Breeding Biology of Atlantic Population Canada Geese in Nunavik, Northern Québec RICHARD C. COTTER,^{1,2} R. JOHN HUGHES,³ PETER MAY,⁴ PAULUSI NOVALINGA,⁵ JIMMY JOHANNES,⁵ LARRY J. HINDMAN⁶ and PAUL I. PADDING⁷

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ABSTRACT. The Atlantic population of Canada Geese (Branta canadensis interior) experienced a sharp decline in numbers in the late 1980s. Management agencies in Canada and the United States responded by implementing several measures, notably closing sport hunting seasons for a number of years in most Atlantic Flyway states and provinces and funding a research project to study the nesting ecology and the factors affecting productivity of this goose population. In this paper we present the nesting phenology and breeding biology of Atlantic population Canada Geese on their tundra nesting grounds in Nunavik, Québec, specifically on a primary study area (32.8 km²) along Hudson Bay (1997–2003) and on several secondary sites (most smaller than 1 km²) distributed along the coastal lowlands of Hudson Bay and Ungava Bay (1996–2005). In the late 1990s the population rebounded, with strong increases in the population of breeding pairs and the density of nests between 1996 and 2001, followed by stabilization of both variables from 2001 to 2005. As a result, there was a near doubling in productivity index (the number of goslings produced per km²) on the primary study area, from 17.9 in 1997 to 32.0 in 2003. Geese start laying eggs soon after snow disappears from their nesting grounds. On the primary study area, for all years pooled, mean clutch initiation date, clutch size, hatching date, and Mayfield nesting success were 27 May, 4.54 eggs, 26 June, and 67.3%, respectively. Among secondary sites along both Hudson Bay and Ungava Bay, we found a correlation between the annual average daily temperature for 4-24 May (the period leading up to egg-laying) and the annual mean clutch initiation date: higher temperatures were correlated with earlier initiation. Similarly, an earlier annual mean clutch initiation date was correlated with large mean clutch size.

Key words: Canada Goose, *Branta canadensis interior*, Atlantic population, breeding biology, nesting success, productivity, Nunavik, Ungava Peninsula, Québec

RÉSUMÉ. La population de l'Atlantique de la bernache du Canada (Branta canadensis interior) a subi un déclin prononcé à la fin des années 1980. Les organismes chargés de la gestion de la faune au Canada et aux États-Unis ont réagi en mettant en place plusieurs mesures. Ils ont notamment fermé la saison de chasse sportive dans la plupart des États et provinces de la voie migratoire de la population de l'Atlantique pendant un certain nombre d'années et financé un projet de recherche sur l'écologie de la nidification et sur les facteurs limitant la productivité de cette population. Dans le présent article, nous décrivons la phénologie de la nidification et la biologie de la reproduction de la population de l'Atlantique de la bernache du Canada dans son aire de nidification de la toundra du Nunavik (Québec), plus précisément dans une aire d'étude principale (32,8 km²) établie en bordure de la baie d'Hudson (1997-2003) et dans plusieurs sites secondaires de superficie plus modeste (dans la plupart des cas, inférieure à 1 km²) disséminés dans les basses-terres côtières de la baie d'Hudson et de la baie d'Ungava (1996-2005). À la fin des années 1990, la population a rebondi, le nombre de couples nicheurs et la densité des nids augmentant fortement entre 1996 et 2001 pour ensuite se stabiliser de 2001 à 2005. Par suite de ce redressement, le nombre d'oisons produits par kilomètre carré a presque doublé (indice de productivité) dans l'aire d'étude principale, passant de 17,9 en 1997 à 32,0 en 2003. La ponte débute peu après la disparition de la neige dans les sites de nidification. Dans l'aire d'étude principale, nous avons enregistré les valeurs moyennes suivantes (années regroupées) : début de la période de ponte : 27 mai; taille des couvées : 4,54 œufs; premières éclosions : 26 juin; succès de la nidification en mai : 67,3 %. Aux sites secondaires, en bordure de la baie d'Hudson et de la baie d'Ungava, nous avons relevé une corrélation entre la température journalière moyenne annuelle pour la période du 4 au 24 mai (période précédant le début de la période de ponte) et la date annuelle moyenne du début de la ponte: les températures plus élevées donnaient une corrélation avec un début de période de ponte plus hâtif. De même, une date annuelle moyenne plus hâtive du début de la ponte a été corrélée avec une grande taille moyenne des couvées.

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Mots clés : bernache du Canada, *Branta canadensis interior*, population de l'Atlantique, biologie de la reproduction, succès de la nidification, productivité, Nunavik, péninsule d'Ungava, Québec

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FIG. 1. Location of the Canada Goose primary study area and the secondary sites (small circles) within the Hudson Bay and Ungava Bay lowlands on the Ungava Peninsula in northern Québec.

INTRODUCTION

Up to the 1980s, the Atlantic population (AP) of Canada Geese (Branta canadensis interior) was the most abundant Canada Goose population in North America, with a midwinter estimate of nearly one million birds in 1981 (Hindman and Ferrigno, 1990) and an annual sport harvest in the Atlantic Flyway estimated at more than 400000 birds (Malecki and Trost, 1990). This population nests entirely in Québec, with more than 80% breeding in Nunavik, Québec's Arctic region north of 55°N, and the remainder nesting in the taiga and northern boreal forest as far south as 48° N. Its major wintering areas are the Delmarva Peninsula of Maryland and Delaware and portions of New York, Pennsylvania, New Jersey, and Virginia (Dickson, 2000; Atlantic Flyway Council, 2008). In the late 1980s and early 1990s, this population experienced a dramatic decline in size as a result of high harvest rates and a number of breeding seasons with poor productivity. The first aerial survey

of the breeding grounds on the Ungava Peninsula in Nunavik, in 1988, counted 118000 (± 15 144 [SE]) nesting pairs (Malecki and Trost, 1990), but an aerial survey in 1995 counted only 33 995 (± 3045) pairs (Harvey and Rodrigue, 2012). This decline prompted wildlife management agencies in Canada and the United States to close sport hunting seasons throughout most of the Atlantic Flyway in 1995 and to produce the Action Plan for the Atlantic Population of Canada Geese (Atlantic Flyway Council, 1996), which detailed objectives and strategies for the recovery of the population, including monitoring and research needs. A key objective was to document recruitment parameters such as nesting phenology, clutch size, and nesting success. The Action Plan therefore recommended a multi-year study of the breeding ecology (primary study area) and the implementation of an annual monitoring program to measure breeding effort and success at key locations (secondary sites) on the Ungava Peninsula. The monitoring program was established in 1996, and the research study was conducted from 1997 to 2003. This paper presents the key reproductive parameters from the breeding ecology study and the first 10 years of the nesting monitoring program, 1996 to 2005.

