

Vegetation Correlates of the History and Density of Nesting by Ross's Geese and Lesser Snow Geese at Karrak Lake, Nunavut

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ABSTRACT. Growth in populations of Ross's geese (*Chen rossii*) and lesser snow geese (*C. caerulescens*) has led to concerns about destructive grazing of Arctic ecosystems. We estimated the extent and composition of plant communities at Karrak Lake, Nunavut, where populations of both goose species have grown geometrically over the past three decades. Proportion of land covered by vegetation was lower in areas where geese had nested for more than 20 years than in areas with no previous nesting history. Vegetative cover also declined with increasing nest density of both species. Species richness and diversity of vegetation was higher in more recently colonized areas of nesting than in areas with over 20 years of goose nesting. Exposed mineral substrate, exposed peat, and *Senecio congestus* were more prevalent in areas with a 10-year or longer history of goose nesting than in areas with less than 10 years of nesting. These patterns confirm that increasing numbers of nesting Ross's geese and lesser snow geese have altered the spatial distribution of vegetation surrounding Karrak Lake and reduced the species richness of local plant communities.

Key words: geese, Queen Maud Gulf, herbivory, vegetation, ecosystem, community, richness, diversity

RÉSUMÉ. La croissance des populations d'oie de Ross (*Chen rossii*) et de petite oie des neiges (*C. caerulescens*) engendre des préoccupations en matière de broutage destructif des écosystèmes de l'Arctique. Nous avons estimé l'ampleur et la composition des peuplements végétaux du lac Karrak, au Nunavut, où les populations de ces deux espèces d'oies ont augmenté de manière géométrique au cours des trois dernières décennies. La proportion de terre couverte par la végétation était moins élevée dans les régions où les oies avaient niché pendant plus de 20 ans que dans les régions où ces oies n'avaient jamais niché. Par ailleurs, la couverture végétale affichait une baisse là où la densité de nidification des deux espèces augmentait. La richesse des espèces et la diversité de la végétation étaient plus grandes dans les lieux de nidification colonisés plus récemment que dans les lieux de nidification colonisés il y a une vingtaine d'années. Les substrats de minéraux à découvert, la tourbe à découvert et le *Senecio congestus* se voyaient plus souvent dans les régions où les oies avaient niché pendant dix ans ou plus que dans les régions où les oies avaient niché pendant moins de dix ans. Ces tendances confirment que les populations croissantes d'oies de Ross et de petites oies des neiges ont altéré la répartition spatiale de la végétation entourant le lac Karrak, en plus de réduire la richesse des espèces et des peuplements végétaux des environs.

Mots clés : oies, golfe de la Reine-Maud, herbivorisme, végétation, écosystème, peuplement, richesse, diversité

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INTRODUCTION

Intense grazing can lead to change in the structure and assemblage of plant communities. While moderate grazing may result in higher nitrogen availability and increased growth rate of individuals in early successional plant communities (Jefferies et al., 1994; Abraham and Jefferies, 1997), intense grazing, together with poor environmental conditions, can degrade or destroy some plant communities (Arnalds, 1987; Jefferies, 1988; Srivastava and Jefferies, 1996). Reduction or loss of food and habitat resources, in turn, may adversely affect other species (Milakovic and Jefferies, 2003; Rockwell et al., 2003), as

well as those responsible for the degradation (Cooch et al., 1991; Francis et al., 1992; Jefferies et al., 1994).

Several North American goose populations have increased significantly over the past three decades (reviewed by Abraham and Jefferies, 1997). In particular, the mid-continent population of lesser snow geese (*Chen caerulescens*; hereafter, snow geese) at known Arctic breeding colonies has grown from about 1.3–1.9 million in 1969 (Kerbes, 1975; Boyd et al., 1982) to 4.5–6 million in 1997 (Abraham and Jefferies, 1997). The Ross's goose (*Chen rossii*) population has also grown substantially, from under 6000 in the 1930s to over 1 million in 1998 (Dzubin, 1965; Kelley et al., 2001). Population growth of

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both Ross's geese and snow geese (collectively referred to as "light geese") has been attributed to increased agricultural production in the southern United States, an increased number of refugia, and a decline in hunting pressure (Ankney, 1996; Abraham and Jefferies, 1997; Jefferies et al., 2003).

Increasing numbers of light geese now stage, nest, and brood their young in Arctic and Subarctic regions, resulting in adverse effects on plant communities (Kerbes et al., 1990; Abraham and Jefferies, 1997; Handa et al., 2002). Such negative impacts have been documented primarily in Subarctic coastal marshes of James Bay and southern and western Hudson Bay. In addition to the birds that breed locally, these marshes support migrating geese that stage there and feed intensively while en route to more northerly breeding colonies. Intense grazing of shoots, shoot-pulling, grubbing of roots and rhizomes, nest building, and trampling, coupled with a short growing season, have led to irreversible loss of vegetation, increased soil salinity, erosion, and desertification (Srivastava and Jefferies, 1996; Abraham and Jefferies, 1997; Jefferies and Rockwell, 2002).

Most studies of the impact of light goose populations on Arctic habitats have been conducted on the west coast of Hudson Bay (Abraham and Jefferies, 1997; Jefferies et al., 2003), with little research at other Arctic locations (but see Giroux et al., 1998, for greater snow geese (*C. c. atlantica*) and Samelius et al., in press, for lesser snow geese). To determine whether such impacts are prevalent throughout the breeding range of light geese, studies over a much wider area are needed. Our objective was to estimate change in plant communities at a large nesting colony of Ross's geese and snow geese in the central Canadian Arctic. Specifically, we examined spatial variability in plant community assemblages, species richness, and indicators of damaged habitat, such as exposed peat and mineral substrate. We predicted that geese had greatly influenced the structure and assemblage of plant communities in older, more central parts of the colony, resulting in loss of plant species and expansion of degraded habitats compared to the more recently colonized periphery and areas outside of the colony.

