ARCTIC
VOL. 51, NO. 4 (DECEMBER 1998) P. 350–360

# Breeding, Moulting, and Site Fidelity of Brant *(Branta bernicla)* on Bathurst and Seymour Islands in the Canadian High Arctic

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(*Received 25 July 1994; accepted in revised form 8 April 1998*)

ABSTRACT. We studied the breeding and moulting ecology of eastern High Arctic brant *Branta bernicla hrota* on Bathurst and Seymour Islands in the central Canadian High Arctic from 1968 to 1989. In most years, brant arrived in Polar Bear Pass, Bathurst Island, during the first few days of June (earliest 28 May 1977), where they fed for several days in small flocks before dispersing to nesting areas. First eggs were usually laid on 13 June and the peak of nest initiation occurred about 16 June. The mean clutch size was 4.5 eggs, and the mean incubation period 23 days. Broods were raised along the shorelines of lakes, ponds, estuaries, and rivers. Goslings were capable of flight by 42–43 days. During the 10 years when the studies were most intensive (1974–77 and 1984–89), there were three years in which brant did not attempt to nest (1974, 1986, 1988); they nested in all other years and were known to produce fledged young in at least four of them. Nesting was not attempted when the mean temperature for the period 1–20 June was below -3˚C. On Bathurst Island in 1987, arctic foxes *(Alopex lagopus)* preyed heavily on brant eggs, and no young were fledged. Nonbreeding adults assembled in small flocks to moult around nearby inland lakes, in river valleys, and at the mouths of estuaries, and concentrated in the latter in cold summers when inland sites had heavier ice cover. The flightless period began about 6 July and lasted 20–22 days. The recapture or resighting of brant marked on Bathurst Island showed that many adults returned in subsequent years to the same breeding territories, and in nonbreeding years they moulted nearby. A smaller proportion of the brant that had been marked as goslings and yearlings also returned to the island. In comparison with most other stocks of North American brant, those we studied bred at high latitude. That choice of breeding site subjected them to periodic breeding failures caused by cold springs and to a reduced availability of plant biomass, but it offered the advantage of reduced spring snow depth and a full 24 h of daylight for feeding during nesting and brood rearing. By using small wetlands which thaw early in close proximity to nesting sites, these brant were able to initiate egg laying relatively early and produce large clutches in most years. The low availability of plant biomass in the High Arctic probably explained the wide dispersal and low densities of these brant during breeding and moulting.

Key words: Bathurst Island, brant, *Branta bernicla hrota*, breeding, brood rearing, moulting, Seymour Island, site fidelity

RÉSUMÉ. De 1968 à 1989, nous avons étudié l'écologie de reproduction et de mue de la bernache cravant à ventre pâle *Branta bernicla hrota* dans les îles Bathurst et Seymour situées dans la partie centrale de l'Extrême-Arctique canadien. En général, les bernaches cravants arrivaient dans la vallée Polar Bear de l'île Bathurst durant les premiers jours de juin (le plus tôt étant le 28 mai 1977); elles s'alimentaient par petits groupes pendant plusieurs jours avant de se disperser vers les sites de nidification. Les premiers oeufs étaient généralement pondus le 13 juin et le pic du début de la ponte se situait vers le 16 juin. La taille moyenne de la couvée était de 4,5 oeufs/nid et la durée moyenne d'incubation était de 23 jours. Les couvées étaient élevées en bordure des lacs, des étangs, des estuaires et des cours d'eau. Les oisons étaient capables de voler à 42 ou 43 jours. Au cours des 10 années d'étude intensive (1974-77 et 1984-89), il y en a eu trois pendant lesquelles les bernaches cravants n'ont pas essayé de nicher (1974, 1986, 1988); par contre, elles ont niché toutes les autres années et ont réussi à élever des oisons jusqu'à l'âge d'envol au moins quatre de ces années. Les bernaches cravants n'ont pas essayé de nicher les années où la température moyenne pour la période allant du 1er au 20 juin était inférieure à -3 °C. En 1987, des renards arctiques *Alopex lagopus* ont prélevé quantité d'oeufs de bernaches cravants dans l'île Bathurst et aucun oison n'a survécu jusqu'à l'âge d'envol. Des adultes non reproducteurs se rassemblaient localement en petits groupes pour muer près des lacs, des rivières et de l'embouchure des estuaires, préférant, durant les étés froids, des estuaires normalement plus dégagés de glace que des sites à l'intérieur des terres. La période de mue débutait autour du 6 juillet et durait de 20 à 22 jours environ. Des bernaches cravants qui avaient été marquées dans l'île Bathurst y ont été observées de nouveau ou y ont été recapturées durant les années subséquentes, prouvant ainsi qu'un grand nombre d'adultes reviennent sur les mêmes aires de reproduction et, pendant les années de non-reproduction, elles muaient à proximité. Une proportion moindre de bernaches cravants marquées au stade juvénile (soit < 2 mois, soit à l'âge d'un an) sont aussi revenues à

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PCSP/EPCP Publication No. 011-98

l'île Bathrust. Comparées à d'autres populations nord-américaines de bernaches, celles que nous avons étudiées se reproduisent à une latitude élevée. En nichant dans l'Extrême-Arctique, cette population était sujette à des échecs périodiques dus à des printemps froids ainsi qu'à une disponibilité réduite de biomasse végétale. Elle bénéficiait par contre d'une faible accumulation de neige au printemps et de 24 heures quotidiennes de clarté pour se nourrir pendant la nidification et l'élevage des oisons. En exploitant de petites superficies de terres humides qui dégèlent tôt, à proximité des sites de nidification, ces bernaches cravants pouvaient, la plupart des années, pondre relativement tôt en saison et produire des couvées de bonne taille. La disponibilité réduite de biomasse végétale dans l'Extrême-Arctique expliquait probablement la dispersion étendue et les faibles densités de ces bernaches cravants en période de reproduction et de mue.

Mots clés: île Bathurst, bernache cravant, *Branta bernicla hrota,* nidification, élevage des couvées, mue, île Seymour, fidélité au site

## INTRODUCTION

Brant (*Branta bernicla*) have a circumpolar Arctic breeding range (Cramp and Simmons, 1977; Ogilvie, 1978). In North America these small geese breed and moult in many locations throughout the Canadian Arctic, in Alaska, and in Greenland (Bellrose, 1980; Boertmannm, 1994; Reed et al., 1998). Those found in the eastern Canadian Arctic are of the light-bellied form (*B. bernicla hrota*), with two recognizable subpopulations or stocks. One stock, known as the eastern High Arctic brant (Reed et al., 1998), breeds and moults principally on the central and eastern Queen Elizabeth Islands (Bathurst, Ellesmere, Axel Heiberg, and Devon Islands) in the Canadian High Arctic and migrates via Iceland to winter quarters in Ireland (Maltby-Prevett et al., 1975; Boyd and Maltby, 1979; O'Briain and Healy, 1991). The other stock (Atlantic brant) nests mainly along the coasts of Foxe Basin and Southampton Island in the eastern Canadian Low Arctic and overwinters in the northeastern United States (Bellrose, 1980; Reed et al., 1998). Similarly, in western North America there are two stocks: the western High Arctic brant, which nest mainly on Melville and Prince Patrick Islands and winter chiefly in Puget Sound, Washington (Boyd and Maltby, 1979; Reed et al., 1989), and the black brant *B. b. nigricans*, which breed chiefly in Alaska and the western Canadian Low Arctic and winter in Mexico (Bellrose, 1980; Sedinger et al., 1993).

