ARCTIC
VOL. 54, NO. 4 (DECEMBER 2001) P. 357–366

Breeding Biology of Brant on Banks Island, Northwest Territories, Canada

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(*Received 3 April 2000; accepted in revised form 30 November 2000*)

ABSTRACT. The numbers of brant (*Branta bernicla*) in the Pacific Flyway are relatively small compared to other populations of arctic geese and have declined from historic levels. Little information is available on brant from Banks Island, although the size of the island and its location in the western Canadian Arctic make it a potentially important nesting area for this species. In 1992–93, we documented the distribution of nesting brant on the southern half of Banks Island through aerial surveys and carried out ground studies at the colonies to document nesting chronology and reproductive parameters. Ten colonies were found in 1992 (n = 159 nests) and 42 colonies (including seven colonies that had been active in 1992) and five solitary nests were found in 1993 (n = 514 nests). Two-thirds (67%) of the nesting locations supported 10 or fewer nests. Most colonies (36 of 45) were located on small islands (mean = 248 m^2) in inland lakes or large ponds, and the remaining colonies (n = 9) were located on the mainland near active snowy owl (*Nyctea scandiaca*) nests. In 1993, when June temperatures were milder and snow melted sooner than in 1992, mean date of clutch initiation was significantly earlier (12 June vs. 20 June in 1992; $p < 0.001$) and mean clutch size was significantly larger (3.8 vs. 3.5 in 1992; $p = 0.02$). An index of productivity for the 21 414 km^2 area surveyed in both years was much higher in 1993 (1339 young) than in the very late spring of 1992 (347 young). The number of adult brant on the survey area was similar in both years, and the lower productivity in 1992 was due primarily to fewer pairs' nesting that year. Smaller clutch size and lower nesting success may also have lowered productivity in 1992, but their effects appeared to be secondary. No correlation was found between colony size and clutch size, mean number of goslings hatched, or the percentage of nests that proved successful.

Key words: brant, *Branta bernicla*, breeding biology, nesting success, productivity, Banks Island, Northwest Territories

RÉSUMÉ. Le nombre de bernaches cravants (*Branta bernicla*) dans la voie migratoire du Pacifique est relativement faible quand on le compare aux autres populations d'oies de l'Arctique, et il a diminué par rapport à ses niveaux historiques. On a peu de renseignements sur la bernache de l'île Banks, même si la taille de l'île et son emplacement dans l'Arctique canadien occidental pourraient en faire une aire de nidification importante pour cette espèce. En 1992 et 1993, on a consigné au moyen de relevés aériens la distribution des bernaches qui nichaient dans la moitié sud de l'île Banks, et on a effectué des études sur le terrain, là où se trouvaient les colonies, afin de consigner la chronologie de nidification et les paramètres de reproduction. En 1992, on a trouvé 10 colonies (n = 159 nids) et, en 1993, 42 colonies (y compris sept qui avaient été actives en 1992), ainsi que cinq nids solitaires (n = 514 nids). Deux tiers (67 p. cent) des sites de nidification accueillaient 10 nids ou moins. La plupart des colonies (36 sur 45) se trouvaient sur des îlots (moyenne = 248 m^2) situés dans des lacs ou de grands étangs de l'île, tandis que le reste (n = 9) étaient situées sur la terre ferme près de nids actifs de harfangs des neiges (*Nyctea scandiaca*). En 1993, avec des températures en juin plus douces et une fonte nivale plus rapide qu'en 1992, la date moyenne du début de la couvée a été nettement plus hâtive (le 12 juin par rapport au 20 juin en 1992; p < 0,001) et la taille moyenne de la couvée a été nettement plus grande (3,8 par rapport à 3,5 en 1992; p = 0,02). Un index de productivité pour les 21 414 km^2 de la zone de relevés des deux années était beaucoup plus élevé en 1993 (1339 petits) qu'au cours du printemps très tardif de 1992 (347 petits). Le nombre de bernaches cravants adultes dans la zone des relevés était semblable dans les deux années, et la productivité plus faible en 1992 était surtout due à un nombre moindre de paires ayant fait un nid cette année-là. La taille plus petite de la couvée et le taux de réussite plus faible quant à l'établissement du nid pourraient aussi expliquer la baisse de productivité de 1992, mais ces effets paraissent secondaires. On n'a trouvé aucune corrélation entre la taille de la colonie et la taille de la couvée, le nombre moyen d'oisons éclos, ou le pourcentage de nids où la reproduction a réussi.

Mots clés: bernache bravant, *Branta bernicla*, biologie de la reproduction, réussite d'établissement du nid, productivité, île Banks, Territoires du Nord-Ouest

Traduit pour la revue *Arctic* par Nésida Loyer.

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INTRODUCTION

The breeding distribution of the Pacific Flyway population of brant (*Branta bernicla*) extends from northeastern Russia, through Alaska, to the western Canadian Arctic. Most of the population is composed of the subspecies *B. b. nigricans* (black brant) and nests in mid to low Arctic areas, including Banks Island (Reed et al., 1998). Much of the population nests in large colonies (> 1000 pairs) on the Yukon-Kuskokwim Delta, Alaska (Subcommittee on Pacific Brant, 1992; Sedinger et al., 1993), where several studies have documented the breeding biology of the species (Shepherd, 1964; Mickelson, 1975; Eisenhauer, 1977; Raveling, 1989; Anthony et al., 1991; Flint, 1993). Elsewhere, however, black brant nest in small colonies (< 100 pairs) or as widely dispersed pairs (Uspenski, 1960; Portenko, 1981; Eldridge et al., 1991; Ward et al., 1993; Stickney and Ritchie, 1996). The delineation of breeding populations in Russia and Canada has been identified as critical to enlightened management of the Pacific Flyway brant population (Sedinger et al., 1993). Similarly, it is important to have information on the breeding biology and productivity of these populations. Because of its large size and its location in the western part of the Canadian Arctic Archipelago, Banks Island is a potentially important nesting area for brant, although few data concerning this species have been collected there. The objective of this study was to document the breeding biology of black brant on Banks Island. Specifically, we investigated nesting chronology, colony size, nesting associations between brant and other species, clutch size, nesting success, causes of nest failure, and overall population productivity.