STUDY AREA

Karrak Lake, Nunavut (67°14' N, 100°15' W), located about 60 km south of Queen Maud Gulf, in the Queen Maud Gulf Bird Sanctuary (QMGBS), is one of the largest known nesting colonies of Ross's geese and snow geese (Alisauskas et al., 1998b). The combined light goose population grew from 17 000 geese in 1965 to about 640 000 in 1998 (Ryder, 1969; Alisauskas et al., 1998b). Correspondingly, the terrestrial area colonized by nesting light geese increased dramatically during the same period, from only a few islands on Karrak Lake to an area encompassing about 140 km² of island and contiguous mainland habitats

(Ryder, 1969; Alisauskas et al., 1998b). In the late 1960s, Ryder (1972) classified habitat at Karrak Lake as marsh tundra (hereafter, wet tussock tundra), dry tundra, and heath tundra. Nomenclature follows Porsild and Cody (1980). (1) *Wet tussock tundra* is characterized by poorly drained, hummocky ground, usually flooded during spring runoff. Mosses such as *Sphagnum* spp., *Aulacomnium turgidum*, *Drepanocladus revolvens*, *Meesia trifaria*, and *Tetraplodon urceolatus* grow at the base of hummocks. Hummocks are well vegetated on sides and tops, primarily with sedges *Eriophorum vaginatum* and *Carex chordorrhiza*, which are interspersed with species such as *Salix* spp., *Ranunculus pallasii*, *Rubus chamaemorus*, *Potentilla hyperarctica*, *Pyrola secunda*, (although we found entirely *P. grandiflora* in this study), and *Pedicularis sudetica*. (2) *Dry tundra* occurs in elevated, well-drained areas that are exposed over winter or become snow-free early in spring. Various lichens and vascular plants such as *Dryopteris fragrans*, *Hierochloe alpina*, *Carex glacialis*, *Luzula confusa*, *Dryas integrifolia*, *Oxytropis maydelliana*, *Empetrum nigrum*, *Arctostaphylos alpina*, *Vaccinium vitis-idaea*, *V. uliginosum*, and *Diapensia lapponica* are common. (3) *Heath tundra* occurs between wet tussock and dry tundra, is generally moist throughout the summer, and may be snow-covered into July. Heath tundra is vegetated primarily by *Carex membranacea*, *Ledum decumbens*, *Cassiope tetragona*, *Arctostaphylos alpina*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, and *Salix reticulata*. Although not mentioned by Ryder (1972), *Betula glandulosa* is also prominent in heath tundra.

METHODS

We constructed a map of history of goose nesting in the colony (Fig. 1a), using the perimeters of the colony for 1966, 1976, 1982, and 1988 from Kerbes (1994) and the boundaries based on our helicopter surveys in 1993–99, which we drew onto 1:250 000 topographic maps each year. Areas where vegetation was surveyed were classified by the number of decades before 1999 that geese had nested in those areas: 0 = no known nesting in the last 33 years, 1 = nesting for 1 to 10 years, 2 = nesting for 11 to 20 years, and 3 = nesting for more than 20 years. We cannot state definitively that nesting was continuous for all areas, particularly from 1966 to 1993, when the colony was not measured annually. However, given that colony boundaries did not regress from 1993 to 1999, we suggest that there was little error in classifying areas by duration of nesting goose occupancy.

During 1999, 176 plots (30 m radius) were sampled throughout the colony (Fig. 1a). Plots were located at corners and centers of a 1 km² Universal Transverse Mercator (Zone 13) grid within a sampling frame determined by the colony boundary. Plot locations were determined using global positioning system (GPS) units or 1:50 000 topographic maps, or both. From 5 to 29 June, we

measured the length and width (± 0.1 mm) of eggs in all goose nests in each plot, and from these data determined the species of geese, following Alisauskas et al. (1998a). Vegetation sampling was conducted from 6 to 28 July, after eggs had hatched. Extending a measuring tape 30 m in each of the four cardinal directions from the center of each plot, we recorded the presence of substrate class or plant species (grasses, sedges, lichens, and mosses were not identified to species) at every meter, at the point where the increment marker on the tape met the substrate (Appendix A). Thus, there were 120 observations per plot.

Additional vegetation sampling was done in late July outside the colony boundary, beginning at the perimeter of the colony and extending north in two 15 km transects spaced 1 km apart. Except at locations that fell in open water, we sampled 30 m plots at every kilometer along each transect ($n = 25$) and conducted vegetation sampling as above.

Statistical Analyses

Data on habitat composition (Appendix A) were converted to proportions for each sample plot. We assumed that exposed bedrock, boulders, cobble, gravel, and pebble were devoid of vegetation previous to occupancy by nesting geese and collectively referred to these as "proportion rock." "Proportion substrate" was the sum of all vegetation types, sand, soil, clay, and exposed peat (i.e., exclusive of rock and water). "Proportion exposed substrate" was the sum of sand, soil, and clay proportions divided by "proportion substrate." "Proportion exposed substrate" and proportions of vegetation species or types and exposed peat were divided by "proportion substrate" to represent these as a fraction of potential occupancy by vegetation. "Proportion vegetation" was the sum of proportions of all vegetation types. Proportions of the family Ericaceae, heath vegetation, including *Ledum decumbens*, *Cassiope tetragona*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Andromeda polifolia*, and *Arctostaphylos alpina*, were grouped for some calculations.

Simpson's (1949) Diversity Index was calculated for each sample plot:

$$1 - \sum_{i=1}^k p^2$$

where p = proportion of vegetation type i for k vegetation types. Species richness of vegetation, grouped as in Appendix A, was also calculated for each plot. We calculated "proportion damaged" by summing occurrences of exposed substrate, exposed peat, and *Senecio congestus* (known as ragwort or mastodon flower), a coarse, weedy species often found in damaged or disturbed areas (Porsild and Cody, 1980; Kerbes et al., 1990). Data were imported into a SPANS GIS (PCI Geomatics, 1999) study area, using an Albers equal area projection, and were used to overlay vegetation characteristics of the colony onto geocorrected satellite imagery (LANDSAT imagery 1989) of

the area that showed the interface between terrestrial habitat (including fens and marshes) and open water (i.e., lakes). Contour maps of vegetation proportions (Fig. 1) were constructed from point data using the SPANS potential mapping program POTMAP. This method of spatial interpolation uses a sampling circle, within which weighted moving averages can be calculated. Interpolated values are a function of vegetation proportions and the properties of the sampling circle, which include the sampling radius (inner radius 1 km, outer radius 2 km), a distance-dependent weighting function (0.5) applied to the outer radius, the number of nearest neighbours (15), and the classification scheme as shown in each legend of Fig. 1.

We used general linear modeling (PROC GLM, SAS Institute, 1996) to compare vegetation proportions, diversity, species richness, and damage among the four classifications of goose occupancy; for each comparison, model $df = 3$ and error $df = 175$. We estimated means $\pm 95\%$ confidence limits for each proportion of vegetation or habitat classification in each stratum of nesting history. We also performed correlation analyses (PROC CORR, SAS Institute, 1996) between various vegetation types or habitat classifications and nest densities of Ross's geese, snow geese, and both species on 148 sample plots.