Most studies on North American brant during summer have been conducted in Low Arctic or Subarctic areas, where they characteristically nest in colonies and moult in large flocks (Barry, 1956, 1962, 1967; Mickelson, 1975; Ankney, 1984; Sedinger and Flint, 1991; Bollinger and Derksen, 1996). Only a few studies have dealt with the summer biology of High Arctic stocks (Boyd and Maltby, 1979, 1980), which not only occupy sites that are difficult to get to, but also often nest in dispersed fashion or moult in small flocks. This study attempts to fill part of that gap by summarizing information collected on eastern High Arctic brant on or near Bathurst Island, Northwest Territories (NWT), from 1968 to 1989. Our data come mainly from three sources: observational records collected by staff working from the Canadian Museum of Nature's (CMN) research station at Polar Bear Pass, Bathurst Island, from 1968 to 1989 (including work on nearby Seymour Island in 1974–77); research results from the University College Dublin's (UCD) Irish Brent Goose Expeditions to Bracebridge Inlet in 1984, 1986, and 1987; and Canadian Wildlife Service (CWS) banding expeditions and surveys to Bracebridge Inlet in 1984–88. We also had access to information from earlier CWS banding expeditions in 1973–75.

## THE STUDY AREA

Bathurst Island (74° 50′N, 99° 30′W), one of the Queen Elizabeth Islands, is situated in the centre of the Canadian Arctic Archipelago (Fig. 1). Most of its 16 000 km$^2$ is less than 300 m above sea level, and it has no permanent ice fields. The coastline is irregular, with several deep inlets. Two inlets, Bracebridge and Goodsir, almost bisect the island from west to east; their inner reaches are separated by a low-lying valley called Polar Bear Pass (Fig. 1). The climate of Bathurst Island, as summarized by Edlund and Alt (1989), is characterized by heavy cloud cover in June and July (75–80%), low mean temperature in summer (-0.3° C in June, 3.5 to 4.8° in July), low summer precipitation (mean total June, July, and August: 40–60 mm), and long duration of snow cover (ca. 300 days). Its vegetation is typical of the High Arctic vegetation zone (Polunin, 1960). Bathurst and its adjacent small islands represent a mosaic of vegetation zones (Edlund and Alt, 1989) ranging from areas of sparse herbaceous cover with low diversity (mainly on northern Bathurst), through areas of increased diversity of herbaceous plant species and the appearance of dwarf shrubs and sedges, to areas dominated by prostrate and matted shrubs in mesic sites and by sedges in wet locations (much of the lowland areas of southern Bathurst).

Most of our observations were conducted in the central portion of Bathurst Island (Fig. 1), an area of about 2500 km$^2$ that included well-vegetated lowlands (valley of Polar Bear Pass with its extensive sedge meadows and numerous ponds, as well as smaller areas in De la Beche Bay and near the mouth of the Variscan River) and rolling uplands, with sparser herbaceous cover characterized by the presence of *Saxifraga oppositifolia* and occasional lakes and braided river valleys.

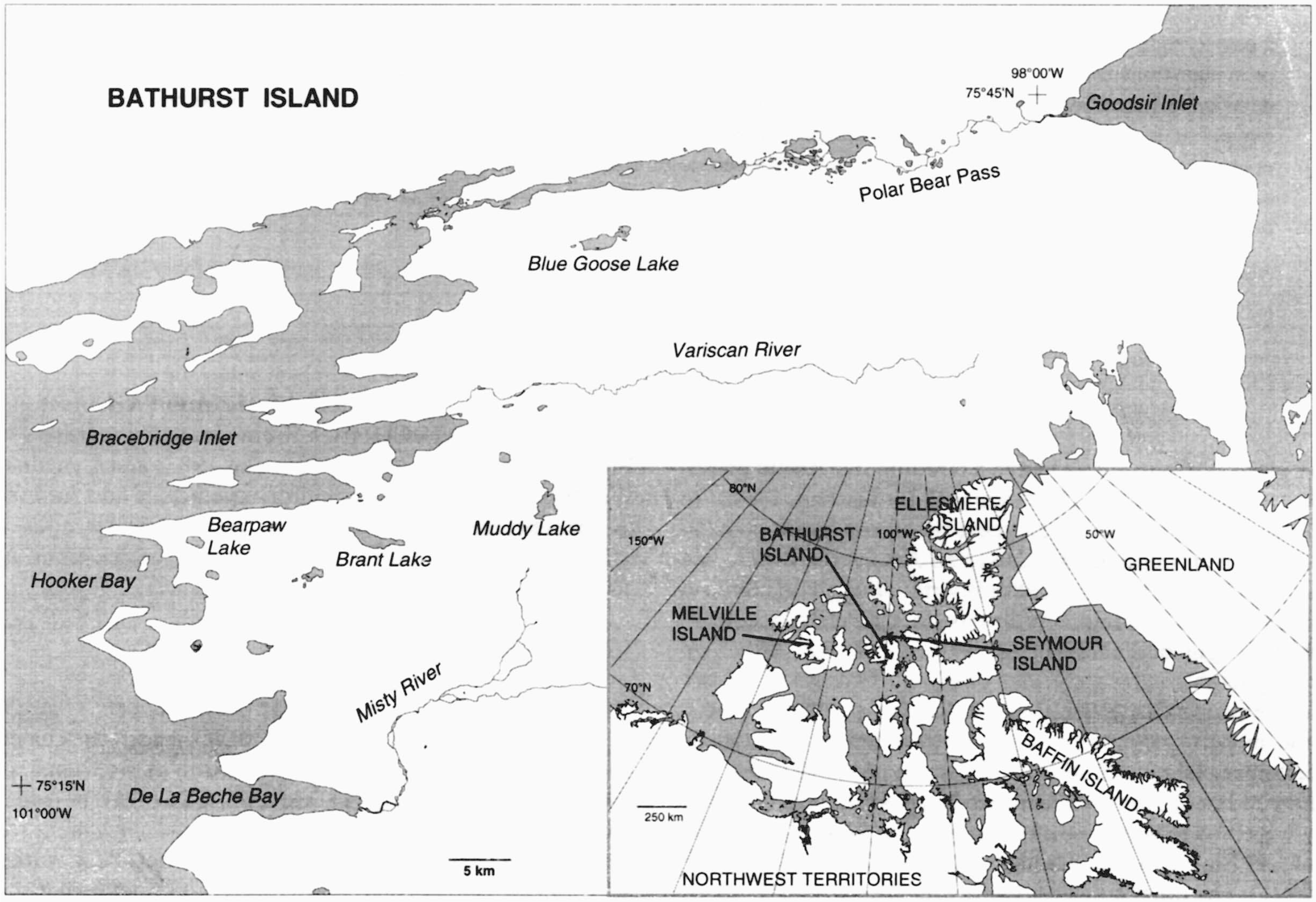


FIG. 1. The Bracebridge Inlet–Polar Bear Pass study area on Bathurst Island, and (inset) the location of Bathurst and Seymour Islands in the Canadian Arctic Archipelago.

Additional observations were conducted on Seymour Island, a smaller (2 km$^2$) low-lying island with sparse herbaceous plant cover, just north of Bathurst Island (Fig. 1).

On Bathurst Island, potential predators of brant or their eggs and chicks include the arctic wolf (*Canis lupus arctos*), arctic fox (*Alopex lagopus*), polar bear (*Ursus maritimus*), snowy owl (*Nyctea scandiaca*), parasitic jaeger (*Stercorarius parasiticus*), long-tailed jaeger (*S. longicaudus*), pomarine jaeger (*S. pomarinus*), Thayer's gull (*Larus thayeri*), glaucous gull (*L. hyperboreus*), and common raven (*Corvus corax*). On Seymour Island, the same predatory species are present, with the exception of arctic foxes and arctic wolves in most years; in addition, ivory gulls (*Pagophila eburnea*) are especially abundant (MacDonald, 1976).

