the local scale. Even if attempts to reduce the numbers of the Mid-Continent Population of lesser snow geese are successful in the short term, the recovery of the coastal vegetation is likely to be long term. A striking temporal asymmetry exists between any sustained reduction in the consumer population and the recovery of damaged vegetation and degraded soils. The simulation model of N flow in an intertidal marsh (Walker et al. 2003) supports the prediction that events that have occurred in the coastal lowlands of the Hudson Bay region and elsewhere during the last 50 years are likely to be repeated at other wetland sites as large number of birds forage in unexploited marshes resulting in alternative stable states of low biological productivity.

Acknowledgements

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