

Lesser Snow Geese, *Chen caerulescens caerulescens*, and Ross's Geese, *Chen rossii*, of Jenny Lind Island, Nunavut

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We surveyed the Lesser Snow (*Chen caerulescens caerulescens*) and Ross's geese (*Chen rossii*) of Jenny Lind Island, Nunavut, using aerial photography in June 1988, 1998, and 2006, and a visual helicopter transect survey in July 1990. The estimated number of nesting geese was $39\,154 \pm SE\,2238$ in 1988, $19\,253 \pm 2323$ in 1998, and $21\,572 \pm 1898$ in 2006. In 1988 an estimated 2.7% of the nesting geese were Ross's. The July 1990 population of adult-plumaged birds was $25\,020 \pm 3114$. The estimated percentage blue morph among Snow and Ross's geese was 19.0% in 1988, 25.1% in 1989, 23.0% in 1990 and 21.1% in 2006. Estimated pre-fledged Snow Goose productivity was 47% young in 1989 and 46% in 1990. Combined numbers of Snow and Ross's geese on Jenny Lind Island grew over 250 fold, from 210 adults in 1962-1966 to 54 100 adults in 1985. Numbers subsequently declined, to 42 200 in 1988, 25 000 in 1990, 20 300 in 1998, and 26 400 in 2006. Population decline between 1985 and 1990 was consistent with anecdotal reports by others that die-offs of Snow Geese occurred in 1984, 1985 and 1989, and with our August 1989 fieldwork which found evidence of habitat degradation and malnourishment of young geese. In spite of limited food resources on Jenny Lind Island, the colony continued to exist in 2006 at near its 1990 and 1998 levels. Further studies there could provide insights for management of the overabundant mid-continent Snow Goose population and its arctic habitats.

Key Words: Lesser Snow Goose, *Chen caerulescens caerulescens*, Ross's Goose, *Chen rossii*, population, overabundance, nesting, Jenny Lind Island, Nunavut.

Jenny Lind Island (JLI), Nunavut in the Central Canadian Arctic (Figure 1), supports a colony of Lesser Snow Geese (*Chen caerulescens caerulescens*) with a small number of associated Ross's Geese (*Chen rossii*) (Kerbes 1994). Although the Snow Geese of JLI are a tiny part (< 1%) of the Midcontinent Snow Goose Population, they illustrate in microcosm the recent concern about the increasing size of that population and its effects on arctic habitats (Abraham and Jefferies 1997). While the number of adults on JLI grew from an estimated 210 in 1962-1966 (Parmelee et al. 1967) to 54 100 in 1985 (McCormick and Poston 1988) and subsequently declined to less than half that number by 1998, the Midcontinent Population increased from approximately 1 million nesting birds in the early 1970s to 3.8 million in 1998 (Kerbes et al. 2006). Grazing and grubbing by Snow Geese in parts of their arctic range on southern and western Hudson Bay have damaged coastal staging, nesting and moulting habitats, with subsequent decreases in the numbers of nesting birds at colonies in those areas (Kerbes et al. 1990; Abraham and Jefferies 1997; Kerbes et al. 2006). Given the very small amount of nesting, moulting, and brood-rearing habitat on JLI, and the "confinement" of flightless moulting adult geese and their young to the island for most of the summer, it might be expected that the JLI colony would have collapsed very quickly (see Kerbes et al. 1990; Cooch et al. 1991; Francis et al. 1992). In this report we describe goose population sur-

veys done on JLI in 1988, 1989, 1990, 1998, and 2006, and review earlier records. We investigate anecdotal reports of large numbers of geese dying on or near the island in the 1980s and speculate on how this colony has continued to exist, despite the island's apparent shortage of habitat.