## STUDY METHODS

Staff of the CMN Polar Bear Pass research station recorded observations of arrival dates, nesting patterns (habitat, egg laying dates, clutch size, hatch dates, brood sizes), and departure dates of brant as part of their routine investigations from 1968 to 1989; in 1968–79, the station was regularly manned from before 23 May to after 14 August, but in subsequent years the schedule of operations was more variable. Most of their observations were conducted in Polar Bear Pass, but sightings in several other parts of the island and on adjacent islands were made occasionally. Of particular interest were their brant observations during seabird studies on Seymour Island in 1974–77, when a crew of two observers spent most of the breeding season on this small island. Similar, but more detailed observations were carried out in an area mainly south of Bracebridge Inlet by members of the Irish Brent Goose Expedition (UCD) in 1984 (6 people from 31 May until 19 August), 1986 (3 people from 6 July to 8 August), and 1987 (2 people from 30 May to 25 June) with assistance from CWS staff in 1986 and 1987. Extensive nest searches were conducted on foot, and marked geese and goose behaviour were observed with the aid of binoculars and telescopes. CWS and UCD crews conducted banding by driving flightless brant with the help of helicopters into corrals made from netting (Maltby, 1977) in July or August 1984–86; standard metal leg bands were placed on one leg, and coloured plastic bands, bearing individual 3-letter codes large enough to be read at a distance with a telescope, on the other. Although we report here only resightings of coloured bands made within our study area, additional sightings on Irish wintering grounds helped establish the social status (paired, unpaired, mate identity) of many marked birds. Surveys were conducted over parts of southern Bathurst Island from a helicopter to examine nesting activity (June 1987) and rearing and moulting activity (July and/or August, 1984–88).

We examined the effects of weather on nesting events using temperature data from the CMN station at Polar Bear Pass on Bathurst Island for most years. In years when data were missing, we interpolated values from the weather station at Resolute Bay, approximately 100 km SE of Bathurst Island. Information on snow depth was available only for Resolute Bay.

## RESULTS

### *Spring Arrival*

First records of migratory arrival of brant near the Polar Bear Pass station, extracted from the station's annual records for 1968–79, were generally made during the first 10 days of June. The earliest arrival was recorded on 28 May 1977. During detailed observations in 1987, first arrivals were seen on 30 May (ca. 45 brant in flight); by 5 June there were 210 brant in a thermal oasis on the valley floor near Goodsir Inlet, and the following day a survey of the entire Polar Bear Pass revealed a total of 475, including 191 at the Goodsir oasis, 229 at another oasis near Bracebridge Inlet, and a flock of ca. 55 along the north coast of Bracebridge Inlet. These thermal oases are areas of low sedge meadow lying below south-facing hills. Dust that blows off the hills and collects there during winter reduces the reflection of solar energy and hastens snowmelt in spring. Brant used these patches of open wet sedge upon arrival; they fed there in flocks before dispersing to nesting territories or moulting sites. After 6 June 1987, numbers of brant in the two thermal oases declined quickly, while small scattered flocks were observed feeding in many newly thawed sites along the north side of Polar Bear Pass. Individual pairs and small flocks were also observed in flight: most of them (99% of 211 geese) were headed in the direction of Bracebridge Inlet, the most important nesting area near Polar Bear Pass.

Of 435 brant that were closely observed on 6 June 1987, 1.2% were yearlings (a proportion similar to that recorded on the Irish wintering grounds the previous winter: O'Briain, unpubl. data), which suggested that both breeding adults and younger geese were present among the early arrivals. Only 18 of the 435 brant were banded, 3.1% of the number of individuals banded near Bracebridge Inlet over the three previous years, which suggested that only a minority of the brant staging at Polar Bear Pass was destined for nesting territories in the Bracebridge area. Similarly, several marked brant that would be recorded breeding in the Bracebridge area later that summer were not present in the few oases we surveyed. Probably other oases and other suitable feeding sites exist elsewhere in the Bacebridge/Polar Bear Pass area, most likely in the Variscan River area.

On Seymour Island, first arrivals were recorded on 7, 12, and 3 June in 1975, 1976, and 1977, respectively, but not until 25 June in 1974, a cold summer when few or no brant nested in the area or elsewhere in the Queen Elizabeth Islands (Boyd and Maltby, 1979).

### *Nesting*

We observed early nesting behaviour in the Bracebridge area in the springs of 1984 and 1987. The first brant, a solitary yearling, was observed on 6 June 1984, while our observation area around Bearpaw Lake was still largely snow-covered. Subsequently, no brant were observed until 12 June, when six arrived, including an apparent family of two adults and two yearlings. By this time snowmelt was underway. On 13 June, the adults chased the two yearlings from the lake. From 16–18 June onward, territorial chases and other manifestations of nesting behaviour were observed, but these did not prevent occasional, brief visits to these lakes by groups of up to seven brant, including yearlings. On 18 June 1987, an aerial survey of the Misty and Variscan river basins in the Bracebridge breeding area revealed that, although both rivers were largely ice-free and occupied by dispersed pairs of brant, snowmelt at potential nesting and feeding areas in the valley bottoms was incomplete at the Variscan River and had scarcely begun in the Misty River/De la Beche Bay area. This suggested that feeding sites in the immediate vicinity of breeding locations on Bathurst Island became available somewhat later than those in the Polar Bear Pass staging area.

The earliest known nest was initiated on 10 June (Seymour I., 1975) and the latest on 22 June (Seymour I., 1976). Nest initiation peaked about 16 June (n = 15 nests, Bathurst and Seymour Islands combined; Table 1). The earliest hatch occurred on 8 July ( Bathurst I., 1989) and the latest on 19 July (Seymour I., 1976), with a peak about 13 July (Table 1). Completed clutches contained from two to six eggs (overall mean = 4.5 eggs, mode = 5; Table 2). The data suggest some annual variation in mean clutch size: larger mean clutches occurred in early nesting years, such as 1977. Incubation periods (from day of laying of last egg to day of hatch) were determined for seven nests on Seymour Island in 1976 and 1977 and for one in Bracebridge Inlet in 1984: three incubations lasted for 22 days, one for 23 days, three for 24 days, and one for 25 days (mean = 23.3 days, SD = 1.16).

On Seymour Island, nests were typically located on gravel ridges, often near a large rock. On Bathurst Island, 10 of 12 nests were on low gravel islands along braided streams (six of eight nests near Bracebridge Inlet in 1984 and 1987, all four nests found near Goodsir Inlet in 1989). Of the two remaining nests, one was on a small islet in a

TABLE 1. Dates of egg laying and hatch for brant on Bathurst and Seymour Islands, 1975–89.

| | | Date of first egg | | Date of hatch | |
|---|---|---|---|---|---|
| Year | Location | earliest nest | latest nest | earliest nest | latest nest |
| 1975 | Seymour I | 10 June (1)[1] | | 10 July (1) | |
| 1976 | Seymour I | 15 June (4) | 22 June | 11 July (3) | 19 July |
| 1977 | Seymour I | 11 June (6) | 19 June | 10 July (6) | 15 July |
| 1984 | Bathurst I | 15 June (1) | | 11 July (1) | |
| 1987 | Bathurst I | 13 June (3) | 16 June | no data | no data |
| 1989 | Bathurst I | no data | no data | 8 July (2) | 15 July |

[1] The value in parentheses is the sample size (number of nests)

TABLE 2. Clutch sizes of brant on Bathurst and Seymour Islands, 1969–89.

| | | Number of nests with eggs | | | | | Number | | |
|---|---|---|---|---|---|---|---|---|---|
| Year | Location | 2[1] | 3[1] | 4[1] | 5[1] | 6[1] | of nests | Mean | SD |
| 1969–75 | Bathurst I | | | | 2 | | 2 | 5.0 | - |
| 1975 | Seymour I | | | 1 | 1 | | 2 | 4.5 | - |
| 1976 | Seymour I | | | 3 | 1 | | 4 | 4.3 | 0.5 |
| 1977 | Seymour I | | | 2 | 5 | 1 | 8 | 4.9 | 0.6 |
| 1984 | Bathurst I | 1 | | | | | 1 | 2.0 | - |
| 1987 | Bathurst I | | 1 | 1 | 1 | | 3 | 4.0 | 1.0 |
| 1989 | Bathurst I | | 1 | | 3 | | 4 | 4.5 | 1.0 |
| Total | | 1 | 2 | 7 | 13 | 1 | 24 | 4.5 | 0.9 |

[1] The number of eggs.

pond and the other was on a gravel beach 20 m from a lake. All nests were exposed, with no concealing cover, although in some cases adjacent rocks probably provided some protection from winds.