RESULTS

Vegetation Use

Proportion of total vegetation declined with increasing duration of nesting by geese ($F = 16.59$, $P < 0.001$, $r^2 = 0.22$, Fig. 2a) and was about twice as high in areas with no history of goose nesting (95% C.L. = 0.91 ± 0.015) as in areas with more than 20 years of occupancy (0.44 ± 0.073). Figure 1b illustrates the reduction in mean proportion of vegetation toward the center, and oldest section, of the colony. Nest densities of both snow geese ($r = -0.24$, $P = 0.004$) and Ross's geese ($r = -0.38$, $P < 0.001$) were negatively correlated with proportion of total vegetation (Table 1). Proportion of grass was highest where goose nesting had not been documented (0.24 ± 0.036), intermediate in areas with 1–10 years of occupancy (0.12 ± 0.016), and lowest in areas with 11–20 years (0.022 ± 0.014) and more than 20 years (0.078 ± 0.055 , $F = 9.70$, $P < 0.001$, $r^2 = 0.14$) of occupancy, although it was highly variable in the oldest regions of the colony (Fig. 2b). Proportion of grass was also negatively correlated with nesting density of snow geese ($r = -0.29$, $P < 0.001$) and Ross's geese ($r = -0.42$, $P < 0.001$) (Table 1). Proportion of lichen was highest in areas with no goose nesting (0.21 ± 0.028) and declined with colony age to 0.013 ± 0.0031 in the oldest portion of the colony ($F = 3.23$, $P = 0.024$, $r^2 = 0.05$, Fig. 2c). Density of Ross's goose nests was negatively correlated ($r = -0.32$, $P < 0.001$) with proportion of lichen, but density of snow goose nests was not (Table 1). Proportion of heather (*Cassiope tetragona*) was

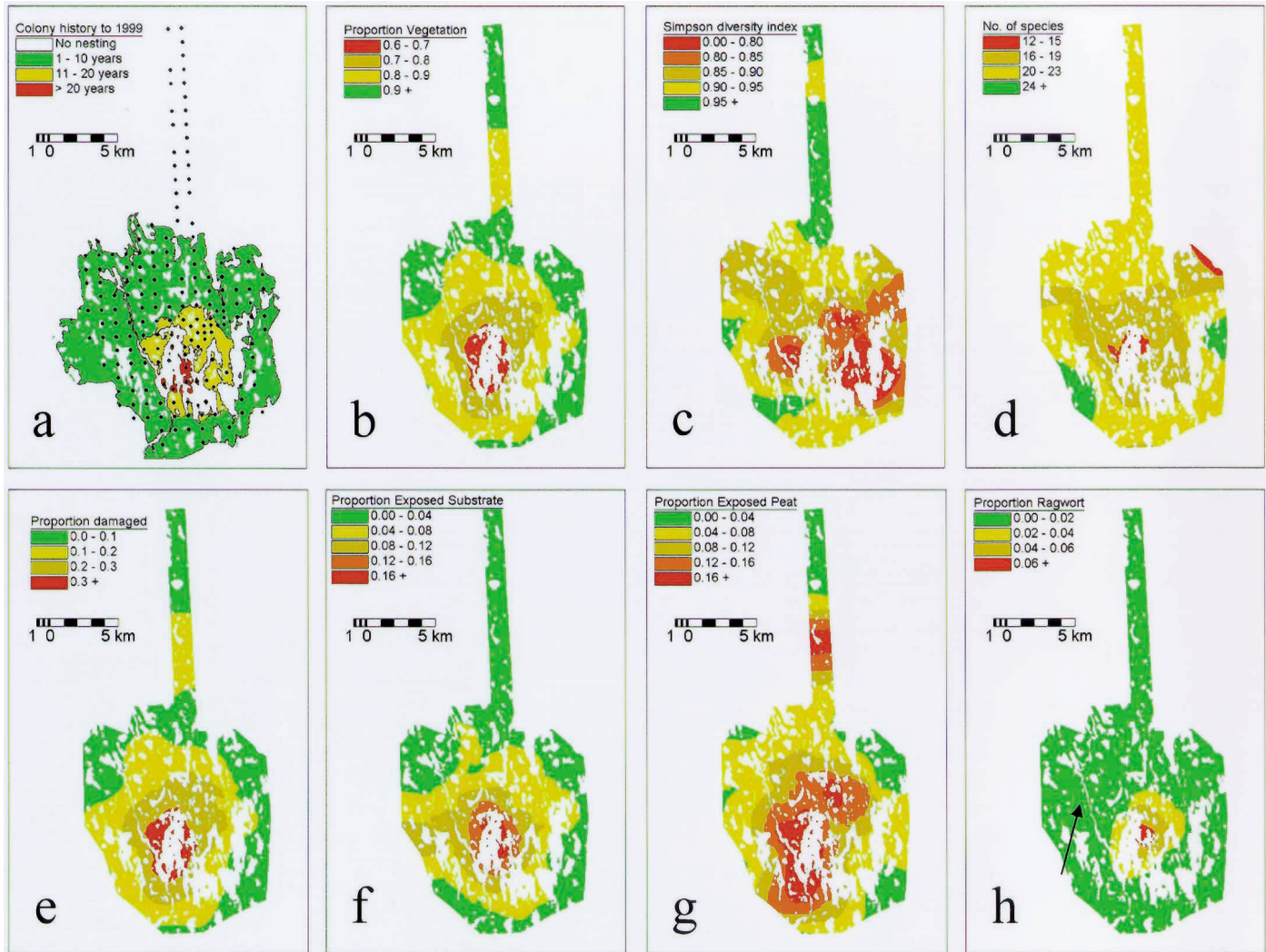


FIG. 1. Maps of the Ross's and lesser snow goose colony at Karrak Lake, Nunavut, showing (a) colony boundaries, 1966–99, with circles denoting locations of vegetation sample plots, (b) vegetation as a proportion of substrate (defined as all vegetation/habitat classifications except rock and water — see Appendix A), (c) Simpson (1949) Diversity Index, (d) number of species (richness), (e) proportion damaged, (f) proportion of exposed substrate, (g) proportion of exposed peat, and (h) proportion of ragwort, *Senecio congestus*. The arrow in (h) points to the location and direction of view (NNE) of photographs in Figure 5.

lowest in the oldest parts of the colony (0.0039 ± 0.0026), and the relevant 95% confidence limits did not overlap those of newer parts of the colony ($F = 1.92$, $P = 0.13$, $r^2 = 0.03$, Fig. 2d). Density of Ross's goose nests was negatively correlated with *Cassiope tetragona* ($r = -0.22$, $P = 0.008$), although no correlation existed for snow geese (Table 1). Proportion of moss was highest in the oldest parts of the colony (0.31 ± 0.081) and lowest in areas where geese had not nested (0.19 ± 0.02 , $F = 3.93$, $P = 0.01$, $r^2 = 0.06$, Fig. 1e). Density of Ross's goose nests was positively correlated ($r = 0.38$, $P < 0.001$) with moss, whereas snow goose nest density and moss were negatively correlated ($r = -0.18$, $P = 0.030$, Table 1).