Study Area

Jenny Lind Island (68°43'N, 101°58'W) in Queen Maud Gulf of the Arctic Ocean covers about 422 km² and measures about 30 km at its widest point (Figures 1 and 2). It lies 100 km north of the Queen Maud Gulf Migratory Bird Sanctuary (QMG), which supports major nesting colonies of Snow and Ross's geese (Kerbes et al. 2006). Part of the Arctic Lowlands Physiographic Region (Bostock 1970), the island is in the Low Arctic Ecoclimatic Region (Ecoregions Working Group 1989). However, the relatively exposed position of the island and the lack of protective relief led Parmelee et al. (1967) to describe the environmental conditions as High Arctic. The island has gently rolling terrain with a maximum elevation of 61 m above sea level. Most of the island has little or no vegetation. Extensive areas of sand and gravel in the southeast, and of gravel and rocks on the northern and western coasts, are almost devoid of vegetation (McCormick and Poston 1988). Extensive areas of lowland sedge tundra occur only in the central-western portion of the island. In general, the vegetation consists of mesic to

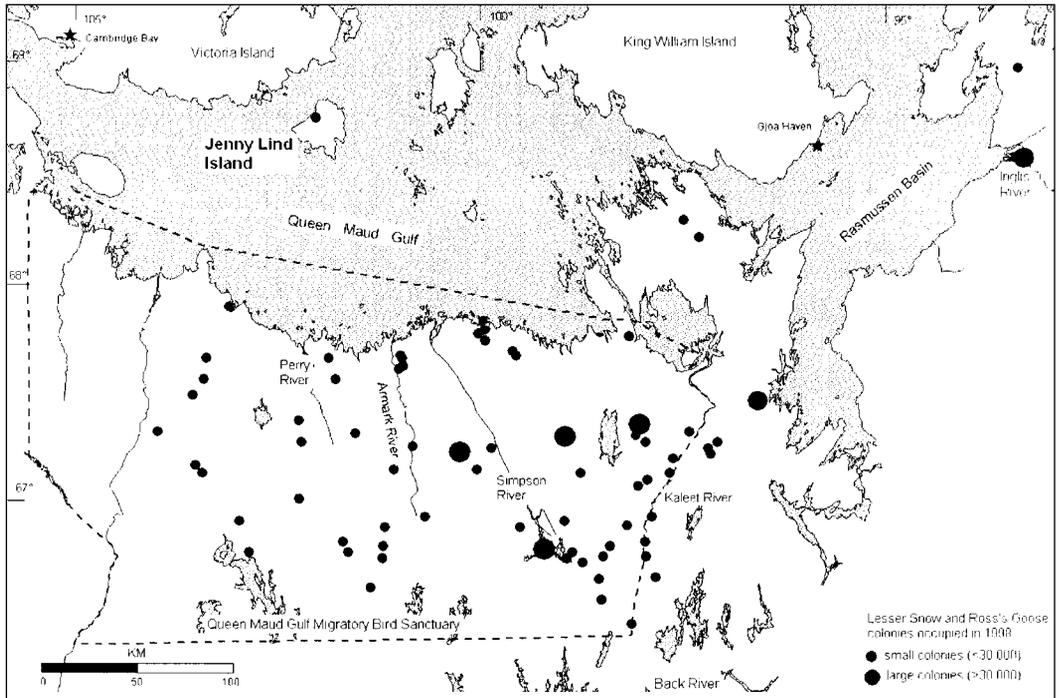


FIGURE 1. Jenny Lind Island, Nunavut, and surrounding area in the central Canadian Arctic, showing Lesser Snow and Ross's goose colonies (dots) active in 1998.

dry/mesic communities dominated by graminoids, forbs and dwarf willows (*Salix* spp.). A Distant Early Warning (DEW) Line station on JLI was occupied from 1952 to 1992.

Methods

Numbers of Snow and Ross's geese nesting on JLI were estimated using large format aerial photography (Kerbes et al. 1983; Kerbes 1994). Prior to obtaining the photos, a reconnaissance of the island was flown to ensure that all nesting areas were covered. Nesting geese were photographed on 18 June 1988 from a DHC Twin Otter aircraft using a Wild RC-10 camera with Panatomic-X and Color Infra Red film; on 22 June 1998 from a Partenavia aircraft using a Zeiss RMK-9 camera with PlusX film; and on 21 June 2006 from a Partenavia using a Zeiss LMK 2000 camera and PlusX film. Each year images of geese from sample areas of the colony were counted visually from the original film negatives, with a Wild M7 binocular microscope. Since they cannot be distinguished separately on the film, the sample counts of white morph Snow Geese and Ross's Geese were combined. They were classified as nesting (on the ground, in pairs or singles) or non-breeding (flying, or on the ground in groups of five or more birds).