Nests were widely dispersed on Bathurst Island. The area of highest nest density known to us was the Variscan River valley, where 6–7 nesting pairs occupied a 10 km stretch of the valley in June 1987. Higher densities occurred on Seymour Island (approximately 2 $km^2$) where eight nests were found in 1977. In all areas, nesting males vigourously chased other pairs that tried to settle in their territories. Potential avian egg predators such as glaucous gulls, Thayer's gulls, long-tailed jaegers, parasitic jaegers, pomarine jaegers and common ravens were also chased. King eiders (*Somateria spectabilis*), red knots (*Calidris canutus*), black-bellied plovers (*Pluvialis squatarola*), oldsquaws (*Clangula hyemalis*), arctic terns (*Sterna paradisaea*), and snow geese (*Anser caerulescens)* were also chased, particularly in the early stages of incubation. Ivory gulls were occasionally chased by territorial males on Seymour Island, but some brant whose nests were established within the gull colony co-existed successfully with the gulls and probably benefited from the aggressive attacks the ivory gulls directed against glaucous gulls (MacDonald, 1976). During nesting, male brant were not seen to react aggressively to passing arctic foxes on Bathurst Island, nor did they react to polar bears on Seymour Island. The brant on Bathurst Island defended territories up to a kilometre in diameter around their nests, whereas territories were much smaller on Seymour Island.

*Brood Rearing*

In the Bracebridge study area, the shorelines of lakes, estuaries and, occasionally, rivers were used for brood rearing. In 1984, 14 broods were raised in eight lakes; in August 1985, 15 broods were present in five lakes, all of which had been used in 1984. The estuary of the Misty River in De la Beche Bay supported 4 broods in 1984 and 15 in 1985. Along the Variscan River valley, five broods were present in 1985, although none had been seen there in 1984. On Seymour Island, broods were raised along shore leads and near freshwater ponds. As the newly hatched broods were led through the ivory gull colony they were unmolested, in contrast to eider broods, which were attacked by ivory gulls; perhaps the brownish colouration of young eiders (similar to that of lemmings, which are regular prey items for ivory gulls) may have elicited the attacks, whereas the grey plumage of young brant (similar to that of young ivory gulls) did not.

On lakes in the Bracebridge area and on Seymour Island, broods were raised singly or in loose groups of 2–3 families (each accompanied by both parents), whereas in rivers and estuaries groups of up to 15 families were observed.

The mean brood size at nest exodus for seven nests on Seymour Island in 1976 and 1977 was 4.3 goslings (SD = 0.76). In the Bracebridge area in 1984, 18 successful pairs were accompanied by 60 young just prior to fledging, with a mean brood size of 3.3 goslings (SD = 1.41). The fledging period was recorded for one brood on Seymour Island in 1977: three goslings flew for the first time 42 days after hatch, and a fourth gosling at age 43 days. Applying that value of age-at-fledging to the hatching dates listed in Table 1, we estimated that fledging generally occurred from 19 to 31 August. This is consistent with the known dates of 22–23 August for the Seymour Island brood mentioned above, and with our observation of three flying broods in the Bracebridge area on 19 August 1984. Dates of migratory departure by families are not known, but presumably those flights occurred shortly after fledging, because there were few sight records of brant by CMN staff in the last week of August. The last sighting occurred on 10 September.

*Reproductive Success*

During the study period on Seymour Island (1974–77), brant did not nest in 1974, but they did so successfully in 1975, 1976, and 1977 (Table 3). In 1976–77, when more detailed records were available, 10 of 12 nests (83%) hatched and two were abandoned. Of the 56 eggs in the 12 nests, 46 hatched (86%), eight were abandoned, one was infertile, and one was taken by an avian predator. No eggs were taken by mammalian predators, although polar bears visited the island in most years. Foxes were present only in 1974, when persistent ice cover allowed access over the

TABLE 3. Nesting effort and breeding success of brant on Seymour Island (1974–77) and on Bathurst Island (1984–89), compared to June temperatures on Bathurst Island.

| Year | Location | Nests initiated | Broods fledged | Mean temp. 1–20 June[1] |
|---|---|---|---|---|
| 1974 | Seymour I | No | No | -7.7 |
| 1975 | Seymour I | Yes | Unknown[2] | 1.5 |
| 1976 | Seymour I | Yes | Unknown | -2.8 |
| 1977 | Seymour I | Yes | Yes | 0.2 |
| 1984 | Bathurst I | Yes | Yes | 0.9 |
| 1985 | Bathurst I | Yes | Yes | 1.3 |
| 1986 | Bathurst I | No | No | -3.9 |
| 1987 | Bathurst I | Yes | No | -1.8 |
| 1988 | Bathurst I | No? | No | -2.2 |
| 1989 | Bathurst I | Yes | Yes | 0.8 |

[1] From weather records in Polar Bear Pass (˚C), except for 1984 and 1985 temperatures, which were interpolated from Resolute Bay records.

[2] Broods were known to have fledged on Bathurst Island.

sea ice (MacDonald, 1976); however, brant did not attempt to nest in that exceptionally cold year.

In the Bracebridge area (1984–88), brant did not nest in 1986, but did so in 1984, 1985, and 1987 (Table 3). The area was not visited during June in 1988, so it was not known whether brant had attempted to nest, but helicopter overflights on 10 July and 14 August revealed no broods. Of five known nests along the Variscan River in 1987, two were destroyed by predators before we found them and at least two of the other three were also destroyed before we left the island in late June. Foxes were frequently observed searching for bird nests that year, and it is likely that they eventually destroyed all brant nests, because no broods could be found during a helicopter survey on 13 August. In 1989, only the Polar Bear Pass area was visited but, exceptionally in that year, four nests were found near Goodsir Inlet (V. Sheridan and D. Gill, pers. comm. 1989), at least two of which hatched.

The two years in which brant did not attempt to nest in our study area, 1974 and 1986, were those with the lowest mean temperatures during 1–20 June for the 10 years of study (≤ -3.9˚C: Table 3, Fig. 2). In the six warmest years (mean temperature 1–20 June > -2˚C), brant laid eggs. In the two remaining years, the weather was moderately cold (1976, -2.8˚C; 1988, -2.2˚C); in 1976 eggs were laid, but few or none appeared to have been laid in 1988. Temperatures were significantly higher in years when eggs were laid (one-tailed Wilcoxon test, $p < 0.03$). Although snow cover was generally correlated with temperature, the average depth of snow over the pre-laying period was not a good predictor of whether or not eggs were laid (Wilcoxon test, $p = 0.26$).