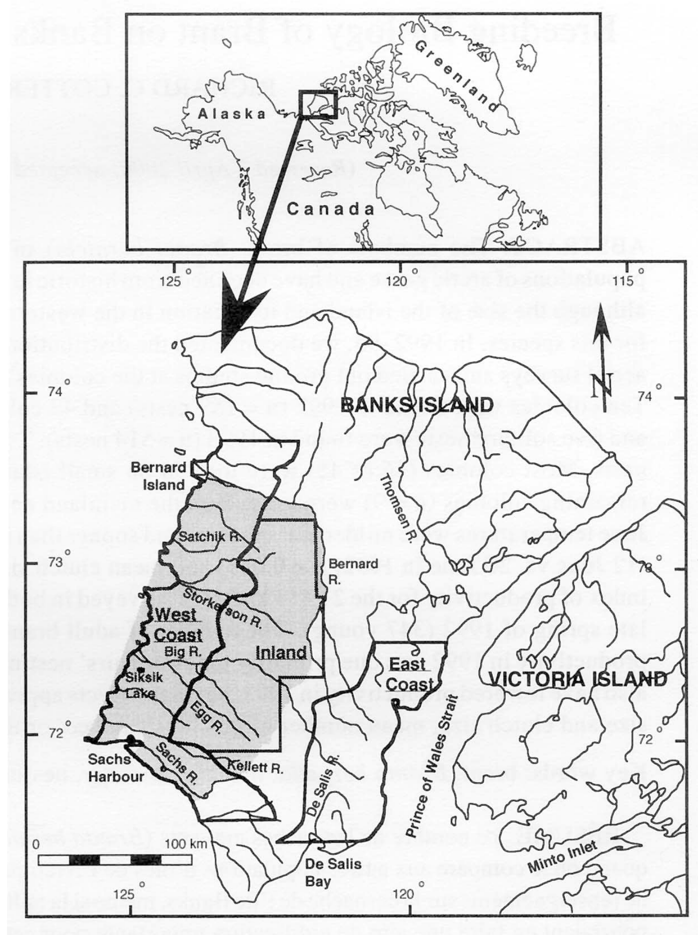

FIG. 1. The location of Banks Island, Banks Island Bird Sanctuary No. 1 (shaded), and the strata (West Coast, Inland, and East Coast) surveyed by helicopter for brant in 1992–93.

STUDY AREA

Banks Island (60 165 km^2) is situated in the southwestern corner of the Canadian Arctic Archipelago (Fig. 1). The climate is dry and cold: from 1955 to 1990 at the coastal community of Sachs Harbour, annual precipitation averaged 127 mm and the mean daily temperatures were -30˚C for January and 6˚C for July (Atmospheric Environment Service, 1993).

Banks Island has three distinct topographic regions: Northern Uplands, Central Lowlands, and Southern Uplands (Vincent, 1982). The Central Lowlands, which cover the western and central parts of the island, were studied in 1992 and 1993. A low plain that rises gradually from sea level along the west coast to 250 m above sea level (asl) in the interior, with rolling hills and shallow valleys, characterizes the topography of this region. Surficial deposits are weakly consolidated sandstone and shale overlain with gravel and sand, glacial deposits, and post-glacial silt, peat, and alluvium (Fyles, 1962). The Central Lowlands are drained by several westward-flowing rivers (most notably the Kellett, Big, Storkerson, and Bernard), which empty into the Beaufort Sea. These rivers become highly braided and broaden into deltas as they approach the coast. On the coastal plains, elevation rarely exceeds 100 m asl, drainage is poor, and tundra ponds and polygons are numerous and widely distributed. Rolling hills characterize the interior of the Central Lowlands. The hills are well drained and dry, and have predominantly barren hilltops (Porsild, 1955). The area studied in southeastern Banks Island in 1993 included two geological regions: the Central Lowlands (described above) and the Southern Uplands. The latter region extends northward in a 50 km wide strip along the east coast of the island to Jesse Harbour and is dominated by a plateau of rolling hills up to 350 m asl in elevation (Fyles, 1962; Vincent, 1982). Here the hills are well drained and dry, and wetland development is poor.

Meadows dominated by grasses and sedges are the dominant vegetation type in low, poorly drained areas in valley bottoms and near the edges of ponds and lakes. Mesic slopes tend to support dwarf shrub-graminoid or hummocky tundra, and dry sites are sparsely vegetated by dwarf shrubs, herbaceous plants, and lichens (Porsild, 1955; Ferguson, 1991).