Non-breeding geese are here defined as the yearlings and some older birds that have not bred, plus birds which have already failed in their nesting attempt

and have abandoned their nest and its territory. *Adult-plumaged geese* include both the successful nesting birds and the non-breeders. Our estimates of total adult-plumaged birds in 1988, 1998 and 2006 included only those non-breeders which were in, or within approximately 500 m of, the occupied nesting area. Our estimate of total adult-plumaged birds was low by an unknown, but probably small, factor in those years because some non-breeders can also be found further from the colony.

On 21 June 1988 helicopter support allowed ground data on species and colour morph composition to be obtained by three observers at each of three sites within the colony. Samples of nests were classified as Snow or Ross's based on egg size, and samples of nesting geese were classified as white Snow, blue Snow or Ross's based on visual examination with binoculars (Kerbes 1994). Limited budget and logistics prevented similar ground information from being collected in 1998 and 2006. The percentage of blue Snow Geese among combined Snow and Ross's geese was estimated in 1988 using nesting birds from low level photos, and in 2006 using flying birds from high level photos. In August 1989 Snow Geese were banded on JLI using helicopter-supported methods (see Timm and Bromley 1976).

On 28 July 1990, following methods used in 1985 by McCormick and Poston (1988), an aerial survey of goose broods and flightless moulting adult-plumaged

geese was conducted with a Bell 206B helicopter on floats, flying straight transects at an altitude of 45 m above ground and a ground speed of 80 km/hr. An observer in the left front seat recorded all sightings of geese within 200 m of the left side of the aircraft and a second observer in the right rear seat recorded sightings within 200 m on the right side. North-south transects were spaced at distances of 2 km and were divided into 3 km segments which served as the basis for recording data. Estimates and standard errors of goose numbers were calculated by the ratio method (Jolly 1969). Because we sampled a relatively large part of the island, a "finite population correction" was applied to improve the precision of the standard error estimates (Cochran 1977: 24). On 29 July 1990, ground observations were made with a 60-power spotting scope to determine age and colour morph ratios among Snow Geese. Nine adult Snow Geese were collected by shotgun and sent to the Western College of Veterinary Medicine, University of Saskatchewan, Saskatoon, for necropsy. General observations on habitat conditions, including evidence of goose grazing pressure, were recorded in 1988, 1989, and 1990.

Results

The estimated number of June-nesting adult Snow and Ross's Geese in the colony declined from $39\,154 \pm SE\ 2238$ in 1988 to $19\,253 \pm 2323$ in 1998, but then increased to $21\,572 \pm 1898$ in 2006 (Table 1). We estimated that $25\,020 \pm SE\ 3114$ adult-plumaged Snow and Ross's geese and 1045 ± 233 Cackling Geese (*Branta hutchinsii*) were present on JLI in July 1990. The ground survey in June 1988 indicated that 2.7% of the nesting Snow and Ross's geese were Ross's, giving an estimate of 1067 ± 430 Ross's and $38\,087 \pm 2238$ Snow. Percentage blue morph among Snow and Ross's geese from ground counts and low-level photos was 19.0% in 1988 (of 2595 nesting adults) and 23.0% in 1990 (of 1472 adult-plumaged birds). In 1989, 25.1% of 506 adult-plumaged birds captured for banding were blue. In 2006, flying non-breeding birds were counted from photos, resulting in 21.1% blue morph (of 655 birds). Nesting Snow and Ross's geese occupied essentially the same area in the central-western part of the island, totalling approximately 38 km² in June 1988, 31 km² in June 1998, and 36 km² in June 2006 (Figure 2). Snow Goose productivity in 1989, estimated from a sample of 643 adult-plumaged birds plus young geese captured on 9 August, was 47% young. Ground observations in 1990 of 29 groups of goslings and adults tallied 1472 adult Snow Geese, 87 adult Cackling Geese, and 1322 goslings of both species. Assuming the goslings occurred in the same ratio as adults of the two species, there were 1248 Snow goslings, and 46% of the Snows were young.