In two of the seven years in which egg laying was known to occur, success through brood rearing could not be determined, but brant were known to fledge young in four other years. In the remaining year, 1987, none of the eggs laid produced fledged young. In 1987, the mean June temperature was close to the long-term average and snow

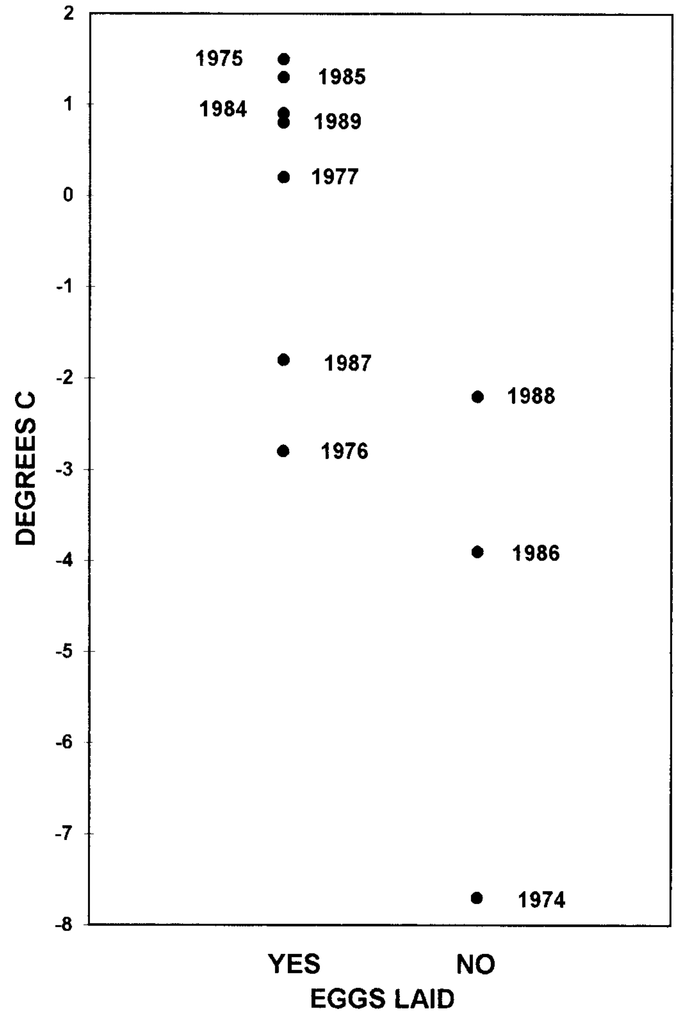


FIG. 2. Relationship between egg laying by brant (Bathurst and Seymour Islands) and mean temperature during 1–20 June (Bathurst Island). In 1988, nonbreeding was inferred from indirect evidence.

cover was light, but heavy egg predation by arctic foxes was observed at our Bracebridge study area. Foxes were abundant and had few alternative prey, because lemmings were not abundant that year; the paucity of lemmings in 1987 was confirmed from D. Gill's (pers. comm. 1987) study of microtine populations in Polar Bear Pass, and by the absence of snowy owls (good indicators of lemming abundance), which had been present and had bred in the previous year. In the four years in which young were known to have fledged, mean temperatures during 1–20 June were warmer than average (> 0˚C).

*Moulting*

Following dispersal from spring staging areas, small flocks of brant formed near lakes and in river valleys in the Bracebridge study area. Brant in these flocks did not display the high level of aggressive behaviour characteristic of territorial breeding pairs and of early spring staging flocks. In June 1984 near Hooker Bay, small groups of ≤ 20 brant, including a high proportion of yearlings, fed around lakes, shifting frequently from lake to lake. Similarly, in June 1987 small groups of nonbreeders and failed breeders (subsequently termed nonbreeders because the two categories cannot be distinguished in moulting flocks observed from a distance) were observed in portions of the Variscan River valley. An aerial survey of the Bracebridge study area on 26 July 1984 revealed the presence of 250–300 nonbreeders, in addition to the actively breeding adults. Another aerial survey (covering a larger area including the north shore of Bracebridge Inlet west to South Snowbird Creek) on 6 July 1986, which was a nonbreeding year, showed a total of 600–650 brant. Flock sizes ranged from 4 to 266 (n = 13, median = 57). Altogether, three coastal and five inland sites were used. Two inland sites were used in one but not both years. Bearpaw Lake was not used by moulting brant in 1984, when a breeding male evicted all nonbreeders from his territory; in 1986, when no breeding territories were established locally, the lake was used by moulting brant. Muddy Lake, farther inland and at a higher elevation, did not thaw until late summer in 1986; as it had no open water when the moult began in that year, it was not used by brant. Probably because of the cold weather and late thaw, coastal sites proved to be of more importance in 1986. A total of 431 moulters was recorded at three estuarine sites, including one flock of 266 brant at South Snowbird Creek. All three estuaries faced south, and shore leads at their mouths opened by late June, probably offering the earliest secure moulting sites in the study area.

At Brant Lake, flocks of nonbreeding brant became flightless about 6 July in both 1984 and 1986, and regained flight 20–22 days later. Within each flock, individual brant appeared to show a high degree of synchrony of moult, but variation of up to a week may have occurred between flocks.

Four main moulting flocks were captured in the Bracebridge study area in 1986. Each contained a similar proportion of yearling brant (pooled n = 288, mean = 26.7%), which corresponded closely with the 23% young estimated in Ireland the previous winter.

Following the wing moult, brant dispersed from the moulting sites. In 1986 flocks of newly banded brant were seen up to 7 km from the moulting sites in July. Most post-moult nonbreeders appeared to have left Bathurst Island by the second week of August, much earlier than the adult breeders and their young. In the nonbreeding year of 1974, the latest observation of brant migrating through Polar Bear Pass was made on 12 August; and in 1987, when breeding failed, no brant were found in the Bracebridge/Polar Bear Pass area on 13 August.

*Fidelity to Breeding and Moulting Areas*

During banding operations on Bathurst Island in 1984–86, we captured six adult brant, all females, that had been banded prior to 1984. One of the birds carried a band too badly worn to be legible, but four of the five others had been banded at Brant Lake on Bathurst Island in 1973 (two individuals) and 1975 (two) and the remaining one on Melville Island in 1974 (a nonbreeding year). All four Bathurst-banded brant were adult females with brood patches when initially banded, which suggested that they had bred locally in the year of banding. In 1984, all four of them were recorded (three as moulters, one with a brood) at the same site where they had been originally banded (Brant Lake). In 1985–86, three of them were again recorded, one with a brood on Muddy Lake in 1985 and as a moulter on Brant Lake in 1986, the two others as moulters on Bearpaw Lake in 1986.

In 1984–87, we banded 554 brant with both individually coded plastic and standard metal leg bands within the Bracebridge study area. From 1985 to 1987, we observed or recaptured 89 individuals (16%) on Bathurst Island (Table 4). Almost half of the brant marked as adult breeders were resighted in subsequent years (34 of 71 individuals = 48%), and of five pairs banded during brood drives on the Variscan River in August 1985, three pairs (60%) were observed nesting or prospecting for nests in the same valley in June 1987. Adults marked as nonbreeders were resighted less frequently (35 of 209 = 17%), but this low proportion is misleading because there were few opportunities to resight the many nonbreeders marked in 1986; indeed, of the 38 nonbreeders marked in 1984, 21 (55%) were recorded on the island in subsequent years. Of 18 pairs trapped as nonbreeders at Brant Lake in 1984, 5 pairs were retrapped at the same site, and 3 pairs less than 10 km away, in 1986. In only 1 of 18 known pairs moulting in the area in 1986 was the male recorded at a moulting site different from that of his mate. Few of those marked as yearlings (7 of 109 = 6%) or goslings (13 of 165 = 8%) were resighted. Brant of both sexes were resighted in more or less equal proportions.