On the basis of topography (Fyles, 1962; Vincent, 1982), the relative availability of potential lowland breeding habitat, and the known distribution of brant on Banks Island (Manning et al., 1956; Barry, 1960), we divided the study area into three strata: West Coast (coastal plains of the Central Lowlands), Inland (interior part of the Central Lowlands), and East Coast (Southern Uplands along the east coast). The West Coast and Inland strata corresponded closely to the Banks Island Bird Sanctuary No. 1 (Fig. 1) and together encompassed an area of 21 414 km^2. The East Coast stratum was 7000 km^2 in area (Fig. 1). The Northern Uplands and the extreme southern part of Banks Island were excluded from this study because those areas contain little lowland habitat (Fyles, 1962; Vincent, 1982) and earlier surveys had reported relatively few nesting brant there (Manning et al., 1956; Barry, 1960).

METHODS

In 1992 and 1993, as part of a population study of brant on Banks Island (Cotter and Hines, 2000), brant nests were found during aerial surveys (Bell 206B helicopter on floats) and reconnaissance flights that involved more than 140 hours of flying and 3300 km of transects each year. In both years, the transects surveyed in the West Coast and Inland strata were identical, and the methodology, timing (16–28 June in 1992; 11–27 June in 1993), search effort, and time employed in the overflights of this area were similar (Cotter and Hines, 2000). In 1993, each of the colony sites found in 1992 was revisited, and those that remained active were included in the sample. The East Coast stratum, added to the study area in 1993, was surveyed in a similar manner, though slightly later—from 29 June to 1 July. (This stratum was not surveyed in 1992 because of logistical and fiscal constraints.)

Colonies located in the overflights were later searched thoroughly from the ground, and a numbered marker was placed next to each nest found. Most nests were first visited after the first week of incubation. In 1992, all nests were revisited 1–2 times; in 1993, however, only 39% (198 of 514 nests) were revisited because of time and fiscal constraints. At each visit, we recorded clutch size and status (i.e., incubating, abandoned, predator-destroyed).

The final visit to each colony was made at or after hatching to record the fate of each nest. Although fate was determined for only a subsample of nests in 1993, we believe that the sample is representative of all nests and that the resulting data were not greatly biased by the attainable resampling efforts. Possible nest fates included successful (at least one egg hatched), abandoned (clutch still intact but eggs cold), or predator-destroyed (complete absence of eggs or presence of broken egg shells without separated membranes). On Banks Island, the most probable egg predators included arctic foxes (*Alopex lagopus*), glaucous gulls (*Larus hyperboreus*), and parasitic jaegers (*Stercorarius parasiticus*) (see Reed et al., 1998).

For each brant nest, the distance to the nearest neighbouring nest was recorded. Each mainland brant colony that we found was centred on an active snowy owl (*Nyctea scandiaca*) nest. Therefore, for these colonies, we also recorded the distance from each brant nest to the snowy owl nest. The length and width of each island with one or more brant nests was measured through the approximate centroid of the island. The area of an island was calculated as the product of its length and width. All distances were recorded with a tape measure.

Colonies were classified according to the presence of other species of birds nesting within the colony: glaucous gull, Sabine's gull (*Xema sabini*), both glaucous and Sabine's gulls, snowy owl, and brant only. A few solitary brant nests were found as well.

The date of initiation of each clutch was estimated by backdating 25 days from the hatch date. This calculation was based on the assumptions that the incubation period was 24 days and that incubation commenced with the laying of the second egg (Flint et al., 1994; Reed et al., 1998). Hatch date was recorded as the current day if goslings were present in the nest, or the following day if pipped eggs were present. If the eggs had already hatched, the median date between the current and the previous visit (interval 4–14 days) was recorded as the hatch date. (Estimates of hatch date become imprecise if visits to colonies are too widely spaced; therefore, hatch dates were not estimated when the interval between nest visits was more than 2 weeks.)

Means and standard errors were calculated for clutch size, number of eggs hatched per nest of known fate, nesting success (percentage of nests in which at least one gosling hatched), percentage of nests depredated, and percentage of nests abandoned. The standard errors (SE) for the last three parameters were based on the binomial distribution. Only nests of seven or fewer eggs were included in some analyses of clutch size because larger clutches may have resulted from nest parasitism (Lindberg et al., 1997:383). Annual differences in clutch initiation dates, clutch sizes, and number of young hatched per nest were evaluated using t-tests (PROC TTEST, SAS Institute, 1990) or Wilcoxon 2-sample tests (PROC NPAR1WAY, SAS Institute, 1990). Annual differences in nesting success and nest losses to predation and abandonment were evaluated using 2 × 2 contingency tables. Contingency table analyses of these and other binomially distributed variables used a G-test of independence with Williams Correction (Sokal and Rohlf, 1981:704).

For the West Coast and Inland strata, which were searched at a similar level of intensity each year, an annual index of population productivity (P) was calculated for 1992 and 1993 as follows:

$$P = N \times S \times H$$

where N is the total number of nests found during our searches, S is nesting success (expressed as a proportion), and H is the mean number of young hatched from all successful nests (both parasitized and non-parasitized).

To determine whether clutch size and nesting success were correlated with colony size, we calculated Pearson correlation coefficients (Sokal and Rohlf, 1981:565). The significance level was $\alpha < 0.05$ for all statistical tests.

RESULTS

Brant Colonies

Ten brant colonies (n = 159 nests) were found in 1992, and 42 colonies (n = 509 nests) were found in 1993 (Table 1). In addition, five solitary nesting brant pairs were found in 1993. Seven of the 10 colonies found in 1992 were active in 1993. In 1993, the number of colonies found in the West Coast and Inland strata (i.e., the same area surveyed in 1992) was 38. Colony size ranged from 2 to 62 brant nests, with a median of 7 and mean of 12.8 (± 1.8 [SE], n = 52) nests, and did not differ significantly between years (t = 0.81, df = 50, $p = 0.42$). Two-thirds of all nesting locations supported 10 or fewer nests; the percentage was similar in 1992 (60.0%) and 1993 (68.1%).