Species Diversity and Richness

The oldest areas of the colony (11–20 and > 20 years of occupation) had the lowest and most variable estimates of vegetation diversity (0.82 ± 0.037 and 0.86 ± 0.054 ,

respectively) compared to areas where nesting by geese had not been documented (0.95 ± 0.010 , $F = 4.22$, $P = 0.007$, $r^2 = 0.07$, Figs. 1c and 2f). Similarly, species richness was highest in areas devoid of goose nesting, which contained an average of seven (i.e., 50%) more species than were found in the oldest areas of the colony ($F = 8.42$, $P < 0.001$, $r^2 = 0.13$, Figs. 1d and 3a). Figure 1d shows low richness in the center of the study area and at its northeastern edge.

Damaged Habitat

Proportion of damaged habitat (sum of exposed substrate, exposed peat, and *Senecio congestus*) was greatest (0.386 ± 0.051) in the oldest parts of the colony and declined to 0.085 ± 0.015 in unoccupied areas ($F = 16.64$, $P < 0.001$, $r^2 = 0.23$, Figs. 1e and 3b). The 95% confidence limits for damaged habitat in areas with no nesting and 1–10 years of nesting did not overlap those for areas with 11–20 and

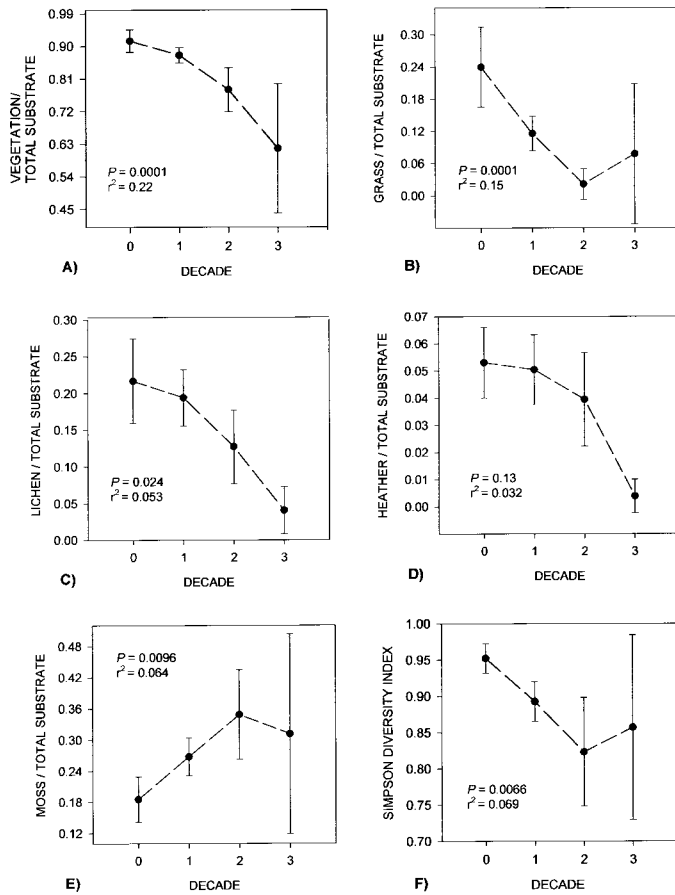


FIG. 2. Means and 95% confidence limits for proportions of vegetation/habitat classifications in relation to duration of nesting by Ross's and lesser snow geese at Karrak Lake, Nunavut, 1966–99. Decade 0 = no nesting documented, 1 = nesting 1–10 years, 2 = nesting 11–20 years, 3 = nesting more than 20 years. Shown are (A) total vegetation, (B) graminoids, (C) lichen, (D) *Cassiope tetragona*, (E) moss, all expressed as proportions of total substrate, and (F) Simpson Diversity Index.

TABLE 1. Correlations¹ of nest density (Ross's geese, lesser snow geese, and combined species) with proportions of selected vegetation and habitat types within the nesting colony at Karrak Lake, Nunavut, during 1999. Sample units ($n = 148$) were 30 m radius plots.

Category	Ross's Geese	Snow Geese	Both Species
Rock	-0.20*	0.21*	-0.71**
Moss	0.38***	-0.18*	0.22**
Lichen	-0.32***	0.04	-0.24**
Grass	-0.29***	-0.42***	-0.40***
<i>Cassiope tetragona</i>	-0.22**	-0.12	-0.22**
<i>Senecio congestus</i>	0.10	< -0.001	0.08
Total Vegetation	-0.24**	-0.38***	-0.34***
Exposed Substrate	-0.05	0.47***	0.15
Exposed Peat	0.31***	0.15	0.31***
Damage	0.25**	0.32***	0.33***
Heath	0.01	0.55***	0.24**

¹ * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

20+ years of occupancy, indicating that most damage occurred in areas occupied by nesting geese for 10 years or more (Fig. 3b). Nest densities of both Ross's geese ($r = 0.25, P = 0.002$) and snow geese ($r = 0.32, P < 0.001$) were