## DISCUSSION

### *Breeding Biology Compared with that of Other Stocks of Brant*

The average dates of arrival and peak egg laying for brant of Bathurst and Seymour Islands (approximately 75° N latitude) were about 3–5 June and 16 June, respectively, compared with 7–10 June and about 20 June for *B. b. hrota* breeding on Southampton Island, NWT, (Barry, 1962; Abraham and Ankney, 1986) which is 11° farther south. Also, *B. b. bernicla* breeding on the Taimyr Peninsula in Siberia (74° N) did not arrive before 10 June (no date of egg laying provided: Ebbinge and Spaans, 1995). The median date of egg laying in *B. b. hrota* breeding on Svalbard (77° N) was 10 June (Madsen et al., 1989). *B. b. nigricans* arrived on the Yukon-Kuskokwim Delta, Alaska (61° N), before 15 May and began egg laying before 1 June, but in late years, peak egg laying was delayed to about 5 June (Mickelson, 1975; Reed et al., 1998). For the

TABLE 4. Numbers of marked brant recaptured or resighted on Bathurst Island, 1985–87.

| Year marked | Age and status | Number marked | Number recaptured or resighted 1985 breed | 1986 moult | 1987 stage | 1987 breed | Total |
|---|---|---|---|---|---|---|---|
| 1984 | Adult breeder | 16 | 2 | 5 | - | - | 6 |
| | Adult nonbreeder | 38 | 9 | 16 | 2 | 1 | 21 |
| | Yearling | 32 | - | 4 | 1 | 1 | 5 |
| | Gosling | 55 | - | 4 | 1 | 1 | 6 |
| 1985 | Adult breeder | 55 | x | 25 | 3 | 5 | 28 |
| | Yearling | 4 | x | 1 | - | - | 1 |
| | Gosling | 110 | x | 7 | - | - | 7 |
| 1986 | Adult nonbreeder | 171 | x | x | 12 | 2 | 14 |
| | Yearling | 73 | x | x | - | 1 | 1 |

same subspecies at the Anderson River Delta, NWT (69˚ N), first egg laying occurred from 2 to 13 June over an eight-year period, and averaged about 6 June (Barry, 1967). On Victoria Island, NWT (68˚ N) the first egg was laid on 9 June (Parmelee et al., 1967). Brant from the western Canadian High Arctic arrived at Prince Patrick Island, NWT, (76˚ N) on 12–17 June (Handley, 1950). Thus breeding phenology in brant is not closely correlated with latitude (Reed et al., 1998). Those breeding on Bathurst and Seymour Islands, at high latitude, initiate their nesting season relatively early.

The average clutch size recorded for Bathurst and Seymour Island brant, 4.5 eggs (n = 24), is among the highest reported. For *B. b. hrota* on Southampton Island, the mean clutch over the three years 1953, 1956, and 1957 was 3.9 eggs (n = 853; Barry, 1962), and in 1979–80 it was 3.5 (n = 851; Abraham and Ankney, 1986), whereas on Svalbard in 1987, 13 nests averaged 4.0 eggs (Madsen et al., 1989). In 1969–72 the average clutch for 130 nests of *B. b. nigricans* on the Yukon-Kuskokwim Delta was 3.3 eggs, and annual means ranged from 2.7 to 4.1 (Mickelson, 1975). Barry (1967) recorded a mean of 3.9 eggs in 700 nests (1958–65) of the same subspecies on the Anderson River Delta. Some of this variation is undoubtedly due to different rates of partial predation and to annual variation in nesting phenology. Barry (1962) found that in a subsample of nests on Southampton Island, for which the extent of partial predation was known, the true clutch size was on average 0.3 to 0.6 eggs greater than in other nests; he also showed that clutch size was larger in years of early nesting. Because we cannot correct for these factors, statistical comparisons between populations and regions would be of limited value, but brant on Bathurst and Seymour Islands appear to incubate larger clutches than those of most other populations.

We recorded a mean incubation period of 23 days (n = 7) which is similar to those recorded for *B. b. hrota* on Southampton Island (mean = 24 days, n = 12; Barry, 1956) and for *B. b. nigricans* on the Yukon-Kuskokwim Delta (range 22–25 days, n = 7; Mickelson, 1975) and on the Anderson River Delta (mean = 24 days; Barry, 1967). Goslings of a brood on Seymour Island were observed to fly at age 42–43 days, which is a younger age than the 45–50 days suggested by Barry (1962) for *B. b. hrota* on Southampton Island, but similar to the 40–45 days reported for *B. b. nigricans* (Barry, 1967; Mickelson, 1975).

*Moulting*

Several populations of brant are known to undertake summer migrations to moulting sites well removed from their breeding areas (Derksen et al., 1982; Bollinger and Derksen, 1996), but Bathurst Island brant did not appear to do so, moulting mainly in local sites with which they had experience during breeding or moulting in earlier years. Yearling brant were also found in these small moulting flocks, but only a small proportion of them had originally been banded locally as goslings. These facts suggest a relatively low rate of philopatry to the natal area and a wider dispersal over the breeding range during the first year of life. Among 318 nonbreeding adults and yearlings and 71 breeding adult moulters captured in 1984–86, the only evidence of intermixing with other brant populations came from the capture of one foreign-banded individual (marked on Melville Island a decade earlier), of one unbanded *B. b. nigricans*, and of two other unbanded, dark-bellied individuals of unknown racial identity. None of the brant banded by us in this study were among the 451 adults captured on Melville and Prince Patrick Islands in August 1987 (A. Reed and H. Boyd, unpubl. data), nor were any found among the several thousand brant captured in a major moulting area near Teshekpuk Lake, Alaska, from 1987 to 1992 (Bollinger and Derksen, 1996). To date, only two of the brant banded by us on Bathurst Island have been recovered in North America outside the Queen Elizabeth Islands and Greenland, further suggesting little intermixing with other populations.

On Bathurst Island in 1984 and 1986, moulting brant were flightless for 20–22 days. This is similar to the 22–25 day period calculated by Boyd and Maltby (1980) for moulting brant on Melville and Prince Patrick Islands, and the 23–24 days reported by Taylor (1995) for black brant in Alaska.

In the contrasting years of 1984 and 1986, the distribution of brant during the moult was different. In the milder year of 1984, many Brant moulted on inland lakes as far as 5 km from the coast, whereas in the colder, nonbreeding year of 1986, the majority moulted at coastal sites. These distributions agree with the results of coastal waterfowl surveys conducted in the central Arctic islands in 1974 and 1975 (McLaren and Alliston, 1985). They found many brant along the coasts of Bathurst and other adjacent islands in the cold, nonbreeding spring of 1974 but few in the milder spring of 1975, when brant were breeding and moulting at inland sites.

*Reproductive Success and Breeding Strategy*

Fox predation has been reported as an important factor in limiting nest success of brant (Barry, 1967; Raveling, 1989; Anthony et al., 1991; Madsen et al., 1992). Using the proportion of young *B. b. bernicla* in wintering flocks as a measure of breeding success, Summers (1986) and Summers and Underhill (1987) hypothesized that heavy fox predation occurred about once every three years, in those years when fox numbers remained high after a crash in the population of lemmings, their principal prey. In three of the six years of our study on Bathurst Island, no young brant were fledged. In two of the three years, failure was attributed to nonbreeding (in 1986 no eggs were laid, and the same situation was inferred for 1988 from low June temperatures and the absence of broods in early August), and in the third (1987), to heavy nest predation by arctic foxes. Thus fox predation appeared to have an important impact on brant production on Bathurst Island only in 1987, and in that year brant breeding elsewhere in the range successfully raised young, as indicated by the presence of many juveniles in the wintering flock (16%; M. O'Briain, unpubl. data). It appears unlikely that fox predation would cause cyclic, large-scale breeding failure in this population, because some brant nest in fox-free areas (such as Seymour Island in most years) and because the fox/lemming cycle is probably not in synchrony throughout the full breeding range (Miller, 1987).