STUDY AREA

This study was carried out on the Ungava Peninsula in the Nunavik territory of northern Québec (Fig. 1) from 1996 to 2005. This tundra region lies within the Arctic Ecoclimatic Province (Canada Committee on Ecological Land Classification, 1989), specifically the Southern Arctic Ecozone, an area characterized by herb-lichen tundra, a very cold, dry climate, and continuous permafrost (Wiken et al., 1996). The highest densities of breeding pairs of AP Canada Geese are found on this peninsula in two regions: the coastal lowlands of eastern Hudson Bay and the coastal lowlands of southwestern Ungava Bay (Malecki and Trost, 1990; Harvey and Rodrigue, 2012), primarily between the Inuit communities of Inukjuak and Akulivik on Hudson Bay and between Kuujjuaq and Kangirsuk on Ungava Bay. We therefore chose the location of our study areas—a large primary study area (1997-2003 only) and smaller secondary study sites along Hudson Bay and Ungava Bay-from these two regions (Fig. 1).

The primary study area, 32.8 km² in size, was situated along the Polemond River at 59° 31.5' N, 77° 36.1' W, approximately 10 km inland from the Hudson Bay coast and 60 km south of Puvirnituq. It is characterized by lichen-heath tundra (approximately 65% of total area), lakes (22%), wet sedge meadows (11%), and ponds and streams (2%) (Cadieux et al., 2005). Lichens, dwarf birch (*Betula glandulosa*), mountain cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are the dominant plant cover in the lichen-heath tundra, whereas wet-sedge meadows are composed mostly of mosses, water sedge (*Carex aquatilis*), and cottongrass (*Eriophorum angustifolium*). Edges of most ponds are dominated by sedges (*Carex spp.*) and cottongrass, whereas along lakes willow (*Salix lanata*) is the dominant plant species (Cadieux et al., 2005).

The secondary study sites were located in two stretches of coastal lowlands, one along Hudson Bay and the other along Ungava Bay, each approximately 180 km long. Along Hudson Bay there were seven secondary sites located between the Mariet River (59° 9' N) in the south and the Korak River (60° 46' N) in the north. These sites ranged in size from 0.35 km² to 0.64 km² and all were surveyed in every year except 1996, when only five sites were surveyed. Along Ungava Bay there were 10 secondary sites; however, no more than six were surveyed in any one year, and only six sites were surveyed in five or more years. With one exception, these sites were located between the Whale River (Rivière à la Baleine), located approximately 40 km east of Kuujjuaq in the south and Aupaluk in the north. The exception was a site located farther east along Ungava Bay, about 30 km northwest of Kangiqsualujjuaq; it was surveyed in only two years, and few nests were found there. On average, the Ungava Bay sites ranged in size between 0.25 km^2 and 2.46 km^2 .

METHODS

Primary Study Area

Inuit from Puvirnituq, the nearest village (60 km distant) to the primary study area, begin observing Canada Geese in the region each year, usually in early to mid May. Each year the field crew timed their arrival to coincide with the start of egg laying, but in some years they had to wait to begin nest searches because of delayed snowmelt (Table 1). As soon as it was apparent that some geese had initiated nesting, the field crew (five or six people, depending on the year) began to search for nests: members walked approximately 50 m apart and searched the study area systematically, with emphasis on a close search of the edges of wetlands and ponds. Three to five days were required to search the entire study area, depending on the weather and the amount of snow cover. When a nest was found, it was assigned a unique number, a 1 m stake (painted fluorescent orange) was placed at a distance of 25 m (to help relocate it on subsequent visits), and each egg in the nest was numbered. The following information was also recorded: geographic coordinates (using a hand-held Global Positioning System [GPS], Garmin models 48, 76; NAD27 datum); date and time; status of nest when found (laying, incubating, hatching, abandoned, destroyed, or unknown); the number of eggs; the status of each egg (warm or cold, intact or broken, in or out of the nest); the mass (nearest g), length (nearest 0.1 mm), and width (nearest 0.1 mm) of each egg; the shortest distance from the nest to water (m); and the three most common plant species within a 1 m radius of the nest, as well as the approximate cover of each species. Furthermore, all nests were classified into two broad habitat categories (dry and wet) based on proximity to a waterbody. Dry nests were more than 10 m away from a waterbody larger than 0.0021 ha (e.g., $3 \text{ m} \times 7 \text{ m}$), and wet nests were within 10 m of such a waterbody.

After the initial visit, we revisited all nests approximately every three days until either no new eggs were found in the nest or the nest was depredated or abandoned. For new eggs, the same information was recorded as during the first visit; if no new eggs had been laid, we assumed laying was completed, the clutch size (CS) for the nest was recorded, and the nest was not revisited until mid-incubation, at which time it was visited every 2–3 days, with the penultimate visit timed to occur with the start of hatching. The last visit occurred 1–2 days after pipping began in order to web-tag each gosling and to record clutch size at hatch (CSH), the number of goslings leaving the nest (GLN), and hatching success (HS = GLN/CS).

Clutch initiation date was defined as the date the first egg was laid and was calculated for each nest by subtracting a

			Nest search date ³						
	Average temperatu	re (°C) ¹ May $4-24$	Arrival at prim	ary study area	First egg laid ²	Primary area	Hudson Bay	Ungava Bay	
Year	Puvirnituq	Kuujjuaq	% snow cover	Date (May)	(May)	(May)	(June)	(June)	
1996	-5.4	-3.2					14-16	7-11	
1997	0.2	2.0	10	22	23	24	6-8	6-9	
1998	2.4	4.3	5	21	17	22	9-11	3-6	
1999	0.9	2.7	25	20	17	21	5 - 8	7 - 10	
2000	-1.4	-0.1	95	20	24	28	10 - 14	5 - 8	
2001	3.5	5.6	5	20	18	21	9-13	4-9	
2002	-4.6	-2.4	95	18	5^{4}	9 ⁴	16 - 20	10 - 14	
2003	0.0	5.5	75	17	22	24	7-12	5-11	
2004	-3.7	-1.1					12-15	11 - 17	
2005	0.2	3.9					10-13	7-8	

TABLE 1. General weather conditions and timing of the field crew arrival and searches for Canada Goose nests at the primary study area and at the secondary study sites along Hudson Bay and Ungava Bay in northern Québec, 1996–2005.