Brant colonies and the different colony types (including solitary nests) were distributed throughout the study area (Fig. 2). Nevertheless, most colonies (8 of 10 in 1992, 31 of 42 in 1993) were located in the West Coast stratum, the largest of the three strata. In this stratum and over the study area as a whole, the largest concentration of colonies was situated in the Big River Valley (Fig. 2). The majority (80%) of colonies and solitary nests were located on islands in large ponds or inland lakes. The remaining colonies were located on the mainland and centred on active snowy owl nests. Most island colonies (33 of 36) had one or more pairs of glaucous or Sabine's gulls (or both) nesting on the islands. The most common colony type was brant-glaucous gull, which comprised 70% (7/10) of all brant colonies in 1992 and 60% (25/42) in 1993 (Table 1). In 1993, five additional colonies supported both nesting glaucous and Sabine's gulls (Table 1). In 1992, most (71%, 5/7) brant-glaucous gull colonies had two or more glaucous gull nests (range 1 – 16; mean = 5.0). In 1993, however, 60% (18/30) of the colonies with glaucous gulls had only one glaucous gull nest (range 1 – 21; mean = 3.4). Few colonies (one in 1992 and three in 1993) had 10 or more glaucous gull nests. Two of the five solitary brant nests were located on islands with active glaucous gull nest(s). Brant-snowy owl colonies were the second most common colony type, followed by brant only colonies (Table 1). The single brant-snowy owl colony site found in 1992 was not used by either snowy owls or brant in 1993. One brant colony, active in both years, occurred in association with Sabine's gulls only (Table 1).

Of the 36 colonies on islands, 22 were each situated on a single island, and the remaining 14, on two or more islands. Among colonies with nests on more than one island, most brant nested on one island, with the remaining pair(s) usually nesting alone (rarely ≥ 2 pairs) on a smaller nearby island. Islands with two or more nests were considerably larger than islands with only one nest: 511 m^2 (± 116, n = 18) versus 96 m^2 (± 20, n = 29), respectively. Combined data from 1992 and 1993 indicated that islands with nesting brant ranged in size from 1 m^2 to 1662 m^2, with a mean area of 248 m^2 (± 52, n = 49).

Because of small sample sizes, we pooled 1992 and 1993 data on distances between neighbouring brant nests. In island colonies, the mean distance was 5.5 m (± 0.4, n = 260), whereas in brant-snowy owl colonies, it was considerably greater (23.8 m ± 3.5, n = 38). All brant-snowy owl colonies were located at least 500 m from the nearest body of water. The distance from brant nests to snowy owl nests ranged from 5.3 m to 225 m, with a mean of 84.0 m (± 10.3, n = 37).

Date of Clutch Initiation and Size

Snow cover on Banks Island was reduced to trace amounts on approximately 18 June in 1992 and 5 June in 1993 (Cotter, unpubl. data; Atmospheric Environment Service, 1993). Brant commenced laying shortly after most snow had melted in both years. Mean date of clutch initiation was 20 June (± 0.1 day, n = 96; range 19–25 June) in 1992 and 12 June (± 0.2 day, n = 52; range 5–15 June) in 1993. This difference was statistically significant (t = 26.97, df = 146, $p < 0.001$).

Clutch size ranged from 1 to 17 eggs in 1992 and 1 to 10 eggs in 1993. Excluding nests with more than seven eggs (i.e., parasitized nests), mean clutch size was significantly larger in 1993 (mean = 3.8 ± 0.1, n = 397) than in 1992 (mean = 3.5 ± 0.1, n = 148) (t = 2.40, df = 543, $p = 0.02$) (Table 2). Similarly, mean size of successful clutches was larger in 1993 (mean = 4.1 ± 0.1, n = 92; range 1 – 7) than in 1992 (mean = 3.6 ± 0.1, n = 96; range 1 – 7) (t = 2.54, df = 186, $p = 0.01$). In 1992, only two nests contained more than seven eggs (one contained 8, and the other, obviously a dump nest, had 17). In 1993, there were five nests with 8 eggs, three with 9 eggs, and one with 10 eggs. In both years, and for both total nests and non-parasitized nests, the mean clutch sizes for successful nests appeared to be greater (by 0.2 – 0.5 egg) than for unsuccessful nests; however, the differences were not statistically significant ($p = 0.10 – 0.40$). Sample size for solitary nesting brant was small and despite the one-egg difference in averages, mean clutch size of solitary, non-parasitized nests (mean = 2.8 ± 0.8, n = 4; range 1 – 4) was not different from the mean clutch size of colonial nests (1993 only: mean = 3.8 ± 0.1, n = 393; range 1–7) (Wilcoxon 2-sample test, Z = 1.44, df = 1, $p = 0.15$).

Nesting Success, Number of Eggs Hatching, and Productivity

Fate was determined for 91% (145 of 159) of the nests studied in 1992. Of these 145 nests, 66.2% were successful, 17.2% were predator-destroyed, and 16.6% were

TABLE 1. The number and percentage of brant colonies of different types found during aerial surveys on Banks Island, Northwest Territories, in 1992–93, and the number and percentage of brant nests found in colonies of each type.