During ground work on the JLI colony in June 1988 we observed evidence of extensive grazing and grub-

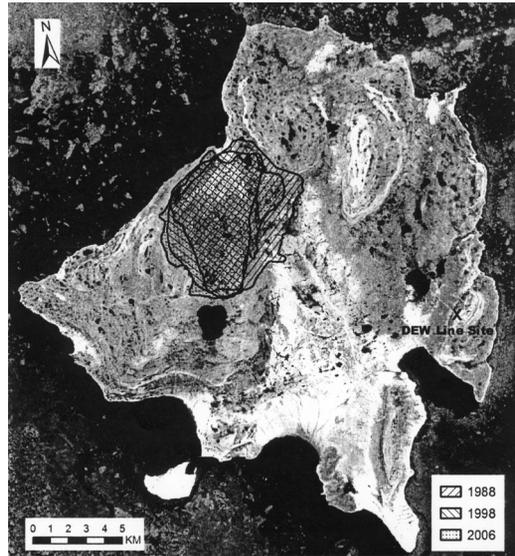


FIGURE 2. Jenny Lind Island, Nunavut, showing area occupied by nesting Lesser Snow and Ross's geese in June 1988, 1998, and 2006, as determined from aerial photography. Landsat 7 image courtesy GeoBase®.

bing in and around the sedge lowland of the central-western part of the island. During banding operations in August 1989 we visited 12 sites throughout the island and observed that virtually all forbs, grasses, and flowering plants had been clipped to near ground level. In general, vegetation on JLI appeared to be retarded and heavily grazed compared to vegetation observed during the previous two weeks in the nearby Queen Maud Gulf Migratory Bird Sanctuary. The relatively small areas of sedge lowland on the island were brown and dry, apparently due to less summer rainfall than usual there. In July 1990, localized destruction of wet tundra habitat was also evident on JLI, with heavily grubbed and grazed areas on the periphery of some ponds, similar to conditions noted by Jefferies et al. (1979) on southwest Hudson Bay. Although this "over-grazed" condition appeared to be localized, most of the sedges and grasses in the wet lowlands had been grazed to some extent by geese.

Discussion

Snow Geese were first reported on JLI by Parmelee et al. (1967), who studied birds on the eastern third of the island in 1962 (19 June to 5 July) and 1966 (31 May to 12 August). They recorded about 70 adult Snow Geese each year, and estimated that the total island population was about 210 adults. Kuyt et al. (1971*) counted 300 adult and 258 young Snow Geese during a 56 km aerial survey of JLI from a Beaver aircraft on 5 August 1971. The counts for 1962, 1966, and 1971 probably reflect minimum numbers of geese present. In any case, 11 years later the island's Snow

TABLE 1. Results of surveys of Lesser Snow and Ross's geese on Jenny Lind Island, Nunavut, 1988, 1990, 1998, and 2006.

Survey date	Total area surveyed km ²	Area sampled km ² (%)	Number of nesting adults		Number with adult plumage ¹		% blue morph	(sample size) ²
				SE		SE		
June 1988 ³	38.3 ⁴	9.40 (24.6)	39 154 ⁵	2238	42 156 ⁵	2445	19.0	(2595)
July 1990 ⁶	422.0 ⁷	100.8 (23.9)	n/a	n/a	25 020	3114	23.0	(1472)
June 1998 ³	30.6 ⁴	4.44 (14.5)	19 253	2323	20 272	2342	n/a	n/a
June 2006 ³	35.6 ⁴	5.73 (16.1)	21 572	1898	26 422	2663	21.1	(655)

¹ Adult-plumaged birds = nesting birds plus non-breeders.

² Number of Snow and Ross's geese in sample used to estimate % blue morph.

³ Air photo survey of nesting Snow and Ross's geese.

⁴ Area occupied by nesting Snow and Ross's geese.

⁵ Includes an estimated 2.7% Ross's from ground survey in 1988 (see text).

⁶ Visual transect survey from helicopter.

⁷ Total area of Jenny Lind Island.

Goose population was much larger. Robert Decker (Northwest Territories Department of the Environment and Natural Resources, personal communication) estimated that 3000 to 4000 adult Snow Geese were present on JLI on 13 July 1982, during a 125 km visual survey from a Cessna 280 aircraft. Only three years later another major increase was reported by McCormick and Poston (1988). On 9 July 1985, they flew helicopter transects which sampled the entire island during the early brood-rearing period, and obtained the first statistically reliable population estimate for the island: 54 100 (SE = 8 100) adult-plumaged Snow Geese (Figure 3). Ross's Geese were first recorded on JLI in 1988 when 2.7% of the nesting geese were estimated to be Ross's. In the other survey years Ross's were not specifically identified, except for 1998 when T. L. Hoar (personal communication), in a separate study of birds on JLI, recorded 45 adult Ross's and one Ross's nest in the Snow Goose colony.