¹ Average of the mean daily temperatures (average of daily maximum and daily minimum) recorded at the Puvirnituq Airport (on Hudson Bay) and Kuujjuaq Airport (on Ungava Bay) (available from http://climate.weatheroffice.gc.ca/).

² Earliest clutch initiated on the primary study area.

³ First day of nest searches on the primary study area and the Hudson Bay and Ungava Bay secondary study sites.

⁴ The month is June (for 2002).

number equal to total clutch size minus one from the date on which incubation began (i.e., the date the last egg was laid). Eggs are laid at intervals of approximately 35 hours (see Mowbray et al., 2002); therefore, for large clutches (four or more eggs) an egg was not subtracted from the total clutch size. Hatch date was defined as the date on which all eggs in the nest had begun pipping (star-pip or hole-pip stage), and length of incubation was calculated by subtracting the start of incubation from the hatch date.

The fate of every nest found was recorded as either successful (at least one egg hatched), abandoned (clutch still intact but eggs cold), destroyed (i.e., predation causing complete absence of eggs or presence of broken egg shells without separated egg membranes), observer destroyed (one nest in 1997 and three nests in 1998), infertile, or unknown. Both apparent nesting success (the percentage of nests initiated that hatched at least one gosling) and Mayfield nesting success (Mayfield, 1961; Johnson, 1979) were calculated. Nests found after they had failed were included in calculating apparent nesting success but excluded for the Mayfield method, which requires a nest to be under observation (i.e., exposure) for at least one day to be included in the calculations. Furthermore, for the Mayfield method, if a nest was observed to have failed between two visits, the date of failure was assumed to be halfway between the two visits (Klett and Johnson, 1982).

At hatch, we fitted each gosling with a uniquely numbered web-tag (size 1, National Band and Tag Co.). Marked goslings and their parents were recaptured four to six weeks later during the annual banding drives. For every brood from which at least one marked gosling was recaptured, we calculated gosling survival from hatch to banding as the proportion of goslings that had left the nest (where status of leaving the nest was either confirmed, probably left the nest, or unknown) and were subsequently recaptured during banding. Goslings that were marked but were known to have died before leaving the nest were excluded. A factor that could bias gosling survival is total brood loss (when no members of a brood survive), which is impossible to distinguish from marked broods simply not being encountered during banding. An indication of annual total brood loss differences is obtained by calculating the proportion of marked broods (% broods recaptured) for which one or more goslings were recaptured.

An annual index of population productivity, the productivity index (PI) or the number of goslings produced per km², was calculated as follows:

PI = nest density • Mayfield nest success • goslings leaving per nest • gosling survival

Each year after hatching had occurred, a crew of two or three observers visited a sector within the study area each day over a four-hour period (0700–1100, 1100–1500, 1500–1900) and recorded the location and size of all individual family broods observed. We considered broods of 10 or more goslings as having goslings from more than one brood and therefore excluded them from the analyses. These observations continued until banding commenced, at which time (for most years) goslings were four to six weeks of age. The distances moved by broods, specifically web-tagged goslings that were captured during the banding drives in late July to mid August, were determined by measuring the distance from the goslings' nests to their banding (catch) locations.

There is evidence from several Arctic sites that small mammal populations fluctuate widely between years and that these fluctuations can have a profound effect on predation rates on goose eggs (Bêty et al., 2001; Wilson and Bromley, 2001). To monitor small mammal populations (primarily Ungava lemming *Dicrostonyx hudsonius*), we followed the protocol established for the Northwest Territories and Nunavut (see Carrière, 1999). In 1997, four 250 m transects were set up in two different habitat types two transects each in lowland and upland habitats. Museum Special snap traps were placed along each transect at 10 m intervals. Each year 100 traps were set and checked once a day, between 0800 and 1000, for 10 days. Trapped individuals were identified to species using Lupien (2002) and Desrosiers et al. (2002). The same trapping transects were used each year, and they were set up in the second half of July.

Secondary Study Sites

Secondary nest sites along Hudson Bay and Ungava Bay were first visited during early incubation, the timing determined from nesting phenology information from the primary study area or from observations of local Inuit. At this visit to a site, two pairs of observers systematically groundsearched the entire area, recorded the location of each nest found and marked it with a stake, numbered each nest and any eggs it contained, and recorded the same information as for nests in the primary study area.

Each site was visited a second time after hatching. To economize on helicopter travel, this visit was carried out during the banding operations in late July to mid August. Each nest was revisited and its fate was recorded as either successful (i.e., egg caps or membranes were present), or abandoned (all eggs were still in the nest), or predator-destroyed (absence of egg shells or presence of egg fragments with membrane attached). The area of each secondary site was calculated using the mapping software ArcView with one of two methods. For sites along Hudson Bay, ArcView was used to map the boundary of each site, which remained constant among years, and then calculate the surface area. The boundaries of Ungava Bay sites, on the other hand, were not fixed, and therefore we plotted the locations of all nests and ArcView calculated the surface area using the nests on the perimeter (Minimum Convex Polygon).

Since most nests were found during incubation, we calculated clutch initiation date by first determining, for each egg in the clutch, the number of days of incubation (DAYS) at the time of the first visit. Basing our method on the principle that eggs gradually lose mass over the course of incubation, we calculated DAYS using an index of egg density (DI) and a regression of density on days, where for each egg:

 $DI = (mass / length \cdot width^2) \cdot 1000, and$ DAYS = (DI of fresh eggs - DI of measured egg) / daily rate of change in density= (0.5551 - DI) / 0.003

Since we had neither a measure of DI for fresh eggs nor the daily rate of change in density for tundra-nesting AP Canada Geese, we used Cooper's (1978) DI value (0.5551 g/cm³) obtained for a Canada Goose population in Manitoba and Hughes et al.'s (2000) rate of change in density