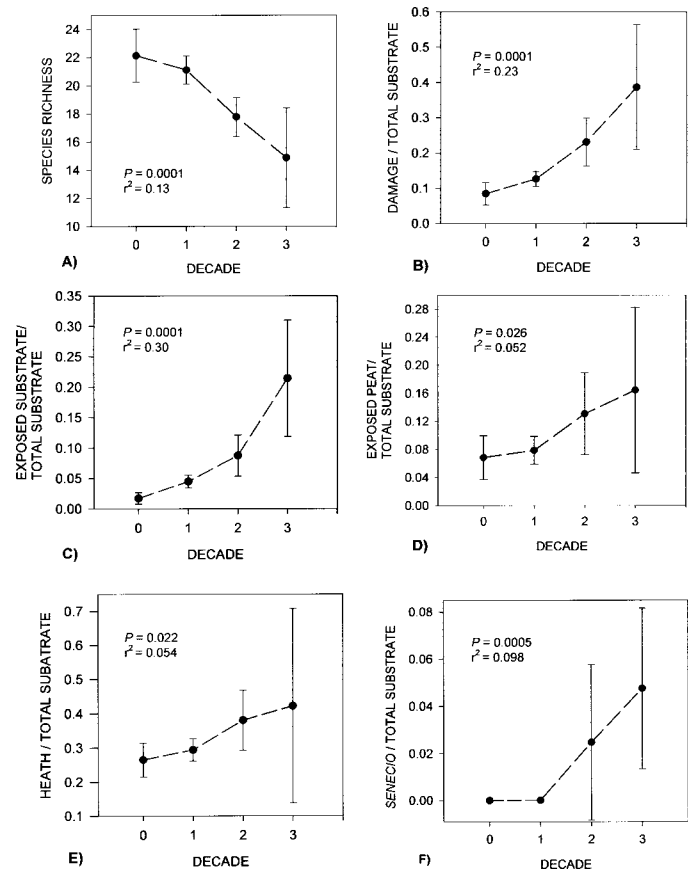


FIG. 3. Means and 95% confidence limits for proportions of vegetation/habitat classifications in relation to duration of nesting by Ross's and lesser snow geese at Karrak Lake, Nunavut, 1966–99. Decades are as in Figure 2. (A) shows number of species (species richness). Also shown are (B) damaged habitat, (C) exposed substrate, (D) exposed peat, (E) heath vegetation, and (F) *Senecio congestus*, all expressed as proportions of total substrate.

positively correlated with proportion of damaged habitat (Table 1). Proportion of exposed substrate was highest (0.14 ± 0.24) in the centre of the colony, where geese had nested the longest, compared to regions where geese had not nested ($0.014 \pm 0.0038, F = 24.07, P < 0.001, r^2 = 0.30$, Figs. 1f and 3c). Snow goose nest density was positively correlated ($r = 0.47, P < 0.001$) with exposed substrate, whereas Ross's goose nest density was not (Table 1). Proportion of exposed peat was highest and most variable (0.10 ± 0.030) in areas occupied by nesting geese for more than 20 years. It was lowest and least variable (0.068 ± 0.015), but still present, where geese were not known to have nested ($F = 3.17, P = 0.026, r^2 = 0.05$, Figs. 1g and 3d). Nest density of Ross's geese was positively correlated ($r = 0.31, P < 0.001$) with exposed peat, but no correlation existed for snow geese (Table 1). Large tracts of exposed peat occurred along the western side of Karrak Lake and in a band north of the colony perimeter (Fig. 1g). The 1989 LANDSAT image (Fig. 4) illustrates the extent of exposed peat within the colony. Proportion of heath vegetation did not differ significantly between areas with differing durations of occupancy ($F = 3.30, P = 0.022, r^2 = 0.05$,

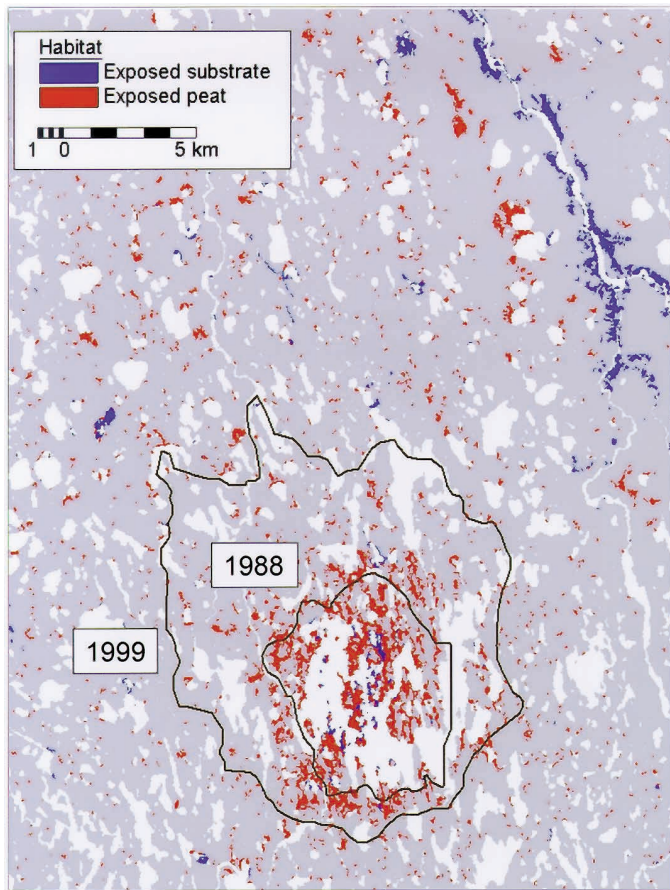


FIG. 4. Exposed substrate and peat habitats classified from LANDSAT imagery of the area surrounding Karrak Lake, Nunavut, in 1989. Note that exposed substrate along banks of Simpson River northeast of Karrak Lake is due to a geomorphic process of solifluction (and not to grazing by geese, as at Karrak Lake). Note also the greater prevalence of exposed peat within the boundaries of the goose colony, shown here for 1988 (inner black line) and 1999 (outer black line).

Fig. 3e) probably because this characteristic was highly variable, particularly in areas with 11–20 and more than 20 years of occupancy. Nest density of snow geese was positively correlated with heath vegetation ($r = 0.55$, $P < 0.001$), but no relationship existed between heath and Ross's geese (Table 1). Finally, proportion of ragwort (*Senecio congestus*), an indicator of disturbance, also was highest and most variable in the oldest parts of the colony (0.047 ± 0.014) and lowest and least variable in areas with no occupancy or only recent occupancy by geese (0.0014 ± 0.0081 , $F = 6.25$, $P = 0.001$, $r^2 = 0.10$, Figs. 1h and 3f). Proportion of *Senecio congestus* was not correlated with nest density of either snow geese or Ross's geese (Table 1).