	1992				1993			
	Colonies		Nests		Colonies		Nests	
Colony Type	n	%	n	%	n	%	n	%
Brant–glaucous gull	7	70.0	89	55.9	25	59.5	272	52.9
Brant–Sabine's gull	1	10.0	44	27.7	1	2.4	47	9.1
Brant–snowy owl	1	10.0	23	14.5	8	19.1	79	15.4
Brant only	1	10.0	3	1.9	3	7.1	73	14.2
Brant–glaucous gull–Sabine's gull	0	0.0	0	0.0	5	11.9	38	7.4
Subtotal	10		159		42		509	
Solitary nest	na		0	0.0	na		5	1.0
Total	10	100.0	159	100.0	42	100.0	514	100.0

abandoned (Table 2). In 1993, within the same area surveyed in 1992, the fate of 38% (155 of 412) of all nests found was determined: 77.4% were successful, 19.4% were predator-destroyed, and 3.2% were abandoned. The fate was determined for only one of the five solitary nests found in 1993. It hatched successfully. Nesting success was significantly greater (G = 4.65, df = 1, $p = 0.03$), loss due to predation was similar (G = 0.22, df = 1, $p = 0.64$), and the proportion of abandoned nests was lower (G = 16.04, df = 1, $p < 0.01$) in 1993 than in 1992.

Hatching was highly synchronous in both 1992 and 1993. All nests hatched within a seven-day period (14–20 July) in 1992, with 91% (n = 96) hatching on 14–16 July. In 1993, all nests hatched within 11 days (30 June–10 July), with most (88%, n = 52) hatching on 5–10 July. The difference between mean dates of hatch (mean = 15 July ± 0.1 day in 1992, mean = 7 July ± 0.3 day in 1993) was significant (t = 26.97, df = 146, $p < 0.001$).

The number of eggs hatched per nest ranged from 0 to 9, with a significantly larger mean in 1993 than in 1992 (Z = 3.66, df = 1, $p < 0.001$) (Table 2). The mean number of eggs hatched per successful nest was 3.3 (± 0.1, n = 96; range 1–7) in 1992 and 4.2 (± 0.2, n = 95; range 1–9) in 1993, and differed significantly between years (t = 4.22, df = 189, $p < 0.001$).

In 1992, the productivity index was estimated as 347 young for all nests found (n = 159) in the 10 colonies. Over the same geographical area in 1993, the productivity index was estimated at 1339 young from 412 nests in 38 colonies and an additional five solitary nests.

Because of the small sample size from 1992, data were pooled for both years to test for an effect of colony size on nesting success. No correlation was found between these two variables (r = -0.15, n = 40, $p = 0.35$). Eliminating potentially parasitized nests (clutches with more than 7 eggs), neither mean clutch size (r = 0.11, n = 55, $p = 0.42$) nor mean number of goslings hatching per nest (r = -0.11, n = 34, $p = 0.55$) was correlated with colony size. This was also true when parasitized nests were pooled with non-parasitized nests (for colony size and clutch size, $p = 0.40$; for colony size and number hatching, $p = 0.92$).

In 1993, nesting success (G = 0.002, df = 1, $p = 0.96$), nest losses due to predation (G = 0.01, df = 1, $p = 0.92$), and the proportion of nests abandoned (G = 0.10, df = 1, $p = 0.75$) were similar in brant-snowy owl colonies and brant-glaucous gull colonies (Table 2). Sample sizes were not large enough for other comparisons.

DISCUSSION

Colony Size, Distribution, and Type

Pacific Flyway brant colonies, outside of those in the Yukon-Kuskokwim Delta, Alaska, where nests number in the thousands, and at the Anderson River and Smoke-Moose River deltas, Northwest Territories, usually consist of fewer than 100 nests (Sedinger et al., 1993; Wiebe and Hines, 2000). The largest colony recorded on Banks Island in 1992–93 was 62 nests, and two-thirds of all nesting locations had 10 or fewer nests. Small colonies also predominate on the Arctic Coastal Plain of Alaska where, from 1989 to 1992, more than 70% of nesting locations supported 5 or fewer nests (Stickney and Ritchie, 1996). Similarly, surveys on the mainland of the western Canadian Arctic, to the south and west of Banks Island, indicate that most brant colonies are relatively small (Wiebe and Hines, 2000).

Although we found only a small number of brant nesting as solitary pairs (5 nests out of 673; < 1%), we suspect that a much higher proportion of the population nested as solitary pairs. During aerial surveys of breeding pairs in 1992 and 1993, the number of pairs recorded as solitary pairs was similar to that of pairs associated with colonies (Cotter and Hines, 2000). In waterfowl surveys of the type we conducted, nests are infrequently sighted from the air, and each single bird sighted is treated as an "indicated breeding pair" (Anonymous, 1987). The underlying assumption is that a nesting female is nearby but not seen by the observers (see also Dzubin, 1969; Wishart, 1983). In 1993, 55% of the solitary pair records (n = 40) were based on the sighting of a single brant, indicating that a significant proportion of the solitary pairs were nesting. In contrast, in the late spring of 1992, only 26% of the pairs recorded (n = 85) occurred as singletons, suggesting that proportionately fewer of the solitary pairs were nesting.