The rate of increase in Snow Goose numbers was about 34% per annum between 1962-1966 and 1985, and 149% per annum between 1982 and 1985 (Figure 4). That was far too great to be explained by increased reproductive success and survival of Snow Geese hatched on JLI. The increase was probably due to immigration from larger colonies elsewhere, such as those at Queen Maud Gulf Migratory Bird Sanctuary or West Hudson Bay (Kerbes et al. 2006).

JLI Snow and Ross's goose numbers appear to have declined overall since their peak of 54 100 in 1985 (Table 1, Figure 4), as might be expected, given the limited food resources for the geese on the island. Subsequent estimates of adult-plumaged birds were: June 1988 = 42 200 (22% less than in 1985); July 1990 = 25 000 (40% less than in 1988); June 1998 = 20 300 (20% less than in 1990); and June 2006 = 26 400 (30% more than in 1998). It seems that the JLI Snow Goose population peaked in the late 1980s, declined in 1990 and remained at about the 1990 level up to 2006.

The limited amount and quality of food plants on JLI is probably the key factor that caused the popula-

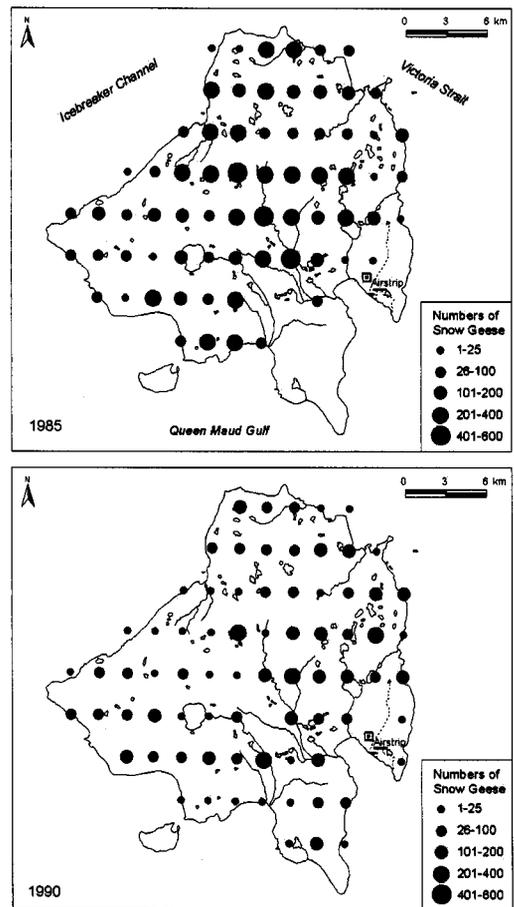


FIGURE 3. Distribution of adult-plumaged Lesser Snow and Ross's geese, per 1.2 km² transect segment from visual helicopter transect surveys, 9 July 1985 (McCormick and Poston 1988) and 28 July 1990.