DISCUSSION

Vegetation communities at some snow goose and Ross's goose colonies on the western coast of Hudson Bay have been severely degraded or destroyed, with desertification resulting from the cumulative effects of foraging and nest-building by



FIG. 5. Photographs showing differences in vegetation at the Ross's and lesser snow goose colony at Karrak Lake, Nunavut, in wet tussock tundra habitat (A) in 1992, when no geese were nesting at that location, and (B) in 2003, after eight years of goose occupation. The arrow in Figure 1h points to the location and direction of view (NNE) of these photographs.

geese (Kerbes et al., 1990; Srivastava and Jefferies, 1996; Kotanen and Jefferies, 1997; Handa et al., 2002). Although the west Hudson Bay studies were conducted in coastal vegetation communities, inland tundra communities at Karrak Lake show similar effects of degradation. We argue that changes in plant communities at Karrak Lake were the direct result of nest building and feeding by breeding geese, cumulatively resulting in altered plant communities. Proportion of vegetative cover and species diversity and richness were lowest in areas with the longest history of goose nesting. We detected differences in plant community structure as well, with decreases in proportions of *Cassiope tetragona*, grasses and sedges, and lichens in areas with longer occupancy by geese. Proportions of damaged habitats (exposed peat and mineral substrate), moss, and the ruderal species *Senecio congestus* increased with goose occupancy. Although it is not known how long the colony had existed before its discovery in 1965 (Ryder, 1969), observations by J.P. Ryder (pers. comm. 1999) in 1993 confirmed that large-scale, visible changes in abundance of vegetation and community composition had occurred since the late 1960s. As the colony expanded north and westward, changes in habitat were

evident after only a few years of goose occupancy (Figs. 5a, b). Specifically, these photographs illustrate loss of vegetation, particularly of grasses and sedges, and the breakup and decomposition of tussocks described by Kotanen and Jefferies (1997). These photographs are important because, although our statistical inferences about the effect of goose nesting on vegetation were based on correlation, the photographs verify the change in vegetation at a location where goose nesting had encroached in the time between the first and second images.

Foraging

At Karrak Lake, vegetation is removed primarily through foraging and nest-building by breeding geese. The large, robust bill of the snow goose is adapted for excavating roots and rhizomes, particularly those of graminoids (Ryder and Alisauskas, 1995; Alisauskas, 1998b), whereas the relatively small bill of Ross's goose is adapted for grazing on leaves and shoots. Ross's geese grub as well (Didiuk et al., 2001), and grubbing and shoot pulling by both species are effective springtime techniques for obtaining nutrient-rich belowground biomass (Abraham and Jefferies, 1997; Carrière et al., 1999). In addition, the shorter bills of Ross's geese may enable grazing of shorter or closely cropped vegetation, further reducing aboveground biomass in already exploited habitats and likely impeding recovery of vegetation (Didiuk et al., 2001).

Unlike some species, which feed for two weeks or more after arrival on nesting grounds before they begin to nest (Gauthier and Tardif, 1991; Carrière et al., 1999), Ross's geese and snow geese normally initiate nesting within a few days of arrival (Gloutney et al., 1999). Thus they rely largely on endogenous nutrient reserves for egg formation and energy during incubation (Ankney and MacInnes, 1978; Bon, 1997; Alisauskas, 1998a). Although geese forage intensively during nesting at Karrak Lake, they don't manage to ingest much food (Ryder and Alisauskas, 1995; Gloutney et al., 2001), probably because past foraging has severely reduced available vegetation. Still, feeding is concentrated around the nest site (McLandsry, 1983) and occurs over a four-week period during egg laying and incubation. We suggest that the negative correlation between proportion of grass and nest density of both species is due to the cumulative effects of decades of foraging during nesting, which have resulted in large-scale reduction in abundance of grasses.

Additional pressure on vegetation occurs when nonbreeding geese forage in the colony until they disperse at the onset of incubation (Ryder and Alisauskas, 1995). In contrast to colonies of west Hudson Bay, Karrak Lake experiences little impact on vegetation from staging birds, as very few light geese travel to more northerly nesting areas (Didiuk et al., 2001). Nonetheless, habitat damage was also evident outside the nesting colony. Exposed peat was visible on 1989 LANDSAT imagery (Fig. 4), and we detected a band of exposed peat north of the colony boundary during vegetation surveys (Fig. 1g). Habitat

damage outside the nesting colony may be attributable to cumulative, multi-year effects of foraging by both nonbreeding and brood-rearing geese. During nesting, groups of non-breeding birds are often observed immediately outside the colony, and following hatch, broods forage intensively as they disperse northward from the colony to feeding grounds near the coast of Queen Maud Gulf (Slattery, 2000). Additionally, some patches of exposed peat may occur naturally, particularly at drier sites.

Nest Building

As vegetation is a primary component of goose nests (McCracken et al., 1997), nest building has likely contributed substantially to habitat degradation at Karrak Lake. Snow geese, which arrive three to four days before Ross's geese, generally occupy elevated habitats of dry tundra, the first habitats exposed by melting snow and available for nesting, whereas Ross's geese usually occupy lower-lying, wet tussock tundra habitats (Ryder and Alisauskas, 1995; Alisauskas, 2001). Density of snow goose nests was also positively correlated with proportion of rock and heath vegetation (typical of xeric upland habitats) and density of Ross's goose nests, with proportion of moss (typical of low-lying, more mesic habitats).

Female geese use their feet and bills to strip and grub vegetation from around nest sites for use as nesting material. In addition to the expected decline of forage species (grasses and sedges), we also detected a decline in unpalatable species (lichens, *Cassiope tetragona*) in older parts of the colony. Decline of lichens and woody plants may occur because they become sensitive to disturbance as forage species are removed (Abraham and Jefferies, 1997), but for ericaceous species, the most likely reason is uprooting by geese for use in nest construction (McCracken et al., 1997). In wet tussock habitats, where mosses are overlain by vascular plants, removal of plant biomass results in the drying, oxidation, and erosion of the underlying moss (Jefferies et al., 2003). On upland habitats, where vegetative biomass is naturally less, the impact of vegetation removal was less evident. Correspondingly, McCracken et al. (1997) found that the size of goose nests was correlated with vegetative biomass in a given habitat: nests in moss habitats were larger than those in rock habitats. Ross's geese generally nest in wet tussock tundra, where vegetative biomass is greater, so they may have played a proportionately greater role than did snow geese in the alteration and destruction of plant communities in such habitats.

Habitat Damage, Species Diversity and Richness

Cumulative effects of foraging, as well as nest-building and maintenance, by light geese have resulted in damaged habitats and lower species diversity and richness in older areas of the colony at Karrak Lake. Removal of insulating vegetation and debris from dead vegetation causes rates of

evaporation to increase, particularly in wet tussock tundra habitats. Many vascular plants cannot survive such conditions (Kerbes et al., 1990; Abraham and Jefferies, 1997), and their demise leaves large tracts of exposed peat, as evident from LANDSAT imagery for 1989. Further, dried-out peat may erode during spring runoff (Kerbes et al., 1990).