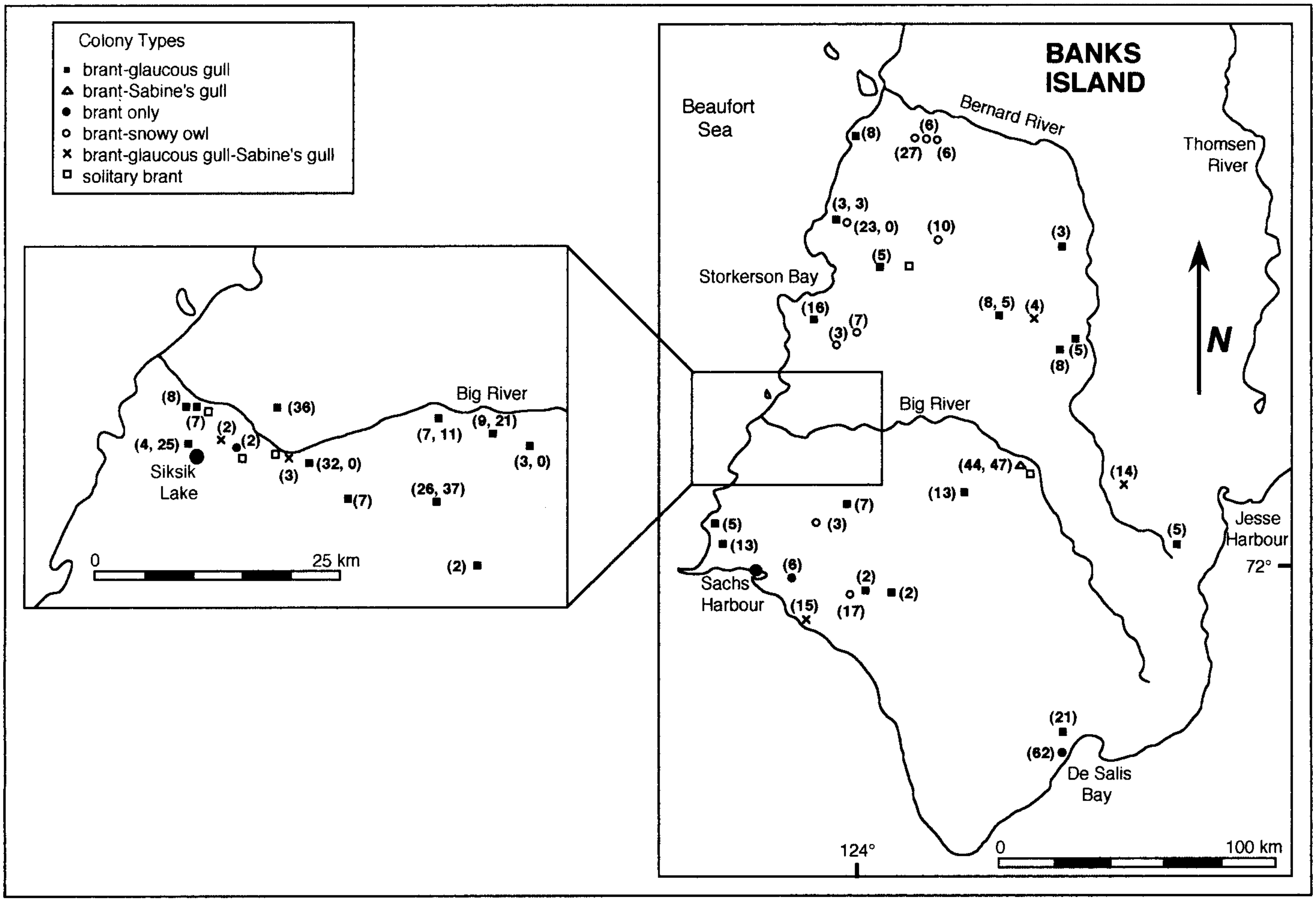

FIG. 2. Locations of five types of brant nesting colonies and solitary nests on Banks Island, Northwest Territories, in 1992–93. The number of nests found at each colony is indicated in parentheses (two numbers indicate colony size for each year of the study).

Colonies were widely distributed throughout the study area. Southern Banks Island is approximately 160 km wide, and several colonies were found in the central part of the island, as far as 80 km from the coast (Fig. 2). Colony locations were apparently determined, at least in part, by the distribution of lakes and ponds containing islands (most numerous in river valleys and coastal areas) and, to a lesser extent, by the presence of active snowy owl nests.

Most (92%) brant colonies and 93% of all the brant nests were located near nesting snowy owls or gulls. Nesting associations between snowy owls and brant, snow geese (*Chen caerulescens*), or king eiders (*Somateria spectabilis*) have been previously documented in northern Canada and Russia (Litvin et al., 1985; Dorogoi, 1990; Summers et al., 1994; Cotter et al., 1997; Tremblay et al., 1997). In Alaska, nesting associations have also been documented between glaucous gulls and common eiders (*S. mollissima*) (Schamel, 1977). The protection against predation by foxes, gulls, or jaegers that a snowy owl provides for its nest and young effectively benefits other species that nest nearby as well (Litvin et al., 1985; Dorogoi, 1990; Summers et al., 1994). Similarly, nest protection is the probable reason that waterfowl frequently nest in larid colonies (Koskimies, 1957; Hildén, 1964; Väänänen, 2000), but such associations have potential costs as well as benefits (Kistchinski and Flint, 1974; Newton and Campbell, 1975; Gerell, 1985; Young and Titman, 1986; Götmark and Ahlund, 1988; Götmark, 1989). Glaucous gulls frequently prey on the eggs and young of brant and other waterfowl (Einarsen, 1965; Barry, 1967; Mickelson, 1975; Armstrong, 1996), but they have also been reported to provide protection from predators for common eider nests (Campbell, 1975; Schamel, 1977).