Over the 10 years of study between 1974 and 1989 on Bathurst and Seymour Islands, brant did not lay eggs in two years and were suspected of not laying in another (1988). The two years of confirmed nonbreeding, 1974 and 1986, had the coldest mean temperatures on Bathurst Island over the first 20 days of June (-7.7 and -3.9˚C, respectively). In 1988, when nonbreeding was also suspected, the mean temperature over the same period (-2.2˚C) was also below average (Fig. 2), but it was also cold (-2.8˚C) in 1976, when brant nested on Seymour Island (Table 3). Boyd (1987), using temperature as an index of snow clearance, found that low June temperatures on the Taimyr Peninsula were closely correlated with poor breeding success in *B. b. bernicla* during the 1950s and early 1960s, but in subsequent years the association weakened.

We conclude that for the brant of Bathurst and adjacent islands, temperature during the period of prelaying and egg laying is the main factor determining whether eggs are laid. Our data suggest a double threshold of June temperatures, with egg laying not occurring when the mean for 1–20 June is below approximately -3˚C, and with egg laying occurring when the mean exceeds about -2˚C. In the intermediate range between -2 and -3˚C, nesting may or may not occur, depending presumably on other factors.

In a High Arctic environment, precipitation is characteristically low, and frequent winds prevent deep accumulation of snow. On Bathurst and Seymour Islands, small patches of open ground are probably available for nest establishment by early June in all but the infrequent years of exceptionally deep snow accumulation and continued heavy spring frost (such as occurred in 1974). More important, however, is the need for larger expanses of suitable ice-free feeding habitat to enable brant to obtain sufficient nutrients for egg production. Although many Arctic-nesting geese rely heavily on nutrient reserves accumulated during spring migration for egg production (Ankney and MacInnes, 1978), brant may depend considerably on food obtained near the nesting area during the pre-laying period (Barry, 1962; Ankney, 1984), because their reserves may be severely depleted during spring migration (Vangilder et al., 1986; Ebbinge and Spaans, 1995). Another High Arctic, long-distance migrant, the greater snow goose (*Anser caerulescens atlanticus*), also relies heavily on nutrients obtained on the breeding grounds (Gauthier, 1993). The availability of suitable feeding sites in the Bathurst Island area is undoubtedly governed by early June temperatures, which influence both the rate of snowmelt and (perhaps more importantly) the thawing of wet sedge meadows and moss carpets. We suggest that breeding success of these brant is strongly influenced by their ability to obtain nutrient reserves during early June, which is in turn linked to the extent of thaw at suitable feeding sites near the nesting areas. But the amount of endogenous nutrients available to brant at the time of egg laying is also influenced by their reserve status upon departure from the staging areas and by wind conditions encountered on migration (Ebbinge and Spaans, 1995). When conditions are especially favourable on spring staging areas and along migration paths, brant may arrive on the breeding ground with better-than-average reserves remaining, enabling them to attain breeding condition even if June temperatures are moderately cold. This may have been the case in 1976, when brant bred successfully on Seymour Island in spite of cold June temperatures and relatively heavy snow in the general area.

Brant of this population arrive in the vicinity of Bathurst Island scarcely a few days after departing the main staging area on Iceland, indicating that the 3000 km flight is conducted almost nonstop. Most of that flight is over open ocean or extensive icefields where feeding is impossible, and the climb to cross the Greenland ice cap adds substantially to the energy demands (Alerstam et al., 1990; Gudmundsson et al.,1995). It is probable that these brant arrive on the breeding islands with insufficient nutrient reserves for egg production and nesting activity. This illustrates the importance for Bathurst Island brant to accumulate large reserves while staging in Iceland and to supplement those reserves by feeding on arrival at or near the nesting area. We suggest that the thermal oases in Polar Bear Pass provide that critical supply of nutrients between arrival and laying. This explains why early June temperatures, through their role in thawing feeding areas, have such a strong influence on reproductive success.

### *Dispersal of Brant and the Food Supply*

An important question remains to be addressed: how do these brant and their goslings cope with the apparently impoverished feeding conditions imposed by the general sparseness of vegetation and low plant biomass characteristic of the High Arctic? Boyd and Maltby (1979) speculated that the low plant biomass at another High Arctic location, Melville Island, could not support brant populations over several consecutive seasons, thus imposing a certain form of nomadism. But in our study, individual sites were generally used in consecutive seasons for breeding and/or moulting; non-use of a traditional wetland in a given year could usually be explained by persistent ice cover. We argue that the low densities of breeding brant and the small size of moulting flocks in High Arctic sites is a consequence of the low plant biomass. We suggest that food resources at individual sites limit the number of brant that can be accommodated, and the balance is mediated through aggression and other social interactions. The wide dispersal of nests on Bathurst and other large islands may provide an additional benefit by reducing the risk of fox predation. Although reduced densities of geese in areas of low plant biomass will have obvious overall benefits, the question of growth requirements of goslings may be more complex. Studies on cackling Canada geese *Branta canadensis minima* and black brant in Alaska (Sedinger and Raveling, 1984; Sedinger and Flint, 1991; Sedinger, 1992) and on greater snow geese on Bylot Island (Manseau and Gauthier, 1993; Lepage et al., 1998) highlight the importance of both abundance and quality of highly digestible graminoid plants for the growth of goslings. The rearing habitats on Bathurst and Seymour Islands are generally characterized by narrow, mossy lake margins and a sparse upland cover of forbs; they lack the dense swards of high-quality *Carex subspathacea, Puccinellia phryganodes*, and *Triglochin palustris* found in Alaska and of *Carex aquatilis, Dupontia fisheri*, and *Eriophorum* spp. found on Bylot Island. For cackling Canada geese, which are similar in size to brant, Sedinger (1992) showed that normal growth rates were attained by goslings feeding during 63% of the 20 h daylight period in Alaska. If brant goslings on Bathurst Island fed at the same rate through the full 24 h of daylight which prevails at that latitude, they would gain 20% more feeding time in comparison to cackling Canada geese in Alaska; this might compensate, at least in part, for the apparently reduced availability and quality of forage plants. It would be rewarding to investigate how goslings of this High Arctic population of brant adjust their diet and behaviour to ensure the assimilation of adequate nutrients for their rapid growth.

## ACKNOWLEDGEMENTS

We are grateful to the many members of the Canadian Museum of Nature's field crews who recorded observations from Polar Bear Pass and from Seymour Island, especially D. Gill and J. Hawkings, who made many of the most pertinent observations as well as extracting and interpreting the data for us. Special thanks are due to the members of the Irish Brent Goose Expedition's research teams: B. Hayes, V. Sheridan, T.D. Carruthers, T. O'Carroll, G. Ford, and W. Clarke. Canadian Wildlife Service crews included H. Boyd, P. Chagnon, and C.-A. Drolet. Substantial logistical support of field activities was provided by the Polar Continental Shelf Project, Energy, Mines and Resources Canada. Financial support for the Irish Brent Goose Expedition came from UNESCO, Ducks Unlimited Inc., the Department of the Environment of Northern Ireland, the Irish National Parks and Wildlife Service, the World Wildlife Fund (Canada), and a large number of individuals contributing through an "adopt-a-goose" scheme.

We received valuable advice and encouragement from H. Boyd, L. Maltby, and F. Miller (Canadian Wildlife Service), B. Healy and E.J. Duke (University College, Dublin), R.A. McCabe (University of Wisconsin), M. Owen (Wildfowl and Wetlands Trust), and D.A. Stroud (Joint Nature Conservation Committee). We are also grateful to B. Ebbinge (Netherlands Institute for Forestry and Nature Research) and two anonymous reviewers for valuable comments on an earlier version.

## REFERENCES

ABRAHAM, K.F., and ANKNEY, C.D. 1986. Summer birds of East Bay, Southampton Island, Northwest Territories. Canadian Field-Naturalist 100:180–185.