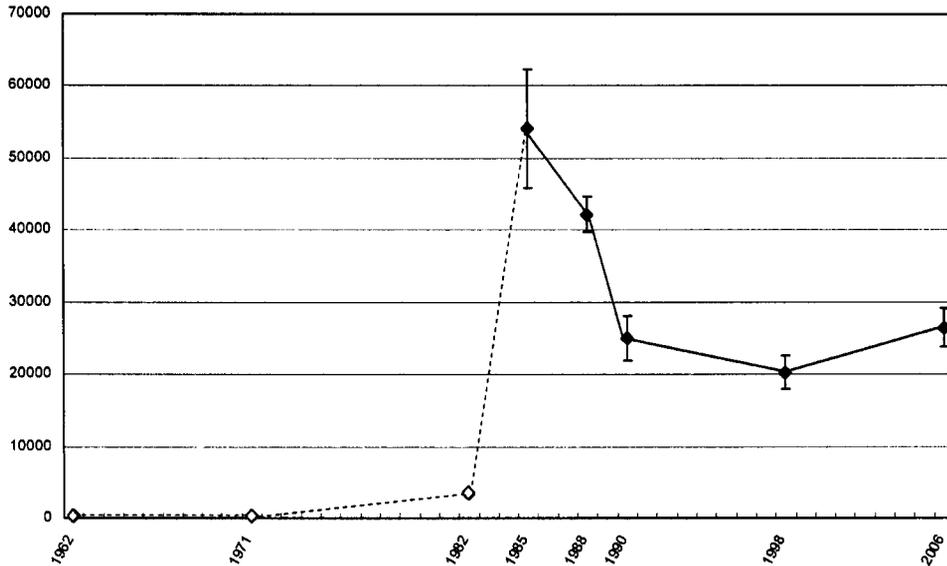


FIGURE 4. Estimated number (\pm SE, for 1985-2006 only) of adult-plumaged Lesser Snow and Ross's geese on Jenny Lind Island, Nunavut, 1962 to 2006.

tion to decline, through decreased survival, lowered productivity, or emigration. Geese were scattered over the entire area of JLI in July of 1985 and 1990 (Figure 3), including areas with little or no vegetation, thus having potential impact on habitat throughout the island. Although we recorded substantial productivity in 1989 (47% young) and 1990 (46% young), we have no information on how successful those young birds were in fledging. During Snow Goose banding operations in 1989, at JLI and QMG, the condition and behaviour of the geese differed remarkably between the two locations. In Queen Maud Gulf Migratory Bird Sanctuary the breeding geese occurred in flocks of families, ranging in size from 50 to several hundred birds each. On JLI most breeding geese occurred as scattered individual families, rather than groups of families, making it difficult to round up a flock of at least 100 for banding. Presumably the low availability of forage caused the high dispersion and low density of feeding geese. The young birds on JLI, although of similar age to those of QMG, were noticeably lighter in weight. Furthermore, both adult and young geese on JLI appeared to be weaker, and the young birds rushed to feed on what little vegetation was available nearby as soon as they were released from the banding pen. That contrasted with the behaviour of young Snow and Ross's geese which we and others (C. D. MacInnes, F. Cooke, R. Alisaukas, personal communication) have observed during arctic banding operations elsewhere. Normally, upon release from the banding pen, both adult and young geese quickly flee rather than attempting to feed.

In 1989 young geese were not banded because they appeared to be weak and underweight, even though

their structural size was normal for their age (approximately four weeks). Nine adult Snow Geese collected in 1990 showed no evidence of unusual nutritional stress (G. Wobeser, Western College of Veterinary Medicine, unpublished pathology report). The average weights of five males ($2267 \pm \text{SE } 128 \text{ g}$) and four females ($2059 \pm 129 \text{ g}$) were similar to those reported by Ankney (1979) for wild birds at the same time of year.

Because JLI is small and sparsely vegetated, overpopulation by geese was expected to lead to destruction of feeding habitats, with serious decline in the condition and numbers of geese. Strong evidence of unusual mortality was not found by McCormick and Poston (1988) in 1985 or in our surveys in 1988, 1989 and 1990. However, at least three anecdotal reports of large die-offs of geese on or near the island in the summers of 1984 and 1985, and in autumn 1989, were received from workers at the DEW Line station or on ships bringing supplies to the station (Kerbes et al. 2005*). They indicated that from hundreds to thousands of geese had died. Although such numbers were unconfirmed, it may be significant that those reports were received during the period when the population grew most rapidly and deterioration in the vegetation caused by over-grazing may have begun to impact the geese on JLI seriously.

On 8 and 9 August 1989, while banding Snow Geese on JLI, we did not observe any evidence of recent mortality. However, on central-eastern and southeastern parts of JLI we observed dried carcasses and other remains of young Snow Geese which apparently had died during the previous year. Similarly, in 1990 scattered remains of a few dead geese from the

previous year were found during ground work. Although we noted only small numbers of carcasses in 1989 and 1990, the actual numbers of geese that had died was probably larger. Mass die-offs can attract avian and mammalian scavengers which reduce the number and visibility of the carcasses (A. J. Erskine and G. Wobeser, personal communication).