(0.003 g/cm³) for AP Canada Geese nesting in the taiga of north-central Québec. This method was used for all sites in all years, except at Hudson Bay sites in 2000, where the stage of incubation was determined by floating eggs and nest age was calculated following Walter and Rusch (1997). The density index method computes the start of incubation for individual eggs within each nest by subtracting the day of incubation (i.e., DAYS, except for Hudson Bay sites in 2000) from the date the egg was measured (presumably the date the nest was found). Taking the average of the eggs in each clutch, we obtained the start of incubation date for each nest. We obtained the clutch initiation date (the start of egg laying) for each nest by subtracting a number of days equal to total eggs in the nest minus one from the date on which incubation began. As for nests on the primary study area, we did not subtract an egg from the total for clutches of four or more eggs. We estimated hatch date by adding 26 days to the first day of incubation. For Hudson Bay sites in 2000, following Walter and Rusch's (1997) method for large Canada Geese, we first calculated the clutch age as equal to $4.333 \times \text{stage} - 2.167$, where stage equals the stage of development of the yolk. Hatch date = date found + (length of incubation clutch age), where length of incubation is 26 days. With respect to stage of yolk development, Walter and Rusch (1997) used the six float stages described by Westerskov (1950) for Ring-necked Pheasants (Phasianus colchi*cus*). In our study, we grouped these six into three stages. Clutch initiation date was then calculated by subtracting (length of incubation + (clutch size -1))—or (length of incubation + clutch size) for clutches of four or more eggsfrom the hatch date.

Statistical Analyses

Annual means (± standard errors, SE) for each reproductive variable were calculated for the primary site and all secondary sites using the following nest criteria: nest density and nest fate (i.e., percentage of total nests initiated that were either successful, abandoned, destroyed, or other) used all nests that were found; clutch initiation date and clutch size for the primary study area used only nests found during egg-laying; clutch initiation date for the secondary sites used all active nests found; clutch size for the secondary sites used only nests found during incubation; and clutch size at hatch, number of goslings leaving the nest, hatching success, and hatching date were determined only for successful nests on the primary study area (whether found during egg-laying or incubation). The annual means of each variable for Hudson Bay and Ungava Bay, with one exception, were calculated by pooling nests from across all sites. The exception was nest density, for which the annual mean was the mean of the nest densities of the individual sites along either Hudson Bay or Ungava Bay (and therefore sample size was equal to the number of sites surveyed). The standard errors for each nest fate (successful, abandoned, destroyed, and other) were based on the binomial distribution:

$$SE = \sqrt{(pq)/n}$$

where, for example, p = the proportion of nests abandoned, q = 1 - p, and n = total number of nests.

For Hudson Bay and Ungava Bay secondary sites, site (fixed variable) and year (random variable) were tested in a two-factor mixed-model analysis of variance (PROC GLM; SAS Institute, 2004) for clutch initiation date, clutch size, and apparent nest success. Correlations between sets of two variables were analyzed by calculating Pearson product-moment correlation coefficients (r) (PROC CORR; SAS Institute, 2004). The significance level was set at $\alpha < 0.05$ for all tests.

RESULTS

Nest Density and Site Characteristics

Over the 10 years of this study, 5898 Canada Goose nests were found: 3085 on the primary study area, 1749 on Hudson Bay secondary sites, and 1064 on Ungava Bay secondary sites. On the primary study area (32.8 km²), nest density increased from 8.9 nests/km² in 1997 to 20.6 nests/km² in 2003 (Table 2), a 131% increase. Nest densities were considerably higher on the smaller secondary sites than on the primary study area, two to five times higher in any given year (Table 2). Between 1997 and 2003, the secondary sites along Hudson Bay experienced a level of increase in nest density (121%) similar to that of the primary study area, from 37.7 nests/km² to 83.4 nests/km². From 1996 to 2005, nest density on these sites increased by 249%, which is very close to the 241% increase in the size of the breeding population recorded by Harvey and Rodrigue (2012) on the Ungava Peninsula over this 10-year period (from $51466 \pm$ 4789 [SE] pairs to 175679 ± 16737 pairs). Both nest density and the size of the breeding population increased strongly up to 2001 but then stabilized in the following years. On the Ungava Bay secondary sites, nest densities increased each year from 1996 to 1999 but afterwards fluctuated considerably (Table 2).

More Canada Goose nests were found in wet habitat than in dry habitat. Wet habitat represented 67% (2073 of 3085 nests) on the primary study area, 85% (1026 of 1207 nests) on Hudson Bay secondary sites, and 60% (429 of 716 nests) on Ungava Bay secondary sites. Wet or dry habitat was not recorded for 157 of 873 nests (18%) of Ungava Bay sites. The mean distance of nests to water was 7.4 m (\pm 23.7 [SD], n = 3078 nests) on the primary study area, 4.1 m (± 7.7, n = 1186 nests) on Hudson Bay secondary sites, and 8.2 m $(\pm 15.3, n = 649 \text{ nests})$ on Ungava Bay secondary sites. At all three areas, the most common plant providing nest cover was dwarf birch; this shrub was ranked first (i.e., providing the most cover) at 54% of all nests at the primary study area (all years and habitat types pooled), 38% at Hudson Bay secondary sites, and 28% at Ungava Bay secondary sites. The next most common plants bordering goose nests were

[ABLE 2. Mean (± SE, n) nest density, clutch initiation date, clutch size, and apparent nesting success of Canada Geese for the primary study area (Primary) and for the secondary 1006 Ouáhan 44 Davi in Day Hudeor ĥ 4