ALERSTAM, T., GUDMUNDSSON, G.A., JONSSON, P.E., KARLSSON, J., and LINDSTRÖM, A. 1990. Orientation, migration routes and flight behaviour of knots, turnstones and brant geese departing from Iceland in spring. Arctic 43: 201–214.

ANKNEY, C.D. 1984. Nutrient reserve dynamics of breeding and molting brant. Auk 101:361–370.

ANKNEY, C.D., and MacINNES, C.D. 1978. Nutrient reserves and reproductive performance in female lesser snow geese. Auk 95:459–471.

ANTHONY, R.M., FLINT, P.L., and SEDINGER, J.S. 1991. Arctic fox removal improves nest success of black brant. Wildlife Society Bulletin 19:176–184.

BARRY, T.W. 1956. Observations of a nesting colony of American brant. Auk 73:193–202.

———. 1962. Effect of late seasons on Atlantic brant reproduction. Journal of Wildlife Management 26:19–26.

———. 1967. Geese of the Anderson River Delta, Northwest Territories. Ph.D. Thesis, University of Alberta, Edmonton. 212 p.

BELLROSE, F.C. 1980. Ducks, geese and swans of North America. Harrisburg, Pennsylvania: Stackpole Books. 544 p.

BOERTMANN, D. 1994. An annotated checklist to the birds of Greenland. Meddelelser om Grønland, Bioscience 38. 63 p.

BOLLINGER, K.S., and DERKSEN, D.V. 1996. Demographic characteristics of molting black brant near Teshekpuk Lake, Alaska. Journal of Field Ornithology 67:141–158.

BOYD, H. 1987. Do June temperatures affect the breeding success of dark-bellied brent geese *Branta b. bernicla*? Bird Study 34:155–159.

BOYD, H., and MALTBY, L.S. 1979. The brant of the western Queen Elizabeth Islands, N.W.T. In: Jarvis, R.L., and Bartonek, J.C., eds. Management and biology of Pacific Flyway geese, A Symposium. Corvallis, Oregon: Oregon State University Book Stores. 5–21.

———. 1980. Weights and primary growth of brent geese moulting in the Queen Elizabeth Islands, N.W.T., Canada. Ornis Scandinavica 11:131–141.

CRAMP, S., and SIMMONS, K.E.L. 1977. The birds of the western Palearctic Vol. 1. Oxford: Oxford University Press. 722 p.

DERKSEN, D.V., ELDRIDGE, W.D., and WELLER, M.W. 1982. Habitat ecology of Pacific black brant and other geese moulting near Teshekpuk Lake, Alaska. Wildfowl 33:39–57.

EBBINGE, B.S., and SPAANS, B. 1995. The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the High Arctic. Journal of Avian Biology 26:105–113.

EDLUND, S.E., and ALT, B.T. 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic 42:3–23.

GAUTHIER, G. 1993. Feeding ecology of nesting greater snow geese. Journal of Wildlife Management 57:216–223.

GUDMUNDSSON, G.A., BENVENUTI, S., ALERSTAM, T., PAPI, F., LILLIENDAHL, K., and ÅKESSON, S. 1995. Examining the limits of flight orientation performance:Satellite tracking of brent geese migrating across the Greenland ice-cap. Proceedings of the Royal Society of London B(261):73–79.

HANDLEY, C.O. 1950. The brant of Prince Patrick Island, Northwest Territories. Wilson Bulletin 62:128–132.

LEPAGE, D., GAUTHIER, G., and REED, A. 1998. Seasonal variation in growth of greater snow goose goslings: The role of food supply. Oecologia 114:226–235.

MacDONALD, S.D. 1976. Phantoms of the polar pack ice. Audubon Magazine 78(3):2–19.

MADSEN, J., BREGNBALLE, T., and MEHLUM, F. 1989. Study of the breeding ecology and behaviour of the Svalbard population of light-bellied brent goose *Branta bernicla hrota.* Polar Research 7:1–21.

MADSEN, J., BREGNBALLE, T., and HASTRUP, A. 1992. Impact of arctic fox *Alopex lagopus* on nesting success of geese in southeast Svalbard, 1989. Polar Research 11:35–39.

MALTBY, L.S. 1977. Techniques used for the capture, handling and marking of brant in the Canadian High Arctic. Canadian Wildlife Service Progress Notes 72. 6 p.

MALTBY-PREVETT, L., BOYD, H., and HEYLAND, J.D. 1975. Observations in Iceland and northwest Europe of brant from the Queen Elizabeth Islands, N.W.T., Canada. Bird Banding 46: 155–161.

MANSEAU, M., and GAUTHIER, G. 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74:2045–2055.

McLAREN, M.A., and ALLISTON, W.G. 1985. Effects of snow and ice on waterfowl distribution in the central Canadian Arctic islands. Arctic 38:43–52.

MICKELSON, P.G. 1975. Breeding biology of cackling geese and associated species on the Yukon-Kuskokwim Delta, Alaska. Wildlife Monographs 45. 35 p.

MILLER, F. 1987. Snowy owl numbers on twelve Queen Elizabeth Islands, Canadian High Arctic. Journal of Raptor Research 21:153–157.

OGILVIE, M. 1978. Wild geese. Berkhamsted: Poyser. 350 p.

O'BRIAIN, M., and HEALY, B. 1991. Winter distribution of light-bellied brent geese *Branta bernicla hrota* in Ireland. Ardea 79:317–326.

PARMELEE, D.F., STEPHENS, H.A., and SCHMIDT, R.H. 1967. The birds of southeastern Victoria Island and adjacent small islands. National Museums of Canada Bulletin No. 222. 229 p.

POLUNIN, N. 1960. Introduction to plant geography and some related sciences. New York: McGraw-Hill. 640 p.

RAVELING, D.G. 1989. Nest-predation rates in relation to colony size of black brant. Journal of Wildlife Management 53:87–90.

REED, A., DAVISON, M.A., and KRAEGE, D.K. 1989. Segregation of brent geese *Branta bernicla* wintering and staging in Puget Sound and the Strait of Georgia. Wildfowl 40:22–31.

REED, A., WARD, D.H., DERKSEN, D.V., and SEDINGER, J.S. 1998. Brant (*Branta bernicla*). In: Poole, A., and Gill, F., eds. The birds of North America. Washington, D.C.: The Academy of Natural Sciences and Philadelphia, Pennsylvania: The American Ornithologists' Union. No. 337. 32 p.

SEDINGER, J.S. 1992. Ecology of prefledging waterfowl. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A., and Krapu, G.L., eds. Ecology and management of breeding waterfowl. Minneapolis, Minnesota: University of Minnesota Press. 109–127.

SEDINGER, J.S., and FLINT, P. 1991. Growth rate negatively correlated with hatch date in black brant. Ecology 72:496–502.

SEDINGER, J.S., and RAVELING, D.G. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101:295–306.

SEDINGER, J.S., LENSINK, C.J., WARD, D.H., ANTHONY, R.M., WEGE, M.L., and BYRD, G.V. 1993. Current status and recent dynamics of the black brant *Branta bernicla* breeding population. Wildfowl 44:49–59.

SUMMERS, R.W. 1986. Breeding production of dark-bellied brent geese *Branta b. bernicla* in relation to lemming cycles. Bird Study 33:105–108.

SUMMERS, R.W., and UNDERHILL, L.G. 1987. Factors related to breeding production of brent geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. Bird Study 34:161–171.

TAYLOR, E.J. 1995. Molt of black brant (*Branta bernicla nigricans*) on the Arctic Coastal Plain, Alaska. Auk 112:904–919.

VANGILDER, L.D., SMITH, L.M., and LAWRENCE, R.K. 1986. Nutrient reserves of premigratory brant during spring. Auk 103:237–241.