It is difficult to accept that the limited food resources of Jenny Lind Island are abundant enough to allow significant numbers of newly hatched young to survive to fledging. Possibly, the persistence of this colony is due solely to immigration from the large and increased numbers of Snow Geese in the QMG region and elsewhere in the Canadian Arctic (Kerbes et al. 2006). Further study of JLI and its geese could provide valuable insights for managing the Midcontinent Snow Goose Population and its arctic habitats. JLI is like an isolated laboratory where newly hatched geese and their flightless parents are "trapped" on an island with a limited and probably dwindling food supply. It offers a good opportunity to evaluate the interactions of geese and their habitat and the resilience of both the goose populations and their habitat. We recommend continued monitoring of the numbers of the Snow and Ross's geese there, a general habitat survey with detailed ground studies of the vegetation, and banding of the geese to determine body condition, survival rates, and, possibly, levels of immigration.

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Documents Cited (marked * in text)

- Kerbes, R. H., K. M. Meeres, J. E. Hines, and D. G. Kay.** 2005. Surveys of Lesser Snow and Ross's geese on Jenny Lind Island, Nunavut, 1962 to 1998. Unpublished Report, Canadian Wildlife Service, Saskatoon, Saskatchewan.
- Kuyt, E., C. H. Schroeder, and A. R. Brazda.** 1971. Aerial waterfowl survey, Queen Maud Gulf, NWT: July-August 1971. Unpublished Report, Canadian Wildlife Service, Edmonton, Alberta.

Literature Cited

- Abraham, K. F., and R. L. Jefferies.** 1997. High goose populations: causes, impacts and implications. Pages 7-

72 in Arctic ecosystems in peril: report to the Arctic Goose Habitat Working Group. Edited by B. D. J. Batt. Arctic Joint Venture Special Publication. United States Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario. 120 pages.

- Ankney, C. D.** 1979. Does the wing moult cause nutritional stress in Lesser Snow Geese? *Auk* 96: 68-72.
- Bostock, H. S.** 1970. Physiographic subdivisions of Canada. Pages 10-30 in *Geology and economic minerals in Canada*. Economic Geology Report (1), 5th edition. Edited by R. W. J. Douglas. Geological Survey of Canada, Ottawa, Ontario.
- Cochran, W. G.** 1977. Sampling techniques. 3rd edition. John Wiley and Sons, New York.
- Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke.** 1991. Long-term decline in body size in a Snow Goose population: Evidence of environmental degradation? *Journal of Animal Ecology* 60: 483-496.
- Ecoregions Working Group.** 1989. Ecoclimatic regions of Canada. Ecological Land Classification series 23. Canadian Wildlife Service, Ottawa, Ontario.
- Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell.** 1992. Long-term changes in survival rates of lesser snow geese. *Ecology* 73: 1346-1362.
- Jefferies, R. L., A. Jensen, and K. F. Abraham.** 1979. Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. *Canadian Journal of Botany* 57: 1439-1450.
- Jolly, G. M.** 1969. Sampling methods for aerial censuses of wildlife populations. *East African Agriculture and Forestry Journal* 34: 46-49.
- Kerbes, R. H.** 1994. Colonies and numbers of Ross' Geese and Lesser Snow Geese in the Queen Maud Gulf Migratory Bird Sanctuary. Canadian Wildlife Service Occasional Paper Number 81. 47 pages.
- Kerbes, R. H., M. R. McLandress, G. E. J. Smith, G. W. Beyersbergen, and B. Godwin.** 1983. Ross' Goose and Lesser Snow Goose colonies in the central Canadian Arctic. *Canadian Journal of Zoology* 61: 168-173.
- Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies.** 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.
- Kerbes, R. H., K. M. Meeres, R. T. Alisauskas, F. D. Caswell, K. F. Abraham, and R. K. Ross.** 2006. Surveys of Nesting Mid-continent Lesser Snow Geese and Ross's Geese in Eastern and Central Arctic Canada, 1997-98. Technical Report Series No. 447, Canadian Wildlife Service, Prairie and Northern Region, Saskatoon, Saskatchewan.
- McCormick, K. J., and B. Poston.** 1988. Lesser Snow Geese (*Anser c. caerulescens*) nesting on Jenny Lind Island, Northwest Territories. *Canadian Field-Naturalist* 102: 530-532.
- Parmelee, P. F., H. A. Stephens, and R. H. Schmidt.** 1967. The birds of southeastern Victoria Island and adjacent 78, National Museum of Canada, Ottawa, Ontario.
- Timm, D. E., and R. G. Bromley.** 1976. Driving Canada Geese by helicopter. *Wildlife Society Bulletin* 4: 180-181.

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