success (%)	son Bay Ungava Bay	72.4 12.5	$5.9, 58) (\pm 8.5, 16)$	78.0 60.7	(.7, 123) (± 9.4, 28)	89.8 77.0	2.7,127) (± 5.4,61)	77.7 60.2	(.7, 130) (± 4.6, 113)	49.7 27.5	$(0, 159)$ $(\pm 5.0, 80)$	85.5 49.7	(±3, 228) (± 3.7, 181)	68.3 22.7	(6, 167) (± 3.1, 185)	75.1 63.6	(.6, 273) (± 3.2, 225)	82.9 20.3	$(.8, 187)$ $(\pm 5.3, 59)$	83.8 56.9	(.1, 297) (± 4.6, 116)
Nesting	Primary Hud		; =)	82.5	(± 2.2, 292) (± 3	86.8	$(\pm 1.8, 348) (\pm 2$	64.3	(± 2.3, 423) (± 3	23.0	(± 2.2, 383) (± 4	84.2	$(\pm 1.4, 639)$ $(\pm 2$	55.1	(± 2.8, 325) (± 3	75.7	(± 1.7, 675) (± 2		(主 2		(主 2
	Ungava Bay	3.89	$(\pm 0.39, 9)$	4.36	$(\pm 0.30, 22)$	4.22	$(\pm 0.20,55)$	4.23	$(\pm 0.13, 91)$	3.69	$(\pm 0.15, 67)$	4.07	$(\pm 0.11, 142)$	3.47	$(\pm 0.10, 136)$	4.34	$(\pm 0.10, 187)$	3.42	$(\pm 0.23, 33)$	4.31	$(\pm 0.15, 81)$
Clutch size	Hudson Bay	3.53	$(\pm 0.17, 55)$	4.55	$(\pm 0.10, 108)$	4.66	$(\pm 0.10, 121)$	4.15	$(\pm 0.11, 120)$	3.95	$(\pm 0.10, 128)$	4.52	$(\pm 0.08, 208)$	3.21	$(\pm 0.08, 141)$	4.25	$(\pm 0.07, 251)$	3.11	$(\pm 0.07, 176)$	4.38	$(\pm 0.07, 280)$
	Primary			4.98	$(\pm 0.09, 113)$	5.29	$(\pm 0.10, 102)$	4.65	$(\pm 0.07, 162)$	4.05	$(\pm 0.11, 111)$	4.49	$(\pm 0.07, 322)$	3.63	$(\pm 0.12, 73)$	4.52	$(\pm 0.06, 248)$				
ate	Ungava Bay	01 June	$(\pm 1.4, 12)$	24 May	$(\pm 1.0, 19)$	22 May	$(\pm 0.8, 55)$	24 May	$(\pm 0.6, 91)$	30 May	$(\pm 0.4, 72)$	20 May	$(\pm 0.5, 142)$	11 June	$(\pm 0.9, 137)$	20 May	$(\pm 0.9, 168)$	07 June	$(\pm 1.0, 27)$	24 May	$(\pm 0.7, 82)$
atch initiation da	Hudson Bay	05 June	$(\pm 0.5, 55)$	28 May	$(\pm 0.4, 109)$	19 May	$(\pm 0.4, 114)$	22 May	$(\pm 0.6, 121)$	01 June	$(\pm 0.3, 125)$	23 May	$(\pm 0.3, 208)$	09 June	$(\pm 0.5, 153)$	01 June	$(\pm 0.6, 251)$	05 June	$(\pm 0.4, 176)$	28 May	$(\pm 0.5, 280)$
Ch	Primary			29 May	$(\pm 0.2, 127)$	21 May	$(\pm 0.2, 110)$	23 May	$(\pm 0.2, 199)$	31 May	$(\pm 0.2, 178)$	24 May	$(\pm 0.1, 322)$	11 June	$(\pm 0.2, 99)$	28 May	$(\pm 0.2, 284)$				
1 ²)	Ungava Bay	3.5	(16)	14.2	(28)	21.2	(61)	67.1	(113)	38.4	(80)	40.7	(181)	19.4	(185)	19.1	(225)	24.5	(59)	43.3	(116)
est density (n/kn	Hudson Bay	25.5	(58)	37.7	(123)	38.7	(127)	40.2	(130)	49.2	(159)	71.1	(228)	51.2	(167)	83.4	(273)	56.4	(187)	88.9	(297)
Ne	Primary			8.9	(292)	10.6	(348)	12.9	(423)	11.7	(383)	19.5	(639)	9.9	(325)	20.6	(675)				
	Year	1996		1997		1998		1999		2000		2001		2002		2003		2004		2005	

crowberry at the primary study area, grasses (Graminae spp.) at Hudson Bay, and willow and sedge at Ungava Bay.

Nesting Phenology, Egg Size, Clutch Size, and Hatching Success

On the primary study area, 80% (10th to 90th percentile) of nests over all years were initiated (i.e., first egg laid) during a 15-day period from 21 May to 4 June (Fig. 2), and the overall mean date of initiation was 27 May (± 0.2 , n = 1319 nests). Among years we observed a three-week difference between the earliest year (80% initiation: 18–24 May 1998) and the latest year (9-13 June 2002) (Fig. 2). In any one year, 80% of all nests were initiated over a five- to nine-day period. This period was longer for the secondary sites: 9 to 24 days for Hudson Bay and 9 to 26 days for Ungava Bay. At both secondary areas, there was a non-significant site effect (Hudson Bay: F = 2.04, df = 6, p = 0.08; Ungava Bay: F = 1.15, df = 9, p = 0.36), but there were significant effects of year (Hudson Bay: F = 35.94, df = 9, p < 0.01; Ungava Bay: F = 19.20, df = 9, p < 0.01) and interaction effects (Hudson Bay: F = 4.86, df = 52, p < 0.01; Ungava Bay: F =1.61, df = 20, p = 0.04). Overall mean clutch initiation date was 27 May (± 0.4 , n = 805 nests, 95% CI = 26-27 May) at Ungava Bay and 30 May (± 0.2 , n = 1592 nests, 95% CI = 29-30 May) at Hudson Bay.

Annual mean clutch initiation date was negatively correlated with the mean of the average daily temperatures (i.e., average of the daily minimum and maximum temperatures) at both Hudson Bay and Ungava Bay (temperatures recorded at Puvirnituq and Kuujjuaq airports, respectively) for the three-week period leading up to egg laying (4-24 May): primary study area (r = 0.94, n = 7 years), Hudson Bay secondary sites (r = 0.91, n = 10 years), and Ungava Bay secondary sites (r = 0.90, n = 10 years). With this mean temperature (4-24 May), the following model can be used to calculate a predicted mean clutch initiation date = -2.1043 • temperature + 27.9376, and for Ungava Bay, clutch initiation date = -2.1194 • temperature + 31.2453.

The mean length of incubation on the primary study area was 26 days in every year except 2003, when it was 25 days. Across years the mean date of hatching was 26 June, with annual means ranging from 20 June to 10 July (Table 3).