Presumably, it might be more beneficial for brant to nest in association with one species than with another. However, in the one year of our study with an adequate sample size, 1993, there was no difference in nest success of brant at snowy owl and glaucous gull colony types.

Reproductive Success

Reproductive success of brant on Banks Island was much higher in 1993 than in 1992, and the most obvious difference between the two breeding seasons was the weather. Our data suggest that spring weather may have influenced brant reproductive success and overall population productivity through its impact on the number of pairs that nested, clutch size, and nesting success.

TABLE 2. Reproductive parameters for brant nests at brant–glaucous gull, brant–snowy owl, and all-brant colonies on Banks Island, Northwest Territories, 1992–93.

		1992		1993		Both Years	
Colony Type	Parameter	Mean ± SE	(n[1])	Mean ± SE	(n)	Mean ± SE	(n)
Brant–glaucous gull	Clutch size (all nests)[2]	3.6 ± 0.2	(82)	3.9 ± 0.1	(235)	3.8 ± 0.1	(317)
	Clutch size (non-parasitized)	3.6 ± 0.2	(81)	3.7 ± 0.1	(227)	3.7 ± 0.1	(308)
	Number of eggs hatched (all nests)[3]	1.9 ± 0.2	(79)	3.0 ± 0.2	(99)	2.5 ± 0.2	(178)
	Successful nests (%)	55.7 ± 5.6	(79)	75.5 ± 4.1	(110)	67.2 ± 3.4	(189)
	Depredated nests (%)	21.5 ± 4.6	(79)	21.8 ± 3.9	(110)	21.7 ± 3.0	(189)
	Abandoned nests (%)	22.8 ± 4.7	(79)	2.7 ± 1.6	(110)	11.1 ± 2.3	(189)
Brant–snowy owl	Clutch size (all nests)	3.0 ± 0.3	(21)	4.0 ± 0.2	(67)	3.7 ± 0.2	(88)
	Clutch size (non-parasitized)	3.0 ± 0.3	(21)	4.0 ± 0.2	(67)	3.7 ± 0.2	(88)
	Number of eggs hatched (all nests)[3]	2.8 ± 0.3	(20)	3.1 ± 0.5	(22)	3.0 ± 0.3	(42)
	Successful nests (%)	90.0 ± 6.7	(20)	75.0 ± 8.8	(24)	81.8 ± 5.8	(44)
	Depredated nests (%)	0.0	(20)	20.8 ± 8.3	(24)	11.4 ± 4.8	(44)
	Abandoned nests (%)	10.0 ± 6.7	(20)	4.2 ± 4.1	(24)	6.8 ± 3.8	(44)
All brant colonies	Clutch size (all nests)[2]	3.5 ± 0.1	(149)	3.9 ± 0.1	(406)	3.8 ± 0.1	(555)
	Clutch size (non-parasitized)	3.5 ± 0.1	(148)	3.8 ± 0.1	(397)	3.7 ± 0.1	(545)
	Number of eggs hatched (all nests)[3]	2.2 ± 0.2	(145)	3.1 ± 0.2	(128)	2.6 ± 0.1	(273)
	Successful nests (%)[4]	66.2 ± 3.9	(145)	77.4 ± 3.4	(155)	72.0 ± 2.6	(300)
	Depredated nests (%)[4]	17.2 ± 3.1	(145)	19.4 ± 3.2	(155)	18.3 ± 2.2	(300)
	Abandoned nests (%)[4]	16.6 ± 3.1	(145)	3.2 ± 1.4	(155)	9.7 ± 1.7	(300)

[1] Number of nests.

[2] Excluding an abandoned dump nest with 17 eggs in 1992.

[3] Mean number hatched for non-parasitized nests only (i.e., excluding all nests with clutch sizes > 7): Brant-glaucous gull—1992: 2.1 ± 0.2 (n = 71); 1993: 2.9 ± 0.2 (n = 95); Both years: 2.6 ± 0.2 (n = 166); Brant–snowy owl—1992: 2.8 ± 0.3 (n = 20); 1993: 3.4 ± 0.4 (n = 20); Both years: 3.1 ± 0.3 (n = 40); All brant colonies: 2.3 ± 0.2 (n = 136); 1993: 3.0 ± 0.2 (n = 122); Both years: 2.7 ± 0.1 (n = 258).

[4] East Coast stratum (surveyed only in 1993) excluded.

Number of Nesting Pairs: On that part of Banks Island surveyed in both 1992 and 1993, brant population densities in both years were virtually the same (0.39 brant/km^2; Cotter and Hines, 2000). Despite this similarity, nearly four times as many nesting colonies were found in 1993 (38) as in 1992 (10) and, as discussed above, proportionally more of the dispersed (non-colonial) pairs of brant appeared to nest in 1993 as well. Spring weather is one of the most important environmental factors limiting reproductive success of arctic geese (Newton, 1977; Ganter and Boyd, 2000), and we suspect that the fewer brant nesting in 1992 can be explained by the late snowmelt (almost two weeks later that year).

Numerous examples of the effects of spring weather on the reproduction of brant and other arctic geese have been reported. For example, Barry (1962) found that fewer Atlantic brant (*B. b. hrota*) nested in late springs on Southampton Island (64˚ N), and O'Briain et al. (1998) reported that farther north, on Bathurst and Seymour Islands (ca. 75˚ N) in the Canadian High Arctic, brant did not nest at all in some late springs. Over a 10-year period, O'Briain et al. (1998) found that brant failed to nest in three years and that temperature during the period 1–20 June (peak nest initiation date was 16 June) was significantly lower in years when no nesting occurred. Similarly, during the late spring of 1973 on Wrangel Island, Russia, only 6000 nests were produced by the 87 000 adult lesser snow geese (*C. c. caerulescens*) present (Bousfield and Syroechkovskiy, 1985).