Abraham and Jefferies (1997) suggested that grazing of a salt marsh community inhibits succession by impeding the development of dicotyledonous plants, and low species diversity is therefore an indicator of intense goose foraging on some graminoid communities. Although succession of plant communities at Karrak Lake may not be affected, low species diversity may still indicate intense habitat use simply because many species are consumed or uprooted for nest material. Particularly in older areas of the colony, we detected increasing homogeneity through greater proportions of exposed peat and mineral substrate, *Senecio congestus*, and moss, and the reduction or loss of other species. We did, however, find a slight but non-significant increase in diversity in areas with a nesting history of more than 20 years. Initially, vegetation in disturbed areas consists of ruderal species such as *Senecio congestus* and the mosses *Drepanocladus uncinatus* and *Aulaacomnium* spp. (Kerbes et al., 1990; Abraham and Jefferies, 1997) as well as late successional plants, and as the proportion of ruderal species approaches that of other species, the community becomes more “even” and diversity is inflated. Apparently increased diversity in areas with goose occupancy for over 20 years may have been due partially to establishment of *Senecio congestus*; high variability in the mean estimate of diversity in such areas may also have resulted from a relatively low sample size compared to those areas with shorter nesting histories.

Moss carpets of *Drepanocladus uncinatus* and *Aulaacomnium* spp. found in damaged habitats on west Hudson Bay are not eaten by geese and are thought to impede growth of sedges (Abraham and Jefferies, 1997). Similarly, Ryder (1972) observed blankets of *Aulaacomnium* spp. on islands used by nesting geese at Karrak Lake in the 1960s. We observed moss carpets in damaged areas of the colony, but we did not distinguish among moss species in our surveys. If we had distinguished between moss carpets that result from intense goose use and intact moss communities, we might have been able to demonstrate further the decreased species diversity and higher estimates of damaged habitat in older regions of the colony.

We suggest that plant communities within the goose colony at Karrak Lake have been altered and damaged by breeding Ross’s geese and snow geese, and with the northward and westward expansion of the colony (Fig. 1a), we predict a continued increase of intensely damaged habitat (Fig. 5). Short growing seasons in the Arctic, further shortened by stochastic climatic events, may cause the cumulative, multi-year effects of vegetation removal by geese to persist for decades, or may render such impacts effectively irreversible (Handa et al., 2002). In either case,

the study and estimation of impacts by historically unprecedented populations of Arctic-nesting geese on apparently fragile communities of Arctic vegetation needs to be continued. Smaller, newly pioneered colonies of light geese should be studied for better understanding of the dynamics of Arctic plant communities and increasing numbers of light geese.

APPENDIX A: VEGETATION AND HABITAT TYPES AT KARRAK LAKE, NUNAVUT, 1999

Category/ Common Name	Scientific Name or Description
Exposed Substrate:	
Clay	
Soil	
Sand	
Rock:	
Pebble	more than 50% < 1 cm diameter
Gravel	more than 50% > 1 cm diameter
Cobble	between 1–30 cm diameter
Boulder	> 30 cm diameter
Bedrock	large rock outcrops
Heath and Woody Plants:	
Labrador tea	<i>Ledum decumbens</i>
Cranberry	<i>Vaccinium vitis-idaea</i>
Crowberry	<i>Empetrum nigrum</i>
Bearberry	<i>Arctostaphylos alpina</i>
White arctic heather	<i>Cassiope tetragona</i>
Blueberry	<i>Vaccinium uliginosum</i>
Bog rosemary	<i>Andromeda polifolia</i>
Dwarf birch	<i>Betula glandulosa</i>
Willow	<i>Salix</i> spp.
Damaged Habitat:	
Exposed substrate	defined above
Exposed peat	dead moss
Mastodon flower, ragwort	<i>Senecio congestus</i>
Miscellaneous :	
Moss	any live moss
Grass	grass or sedge, live or dead
Lichen	various species
Wintergreen	<i>Pyrola</i> spp.
Cloudberry	<i>Rubus chamaemorus</i>
Mountain avens	<i>Dryas integrifolia</i>
Marsh cinquefoil	<i>Potentilla palustris</i>
Cinquefoil	other <i>Potentilla</i> spp.
Lousewort	<i>Pedicularis lanata</i>
Mare’s tail	<i>Hippuris vulgaris</i>
Purple rattle	<i>Pedicularis sudetica</i>
Crow foot	<i>Ranunculus</i> spp.
Fern	<i>Dryopteris fragrans</i>
Vetch	<i>Astragalus</i> , <i>Lathyrus</i> , <i>Oxytropis</i> spp.