Overall (years and primary and secondary sites pooled), eggs had a mean length of 83.4 mm (\pm 0.03, n = 18992 eggs), width of 56.3 mm (\pm 0.01, n = 18992 eggs), and mass of 140.0 g (\pm 0.09, n = 18992 eggs). For the Hudson Bay region (i.e., pooling the primary and secondary sites), the mean length, width, and mass were 83.2 mm (\pm 0.03, n = 15711 eggs), 56.1 mm (\pm 0.01, n = 15711 eggs), and 139.3 g (\pm 0.10, n = 15711 eggs), respectively, and for Ungava Bay the same means were 84.2 mm (\pm 0.06, n = 3281 eggs), 56.9 mm (\pm 0.03, n = 3281 eggs), and 143.8 g (\pm 0.25, n = 3281 eggs), respectively.

The annual means for clutch size varied between 3.6 and 5.3 eggs for the primary study area and between 3.1 and 4.7



FIG. 2. Phenology of clutch initiation by Canada Geese at the primary study area in northern Québec, 1997–2003.

eggs for secondary sites on Hudson Bay and Ungava Bay (Table 2). Clutches with 3-6 eggs represented 93% (1052) of 1131 nests) of all clutches in the primary study area, 89% (1409 of 1588 nests) of secondary sites at Hudson Bay, and 83% (686 of 823 nests) of those at Ungava Bay. For the primary study area only, the mean clutch size (CS) across vears was 4.54 eggs, clutch size at hatch (CSH) was 4.08 eggs, and number of goslings leaving the nest (GLN) was 3.66 goslings (Table 3). The mean GLN was 19.4% smaller than the mean CS, and this difference provides an indication of egg loss during incubation and gosling loss during hatching. This loss ranged from 16.0% (2001) to 26.4% (2000). Among secondary sites, across years and sites the mean clutch size was 4.09 eggs (± 0.03 , n = 1588 nests, 95% CI = 4.02 - 4.15) at Hudson Bay and 4.03 eggs (± 0.05, n = 823 nests, 95% CI = 3.94-4.13) at Ungava Bay. There was a significant site effect at Hudson Bay (F = 3.99, df = 6, p =0.002), but not at Ungava Bay (F = 0.49, df = 9, p = 0.87). At Hudson Bay, however, Tukey's Studentized Range test showed that the mean clutch sizes for six of the seven sites were not significantly different. At both areas, there was a significant year effect (Hudson Bay: F = 27.64, df = 9, p <0.01; Ungava Bay: F = 3.08, df = 9, p = 0.001), and there was a significant interaction effect at Hudson Bay (F = 1.45, df = 52, p = 0.02) but not at Ungava Bay (F = 1.46, df = 20, p = 0.09). At all three areas, annual mean clutch size was positively correlated with the annual mean temperature for 4-24 May (primary study area: r = 0.77, n = 7 years; Hudson Bay: r = 0.90, n = 10 years; Ungava Bay: r = 0.77, n =10 years) and negatively correlated with the annual mean clutch initiation date (primary study area: r = 0.83, n = 7years; Hudson Bay: r = 0.85, n = 10 years; Ungava Bay: r = 0.90, n = 10 years). Hatching success (GLN/CS) of clutches at the primary study area, across years, was 80% (\pm 0.7 [SE], n = 923 nests), with annual means ranging from 72% to 88%.

Parameter	1997	1998	1999	2000	2001	2002	2003	Years pooled
Clutch size (CS)	4.98 ± 0.09 (n = 113)	5.29 ± 0.10 (n = 102)	$\begin{array}{c} 4.65 \pm 0.07 \\ (n = 162) \end{array}$	4.05 ± 0.11 (n = 111)	4.49 ± 0.07 (n = 322)	3.63 ± 0.12 (n = 73)	$\begin{array}{c} 4.52 \pm 0.06 \\ (n = 248) \end{array}$	4.54 ± 0.03 (n = 1131)
Clutch size at hatch (CSH)	$\begin{array}{c} 4.47 \pm 0.08 \\ (n = 227) \end{array}$	$\begin{array}{c} 4.72 \pm 0.07 \\ (n = 301) \end{array}$	$\begin{array}{c} 3.75 \pm 0.08 \\ (n = 253) \end{array}$	3.45 ± 0.12 (n = 87)	$\begin{array}{c} 4.30 \pm 0.05 \\ (n = 534) \end{array}$	3.03 ± 0.08 (n = 177)	$\begin{array}{c} 3.93 \pm 0.06 \\ (n = 498) \end{array}$	$\begin{array}{c} 4.08 \pm 0.03 \\ (n = 2077) \end{array}$
Goslings leaving nest (GLN)	$\begin{array}{c} 4.16 \pm 0.09 \\ (n = 231) \end{array}$	$\begin{array}{c} 4.26 \pm 0.07 \\ (n=298) \end{array}$	$\begin{array}{c} 3.45 \pm 0.08 \\ (n = 248) \end{array}$	2.98 ± 0.12 (n = 84)	$\begin{array}{c} 3.77 \pm 0.05 \\ (n = 532) \end{array}$	2.71 ± 0.08 (n = 174)	$\begin{array}{c} 3.51 \pm 0.06 \\ (n = 501) \end{array}$	3.66 ± 0.03 (n = 2068)
Hatching date	29 June ± 0.2	$20 \text{ June} \pm 0.1$	22 June ± 0.2	$30 \text{ June} \pm 0.3$	$24 \text{ June} \pm 0.1$	$10 \text{ July} \pm 0.2$	27 June \pm 0.1	26 June ± 0.1
	(n = 220)	(n = 293)	(n = 245)	(n = 75)	(n = 505)	(n = 170)	(n = 475)	(n = 1983)
Brood size ¹	3.91 ± 0.18 (n = 198)	3.92 ± 0.08 (n = 416)	3.39 ± 0.10 (n = 193)	3.07 ± 0.50 (n = 14)	$\begin{array}{c} 4.19 \pm 0.13 \\ (n = 161) \end{array}$	$\begin{array}{c} 2.71 \pm 0.09 \\ (n=224) \end{array}$	3.33 ± 0.06 (n = 679)	3.53 ± 0.04 (n = 1885)
Brood movements (m)	1554 ± 69	4667 ± 241	7809 ± 546	6384 ± 1684	9359 ± 537	7756 ± 1034	11914 ± 772	7237 ± 239
(nest to banding site)	(n = 215)	(n = 297)	(n = 209)	(n = 16)	(n = 282)	(n = 80)	(n = 265)	(n = 1364)
Mayfield nesting success (%) ²	81.9	89.4	61.3	20.4	81.7	50.8	77.6	67.3
	(n = 35;	(n = 27;	(n = 124;	(n = 239;	(n = 92;	(n = 105;	(n = 102;	(n = 724;
	76.6-87.6)	85.6-93.3)	56.2-67.0)	16.6-25.1)	78.3-85.2)	44.5-57.9)	73.8-81.6)	65.4-69.4)
Successful nests (%)	82.5 ± 2.2	86.8 ± 1.8	64.3 ± 2.3	23.0 ± 2.1	84.2 ± 1.4	55.1 ± 2.8	75.7 ± 1.7	69.1 ± 0.8
(Apparent nesting success)	(n = 292)	(n = 348)	(n = 423)	(n = 383)	(n = 639)	(n = 325)	(n = 675)	(n = 3085)
Abandoned nests (%)	0.7 ± 0.5	0.3 ± 0.3	0.7 ± 0.4	3.4 ± 0.9	0.3 ± 0.2	1.8 ± 0.7	1.3 ± 0.4	1.2 ± 0.2
	(n = 292)	(n = 348)	(n = 423)	(n = 383)	(n = 639)	(n = 325)	(n = 675)	(n = 3085)
Destroyed nests (%)	15.4 ± 2.1	9.8 ± 1.6	34.5 ± 2.3	73.4 ± 2.3	15.5 ± 1.4	43.1 ± 2.7	23.0 ± 1.6	29.2 ± 0.8
	(n = 292)	(n = 348)	(n = 423)	(n = 383)	(n = 639)	(n = 325)	(n = 675)	(n = 3085)
Other $(\%)^3$	1.4 ± 0.7	3.2 ± 0.9	0.5 ± 0.3	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.1
	(n = 292)	(n = 348)	(n = 423)	(n = 383)	(n = 639)	(n = 325)	(n = 675)	(n = 3085)