Ganter and Boyd (2000) interviewed a number of researchers who had carried out multiple-year studies of aquatic birds in the Arctic. In so doing, they documented the widespread nature of the unusually late spring of 1992 and its negative effect on reproduction by waterbirds throughout the circumpolar region. Field researchers interviewed by Ganter and Boyd (2000) attributed the low success or total reproductive failure of waterfowl and shorebirds to below-normal spring and summer temperatures and/or high predation pressure. Breeding parameters most affected by weather were initiation of laying (which was delayed) and numbers (or densities) of breeding pairs in the population (which was lower). On Banks Island, both of these effects were observed in 1992; brant nested eight days later than in 1993, and number of nests in the area surveyed in both years was only 39% of what it was the following year.

Clutch Size: Many of the clutches on Banks Island were well into the incubation period when first visited, and it is possible that some loss of eggs to avian predators or arctic foxes had already occurred by that time. During a three-year study on Southampton Island, Barry (1962) found that predators reduced clutch sizes of brant by 0.2 to 0.7 eggs each year. At the Anderson River delta, under conditions of very high predation pressure, Armstrong (1998) reported that avian predators reduced mean clutch size of successful nests by an average of 0.8 eggs over the nesting period. Thus, the clutch sizes we report, like those from other studies, are possibly biased downward by partial predation of clutches.

While within the range of clutch sizes previously recorded for both Atlantic and black brant (Bent, 1923; Palmer, 1976; Cramp and Simmons, 1977; Bellrose, 1980; Reed et al., 1998), the mean clutch size recorded on Banks Island in the delayed spring of 1992 (3.5) was significantly lower than that recorded in 1993 (3.8). Snowmelt was approximately two weeks later and clutch initiation was about a week later in 1992, so our results are consistent with other studies that reported smaller clutch sizes of brant and other arctic-nesting geese in years when nesting is delayed (e.g., Barry, 1962; Newton, 1977; Owen, 1980; Cooke et al., 1995; Ganter and Boyd, 2000; but see also Bousfield and Syroechkovskiy, 1985; Lindberg et al., 1997; and Ganter and Boyd, 2000 for exceptions).

Other factors, such as partial predation of clutches by arctic foxes or avian predators (Barry, 1962; Armstrong, 1998) and age structure of the population (Flint and Sedinger, 1992), could have brought about the annual differences in clutch sizes. However, we have no information on whether these factors varied annually on Banks Island.

Nesting Success: Nesting success of brant was significantly higher in 1993 (77%) than in 1992 (66%). The percentage of the nests destroyed by predators was similar in the two years (19% in 1993 and 17% in 1992), and the higher rate of nesting success in 1993 can be attributed to the low rate of nest abandonment that year (3%, compared to 17% in 1992).

The nesting success observed in our study is similar to that summarized for the Yukon-Kuskokwim Delta by Bellrose (1980) (74%) for the 1960s and 1970s, when population levels were high (Reed et al., 1998). Nesting success on Banks Island was much higher than that reported for the declining Anderson River Delta colony on the mainland of the western Canadian Arctic (ca. 37%; Armstrong, 1998:25) and for the Yukon-Kuskokwim Delta (<10%) during a period of lower populations in the mid-1980s (see Reed et al., 1998). In both 1992 and 1993, the mean number of goslings hatched per successful nest on Banks Island (3.3 and 4.2, respectively) was higher than the 2.9 reported for the Yukon-Kuskokwim Delta by Mickelson (1975) and much higher than the ca. 2.3 reported at Anderson River (Armstrong, 1998).

Overall Productivity: Overall productivity (the estimated number of young hatched for all nests found in the area surveyed in both years) was markedly lower in 1992 (347 young) than in 1993 (1339 young). The 8% smaller clutch size and 14% lower nesting success in 1992 would have accounted for a relatively small part of this difference in productivity. The main cause of lower productivity in 1992 was that far fewer pairs nested that year (159 vs 514 in 1993, 69% lower) and, as summarized by Ganter and Boyd (2000) for other parts of the circumpolar region, this undoubtedly was caused by the almost two-week delay in snowmelt that occurred on Banks Island that year.

ACKNOWLEDGEMENTS

This project was funded jointly through the Inuvialuit Final Agreement and the Canadian Wildlife Service. This study would not have been possible without the cooperation and assistance of the Sachs Harbour Hunters and Trappers Committee. Field assistance was provided by Bradley Carpenter, Greg Green, James Harry, David Kay, Mark Kornder, Jorge Fernandez Layna, Tony Lucas, Trevor Lucas, and Geddes Wolki. The assistance of David Kay was especially instrumental in initiating the study in 1992. We would like to thank Canadian Helicopters and their pilots who ferried us safely throughout Banks Island. We also wish to thank the Polar Continental Shelf Project, Tuktoyaktuk, for their nightly radio communication with our camp and other logistical support. We thank the Royal Canadian Mounted Police for storing our gear in Sachs Harbour over the winter, and the Inuvik Research Center for accommodation and logistical support. We would like to thank Maureen Kay for her assistance with data analysis, and Cindy J. Gratto, Myra Wiebe, and three anonymous reviewers for their comments on the manuscript.

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