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REFERENCES

- ABRAHAM, K.F., and JEFFERIES, R.L. 1997. High goose populations: Causes, impacts and implications. In: Batt, B.D.J., ed. Arctic ecosystems in peril: Report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. Washington, D.C.: U.S. Fish and Wildlife Service and Ottawa: Canadian Wildlife Service. 7–72.
- ALISAUSKAS, R.T. 1998a. Nutritional ecology and population biology of Ross's geese: Progress report and proposal for continued research. Unpubl. progress report. Available at Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4.
- . 1998b. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. *Auk* 115:851–862.
- . 2001. Species description and biology. In: Moser, T.J., ed. The status of Ross's geese. Arctic Goose Joint Venture Special Publication. Washington, D.C.: U.S. Fish and Wildlife Service and Ottawa: Canadian Wildlife Service. 5–9.
- ALISAUSKAS, R.T., SLATTERY, S.M., RYDER, J.P., GLOUTNEY, M.L., AFTON, A.D., KERBES, R.H., and McLANDRESS, R.M. 1998a. Discrimination of Ross's and lesser snow goose eggs. *Journal of Field Ornithology* 69: 647–653.
- ALISAUSKAS, R.T., SLATTERY, S.M., KELLETT, D.K., STERN, D., and WARNER, K.D. 1998b. Spatial and temporal dynamics of Ross's and snow goose colonies in Queen Maud Gulf Bird Sanctuary, 1966–1998: Progress report on numbers of geese and colonies. Unpubl. progress report. Available at Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4.
- ANKNEY, C.D. 1996. An embarrassment of riches: Too many geese. *Journal of Wildlife Management* 60:217–223.
- ANKNEY, C.D., and MACINNES, C.D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459–471.
- ARNALDS, A. 1987. Ecosystem disturbance in Iceland. *Arctic and Alpine Research* 19:508–513.
- BON, R.L. 1997. Spring nutritional ecology of migrating and breeding Ross's geese, *Chen rossii*. MS thesis, University of Saskatchewan, Saskatoon.
- BOYD, H., SMITH, G.E.J., and COOCH, F.G. 1982. The lesser snow geese of the eastern Canadian Arctic: Their status during 1964–1979 and their management from 1982–1990. Occasional Paper Number 46. Ottawa: Canadian Wildlife Service.
- CARRIÈRE, S., BROMLEY, R.G., and GAUTHIER, G. 1999. Comparative spring habitat and food use by two Arctic nesting geese. *Wilson Bulletin* 111:166–180.
- COOCH, E.G., LANK, D.B., ROCKWELL, R.F., and COOKE, F. 1991. Long-term decline in body size in a snow goose population: Evidence of environmental degradation? *Journal of Animal Ecology* 60:483–496.
- DIDIUK, A.B., ALISAUSKAS, R.T., and ROCKWELL, R.F. 2001. Interaction with Arctic and Subarctic habitats. In: Moser, T.J., ed. The status of Ross's geese. Arctic Goose Joint Venture Special Publication. Washington, D.C.: U.S. Fish and Wildlife Service and Ottawa: Canadian Wildlife Service. 19–32.
- DZUBIN, A. 1965. A study of migrating Ross geese in western Saskatchewan. *Condor* 67:511–534.
- FRANCIS, C.M., RICHARDS, M.H., and COOKE, F. 1992. Long-term changes in survival rates of lesser snow geese. *Ecology* 73:1346–1362.
- GAUTHIER, G., and TARDIF, J. 1991. Female feeding and male vigilance during nesting in greater snow geese. *Condor* 93: 701–711.
- GIROUX, J.F., GAUTHIER, G., COSTANZO, G., and REED, A. 1998. Impact of geese on natural habitats. In: Batt, B.D.J., ed. The greater snow goose: Report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. Washington, D.C.: U.S. Fish and Wildlife Service and Ottawa: Canadian Wildlife Service. 32–57.
- GLOUTNEY, M.L., ALISAUSKAS, R.T., HOBSON, K.A., and AFTON, A.D. 1999. Use of supplemental food by breeding Ross's geese and lesser snow geese: Evidence for variable anorexia. *Auk* 116:97–108.
- GLOUTNEY, M.L., ALISAUSKAS, R.T., AFTON, A.D., and SLATTERY, S.M. 2001. Foraging time and dietary intake by breeding Ross' and lesser snow geese. *Oecologia* 127:78–86.
- HANDA, I.T., HARMSEN, R., and JEFFERIES, R.L. 2002. Patterns of vegetation change and the recovery potential of degraded areas in a coastal salt marsh system of the Hudson Bay lowlands. *Journal of Ecology* 90:86–99.
- JEFFERIES, R.L. 1988. Pattern and process in Arctic coastal vegetation in response to foraging by lesser snow geese. In: Gottlieb, L.D., and Jain, S.K., eds. Plant evolutionary biology. London: Chapman and Hall. 341–369.
- JEFFERIES, R.L., and ROCKWELL, R.F. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science* 5:7–16.
- JEFFERIES, R.L., KLEIN, D.R., and SHAVER, G.R. 1994. Vertebrate herbivores and northern plant communities: Reciprocal influences and responses. *Oikos* 71:193–206.
- JEFFERIES, R.L., ROCKWELL, R.F., and ABRAHAM, K.F. 2003. The embarrassment of riches: Agricultural food subsidies, high goose numbers, and loss of Arctic wetlands—A continuing saga. *Environmental Reviews* 11:193–232.
- KELLEY, J.R., DUNCAN, D.C., and YPARRAGUIRRE, D.R. 2001. Distribution and abundance. In: Moser, T.J., ed. The status of Ross's geese. Arctic Goose Joint Venture Special Publication. Washington, D.C.: U.S. Fish and Wildlife Service and Ottawa: Canadian Wildlife Service. 11–18.
- KERBES, R.H. 1975. The nesting population of lesser snow geese in the eastern Canadian Arctic. Report Series Number 35. Ottawa: Canadian Wildlife Service.
- . 1994. Colonies and numbers of Ross' Geese and lesser snow geese in the Queen Maud Gulf Migratory Bird Sanctuary. Occasional Paper Number 81. Ottawa: Canadian Wildlife Service.

- KERBES, R.H., KOTANEN, P.M., and JEFFERIES, R.L. 1990. Destruction of wetland habitats by lesser snow geese: A keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* 27:242–258.
- KOTANEN, P.M., and JEFFERIES, R.L. 1997. Long-term destruction of sub-Arctic wetland vegetation by lesser snow geese. *Ecoscience* 4:179–182.
- McCRACKEN, K.G., AFTON, A.D., and ALISAUSKAS, R.T. 1997. Nest morphology and body size of Ross' geese and lesser snow geese. *Auk* 114:610–618.
- McLANDRESS, M.R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and lesser snow geese. *Auk* 100:335–343.
- MILAKOVIC, B., and JEFFERIES, R.L. 2003. The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblages in an Arctic supratidal marsh. *Ecoscience* 10:57–65.
- PCI GEOMATICS. 1999. SPANS 7.1 Technical Reference. Richmond Hill, Ontario: PCI Geomatics.
- PORSILD, A.E., and CODY, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. Ottawa: National Museums of Canada. 667 p.
- ROCKWELL, R.F., WITTE, C.R., JEFFERIES, R.L., and WEATHERHEAD, P.J. 2003. Response of nesting savannah sparrows to 25 years of habitat change in a snow goose colony. *Ecoscience* 10:33–37.
- RYDER, J.P. 1969. Nesting colonies of Ross' Goose. *Auk* 86: 282–292.
- . 1972. Timing and spacing of nests and breeding biology of Ross' goose. PhD thesis, University of Saskatchewan, Saskatoon.
- RYDER, J.P., and ALISAUSKAS, R.T. 1995. Ross' goose (*Chen rossii*). In: Poole, A., and Gill, F., eds. *The birds of North America*, No. 162. Philadelphia: The Academy of Natural Sciences and Washington, D.C.: The American Ornithologists' Union.
- SAMELIUS, G., ALISAUSKAS, R.T., and HINES, J.E. In press. Productivity of lesser snow geese on Banks Island in 1995 to 1998. Canadian Wildlife Service Occasional Paper.
- SAS INSTITUTE. 1996. SAS/STAT user's guide, version 6, 4th ed. Cary, North Carolina: SAS Institute, Inc.
- SIMPSON, E.H. 1949. Measurement of diversity. *Nature* 163:688.
- SLATTERY, S.M. 2000. Factors affecting first-year survival in Ross's geese. PhD thesis, University of Saskatchewan, Saskatoon.
- SRIVASTAVA, D.S., and JEFFERIES, R.L. 1996. A positive feedback: Herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Journal of Ecology* 84:31–42.