TABLE 3. Means (\pm SE) of reproductive parameters of Canada Geese nesting at the primary study area in northern Québec, 1997–2003. Sample sizes are shown in parentheses.

¹ Mean brood size of all broods observed on study area, from hatching up to banding (approximately 4-6 weeks of age).

² Sample size and 95% confidence intervals in parentheses.

³ From 1997 to 2003, other causes were observer destroyed (n = 4 nests), infertility (n = 10 nests), and unknown (n = 4 nests).

Nesting Success and Productivity

The fate was determined for 99.9% (3081 of 3085 nests) of all nests found in the primary study area, 99.5% (1740 of 1749 nests) at Hudson Bay secondary sites, and 95.5% (1016 of 1064 nests) at Ungava Bay secondary sites. Pooling years, apparent nesting success (the proportion of nests initiated that hatched at least one gosling) was 69.1% for the primary study area, 77.2% (± 1.0, n = 1749 nests, 95% CI = 75.2 - 79.2) for Hudson Bay, and 47.8% (± 1.5 , n = 1064 nests, 95% CI = 44.8-50.8) for Ungava Bay (Table 3). There was no site effect at either Hudson Bay (F = 1.35, df = 6, p = 0.25) or Ungava Bay (F = 1.13, df = 9, p = 0.39), and at Ungava Bay there was no year effect either (F = 2.07, df = 9, p = 0.08). However, there was a year effect at Hudson Bay (F = 5.81, df = 9, p < 0.01) and a significant interaction effect at both Hudson Bay (F = 2.42, df = 52, p < 0.01) and Ungava Bay (F = 3.90, df = 20, p < 0.01). Apparent nesting success was positively correlated with the mean temperature during 4-24 May for Ungava Bay (r = 0.88, n = 10) years), but not for either the primary study area or secondary sites along Hudson Bay (primary study area: r = 0.62,

n = 7 years; secondary sites: r = 0.46, n = 10 years). The mean Mayfield nesting success for the primary study area for all years pooled was 67%, and annual means ranged from a low of 20% in 2000 to a high of 89% in 1998 (Table 3). The proportion of nests abandoned never exceeded 4% in any one year at any of the areas (primary and secondary), except at Ungava Bay in 2000, when 24% (19 of 80 nests) were abandoned. The likely cause was a late-season snowfall in mid-June.

Gosling survival (at approximately four weeks of age) at the primary study area on the Polemond River was relatively stable from year to year, ranging from 57% to 63% in five of the seven years (Table 4). In the other two years, it was much lower: 42% in 2000 and 48% in 2001. In 2000, the primary study area not only had a late spring snowmelt, but also received the most July precipitation (total rainfall recorded at the camp) of any year, 80.9 mm. In contrast, 2001 had the lowest July rainfall, only 18.7 mm. The 2000 nesting season, in addition to having the lowest gosling survival of any year, also had the lowest nesting success and the lowest mean number of goslings leaving the nest (Table 3). The number of goslings produced per km²,

Parameter	1997	1998	1999	2000	2001	2002	2003
Broods marked ¹	211	278	237	75	472	166	455
Broods recaptured ²	89	124	93	10	159	45	142
% broods recaptured	42.2	44.6	39.2	13.3	33.7	27.1	31.2
Goslings marked	842	1166	804	225	1799	465	1558
Goslings recaptured	215	295	210	16	284	81	277
% gosling survival ³	58.9	57.1	63.4	41.7	47.5	58.4	57.0
	(± 3.2)	(± 2.5)	(± 2.9)	(± 8.6)	(± 2.1)	(± 4.3)	(± 2.4)
Productivity index (goslings/km ²)	17.9	23.1	17.3	3.04	28.5	8.0	32.0

TABLE 4. Gosling survival and productivity index of Canada Geese nesting at the primary study area in northern Québec, 1997–2003.

¹ Number of broods in which one or more goslings were marked with a tag.

² Number of broods from which one or more marked goslings were recaptured at banding.

³ Standard error in parentheses and sample size is the number of marked broods recaptured.

⁴ The percentage of marked broods recaptured at banding was much lower than average, suggesting that the rate of total brood loss may have been high.

or productivity index (PI), ranged from a low of only 3.0 goslings/km² in 2000 to a high of 32.0 in 2003 (Table 4) and was not significantly correlated with the annual mean temperature of 4-24 May (r = 0.69, n = 7 years), clutch initiation date (r = -0.59, n = 7 years), or clutch size (r = 0.56, n = 7 years).

The mean size of broods observed on the primary study area (years pooled) declined over the summer periods: 3.58 goslings at hatch to one week old, 3.54 goslings at two weeks, 3.44 goslings at four weeks, and 3.00 goslings at six weeks. The distance moved by goslings from the time they were web-tagged at hatch to the time they were captured at four to six weeks of age during banding drives varied from as little as 56 m to 61 km, with an overall average across years of 7237 m (Table 3). The median distance, pooling years, was 4.0 km, and for single years it ranged from 1.4 to 7.3 km.

Nest Predation and Small Mammal Abundance

The percentage of nests destroyed each year by predators ranged from 10% to 73% at the primary study area (Table 3), 10% to 48% at the Hudson Bay secondary sites, and 16% to 88% at the Ungava Bay secondary sites. Across vears and sites, the mean rate was 29.2% at the primary study area (Table 3), 22.1% (\pm 1.0, n = 1749 nests) at Hudson Bay secondary sites, and 45.8% (± 1.5, n = 1064 nests) at Ungava Bay secondary sites. At the primary study area, there was no correlation between the annual rate of nest predation (%) and either the annual mean clutch initiation date (r = 0.51, n = 7 years) or annual nest density (r = -0.22, n = 7 years). Nevertheless, the two years with latest clutch initiation, 2000 and 2002, experienced the highest predation rates—pooling these two years, the average was 59.4% (\pm 1.8, n = 708 nests) compared with only 20.2% (\pm 0.8, n = 2377 nests) for the other years (pooled).

The number of small mammals captured annually, per 100 trap-nights, was less than 1.0 from 1998 to 2001 (1998: 8 per 938 trap-nights; 1999: 5 per 951 trap-nights; 2000: 5 per 1043 trap-nights; 2001: 5 per 1046 trap-nights),

and then it tripled in the next two years (2002: 32 per 1013 trap-nights; 2003: 30 per 1030 trap-nights). Of the small mammals caught, 92% were Ungava lemmings, and the remainder were either Gapper's red-backed voles (*Clethrionomys gapperi*) or meadow voles (*Microtus pennsylvanicus*). There was no correlation between the number of small mammals captured per 100 trap-nights and the annual mean Mayfield nesting success (r = 0.06, n = 6 years), annual mean brood size (r = -0.58, n = 6 years), or annual productivity index (r = 0.07, n = 6 years).

DISCUSSION

After experiencing a sharp decline in the size of the breeding population in the late 1980s and early 1990s, from an estimated 118000 pairs in 1988 (Malecki and Trost, 1990) to 33 995 pairs in 1995 (Harvey and Rodrigue, 2102), Atlantic Population Canada Geese rebounded strongly over the next six years. This rebound was due to two main factors: 1) the measures implemented by the Atlantic Flyway Council in 1995, notably the closure of sport hunting seasons in most Atlantic Flyway states and provinces between 1995 and 1999 (Atlantic Flyway Council, 2008), and 2) three consecutive breeding seasons of good productivity that occurred while sport hunting seasons were closed (in 1997-99). From the historic low in 1995 to 2001, the size of the breeding population more than quadrupled to 135 196 pairs (Harvey and Rodrigue, 2012). This increase was matched by a strong increase in nest density, as illustrated by an increase of 179% on the Hudson Bay secondary sites between 1996 and 2001. During that period, only 2000 was a poor production year, primarily as a result of low nest success and lower than average clutch size.

The number of breeding pairs began to stabilize after 2001, as the sport harvest had resumed in Atlantic Flyway states and provinces. Interestingly, even though the number of breeding pairs did not change significantly from 2001 to 2005, annual production varied substantially; the productivity index in our primary study area was 28.5 goslings/

km² in 2001, 8.0 in 2002, and 32.0 in 2003. This variation was due to large annual changes in nest density, suggesting that once the population had recovered sufficiently, the main determinant of annual productivity was the propensity of breeding pairs to nest. The highest nest densities occurred during the last year of the study (2003 in the primary study area, 2005 on secondary sites), so nesting habitat did not appear to be limited. Thus, propensity to nest may have been influenced more by the conditions of nesting habitats when the birds arrived on the breeding grounds than by the number of breeding pairs present.

In most years, AP Canada Geese arrive on their breeding grounds in northern Québec during the first two weeks of May (P. Novalinga, J. Johannes, and P. May, pers. obs.), a period when open ground appears as the snow melts and nest sites become available. In our study, we found that the mean temperature during this period, specifically from 4 to 24 May, is an important influence on key breeding parameters. There were significant correlations between this temperature and clutch initiation date (negative) and clutch size (positive), and a weak positive correlation (p = 0.08) with productivity index (PI, number goslings per km²). In their study of factors affecting clutch size in Canada Geese nesting on the western shore of Hudson Bay, MacInnes and Dunn (1988) determined that the interval between arrival and clutch initiation was more important than the lateness of the season per se, as the geese during that interval had to use some of their accumulated energy reserves for maintenance-reserves that otherwise could have been used for egg production.

As has been documented in other populations of Arctic-nesting geese (Mickelson, 1975; Leafloor et al., 2000; Lepage et al., 2000; Ely et al., 2008), in any given year AP Canada Geese were relatively synchronized in nest initiation, with 80% of clutches on the primary study site initiated during a 5- to 9-day period. In most years, the timing of nest initiation of these tundra-nesting AP geese is similar to that of taiga-nesting AP geese, for which Hughes et al. (2000) obtained annual means (1993–96) that ranged from 18 to 25 May on their study area near the Laforge Reservoir (650 km southeast of our primary study area).

Some studies of Arctic nesting geese have shown that nesting success and productivity are directly related to small mammal abundance. In years of low small mammal abundance, predators, especially generalist predators such as Arctic fox (Vulpes lagopus) and Herring Gull (Larus argentatus) (Pierotti and Good, 1994; Angerbjörn et al., 1999; Bêty et al., 2001), both of which are common along both Hudson and Ungava Bays (P. Novalinga, J. Johannes, and P. May, pers. obs.), will switch from small mammals to goose eggs and nests (Bêty et al., 2001). Across the Canadian Arctic, small mammal populations fluctuate in a threeto four-year cycle (Krebs et al., 2002). However, this cycle was not observed on our primary study area along eastern Hudson Bay: for four consecutive years, the population was very low, and then it increased to a level more than four times as high for each of the next two years. We did not

observe any correlation between small mammal abundance and either nesting success or the productivity index.

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