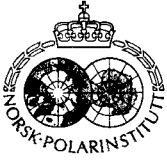


Study of the breeding ecology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota**

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Nesting ecology and behaviour of the Light-bellied Brent Goose was studied on Lurøya and adjacent islands in the Tusenøyane group, SE Svalbard, from 13 June to 30 July 1987.

On Lurøya 38 pairs attempted to nest, and in the whole study area 98 pairs. Estimated median data of laying of first egg was 10 June, and median hatching date 7 July. Mean clutch size in the middle of the incubation period was 4.0 eggs. On Lurøya nesting success was 25.7%, hatching success 28.6%, and hatching success for the whole study area was c. 24%. Most losses were attributed to predation (62% of all eggs), polar bears being the most severe predators. Until mid July the islands were surrounded by drift ice, and bears occurred regularly. Bears not only damaged nests but also created disturbance in the nesting colony, offering Arctic Skuas opportunity to take eggs from deserted nests. Other losses were due to female nest desertion during late incubation. Post-hatching losses were negligible.

17 pairs of Barnacle Geese nested on an island adjacent to Lurøya, and pairs were nest prospecting on Lurøya, but were effectively expelled by territorial Brent males.

During nesting, territorial Brent males spent most of the time in vigilance, followed by grazing and resting. Intruding avian predators and other geese were vigorously chased out of the territories. On average females were attentive to their nests 91% of the time. The rest of the time was spent foraging and preening in the territory. During nesting, time off the nest increased.

Food resources on the islands were poor. Moss constituted the staple part of the diet during nesting and post-hatching, but the geese selected *Cochlearia* and *Saxifraga*. In wet moss carpets where most foraging took place, *Cochlearia* was almost completely depleted.

The high predation pressure observed may be the prime factor responsible for the general low reproductive output of the population, as observed in the Danish wintering quarters. It seems that the Barnacle Goose population on Tusenøyane is expanding, and interspecific competition for nest sites and food may arise.

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The population of Light-bellied Brent Goose *Branta bernicla hrota* breeding in Svalbard and wintering in Denmark and northeast England is one of the smallest goose stocks in the world, numbering 3,000–4,000 individuals (Madsen 1984, 1987). It is characterized by a relatively low reproductive success; in the 1980s the proportion of juveniles in the wintering flocks has varied between 1 and 30%, averaging 12% (Madsen 1987; unpublished). The reasons for the bad performance of the population, however, remain unclear.

In previous centuries the population probably counted in excess of 50,000 geese (Salomonsen 1958), and the Brent were distributed all along

the west coast of Spitsbergen, as well as the coasts of the rest of the Svalbard archipelago (Løvenskiold 1964; Norderhaug 1970). The dramatic population decline occurred at the beginning of this century and possibly even earlier, probably resulting from the impact of several combined factors. First, the Brent were almost completely driven away from the breeding islands in the western part of Spitsbergen due to human exploitation of Eider *Somateria mollissima* down (Gordon 1922; Norderhaug 1970). Second, in 1932–33 the staple food source in the wintering grounds, eelgrass *Zostera marina*, died out over most of the coasts of the North Atlantic, and many Brent died either due to starvation or overshooting, the precise history being unclear (Salomonsen 1958; Madsen 1987).

* Communication No. 226 from the Game Biology Station.

Only within the last decades the remaining breeding haunts of the Brent have been found. A reconnaissance trip to Tusenøyane in the south-eastern part of Svalbard in 1969 revealed that this was a very important area (Norderhaug 1974), and in 1985 it was confirmed that the archipelago holds half or even more of the breeding population (Persen 1986). Therefore, also the information about the breeding ecology of the Brent in Svalbard is very scant. Roi (1911) reported notes on their diet, Løvenskiold (1964) reviewed what was known about nesting and hatching dates, and Nyholm (1965) presented data about nest predators and diet.

In the summer of 1987 the Norwegian Polar Research Institute in collaboration with the Game Biology Station, Denmark undertook a study of the breeding ecology and behaviour of the Light-bellied Brent Geese on Tusenøyane. The aim of the study was 1) to identify factors on the breeding grounds which can contribute to the low and varying reproductive output in the population, and 2) to achieve as much basic knowledge as possible of breeding ecology and behaviour.

In this paper we present data on population composition and breeding success, behaviour during nesting, and diets and exploitation of vegetation zones. A study of post-hatching behaviour will be reported later.

Field work was carried out by Jesper Madsen and Thomas Bregnballe in the period 13 June to 30 July.

Study area

Habitat

The study was carried out on Lurøya and adjacent islands in the Tiholmane island group of Tusenøyane (Fig. 1). The islets are all low and rocky with varying degree of vegetation cover; in this respect Lurøya is outstanding with approximately 60% cover (visually estimated). With its 3.8 km² Lurøya is the largest of the islets. Along the northern and southeastern coast of Lurøya the underlying rock forms ridges, reaching a peak height of 13 m. Between the ridges there is a central low plain, extremely rich in ponds and wet marshes and intervened by gravel heaps and rocky outcrops.

Two vegetation zones predominate on the island: 1) a wet moss carpet with *Bryum* spp., *Philonotis* spp., *Drepanocladus* spp., *Mnium* spp.

and *Andraea* spp. with protruding *Cochlearia officinalis*, and more patchily, *Saxifraga hyperborea*; 2) a fjellmark dominated by mosses and lichens with varying densities of *Saxifraga caespitosa*, *S. oppositifolia* and *Cochlearia*.

In both marshes and fjellmark *Carex subspathacea* and *Phippsia* spp. are irregular. Marshes vary in degree of wetness, and *Cochlearia* is found at highest densities in the transition zone between the wet moss carpet and the fjellmark and in some fjellmark zones. In total we found five species of dicotyledones and 2–3 species of monocotyledones on the island.

On the adjacent Kalvøya the study area comprised a coastal plain with a sparse moss vegetation and protruding *Saxifraga hyperborea* and a small wet marsh fringing a creek. The plain is surrounded by slopes above which there is a plateau with rocky outcrops.

Weather, snow and ice conditions

On our arrival 13 June snow cover was complete in the central plain (Fig. 2), whereas on the ridges it varied between 20 and 80% in coverage. During the following week, snow melt proceeded very fast, and on 25 June the island was almost snow free, apart from the snow leighs. During a snow storm 1–2 July, lasting 18 hours, half the plain became snow covered again. Snow clearance was, however, fast during the following days. In June temperatures varied between –4° and 4°C, in July between –2° and 7°C. In mid June there was dense drift ice in the surrounding Barents Sea. Until mid July there were varying densities of drift ice (usually more than 20% coverage) surrounding Lurøya, whereafter there was virtually no ice.

Potential predators

Potential avian predators to the Brent on Lurøya were: Glaucous Gull *Larus hyperboreus* with 10 breeding pairs on the island, Arctic Skua *Stercorarius parasiticus* with four pairs, and more irregularly non-breeding individuals of Pomarine Skua *Stercorarius pomarinus*, Long-tailed Skua *Stercorarius longicaudus* and Great Skua *Stercorarius skua*. On Kalvøya there was one nesting pair of Arctic Skua and four pairs of Glaucous Gulls.

Polar Bears *Ursus maritimus* were regular on the island while there was drift ice. Bears were

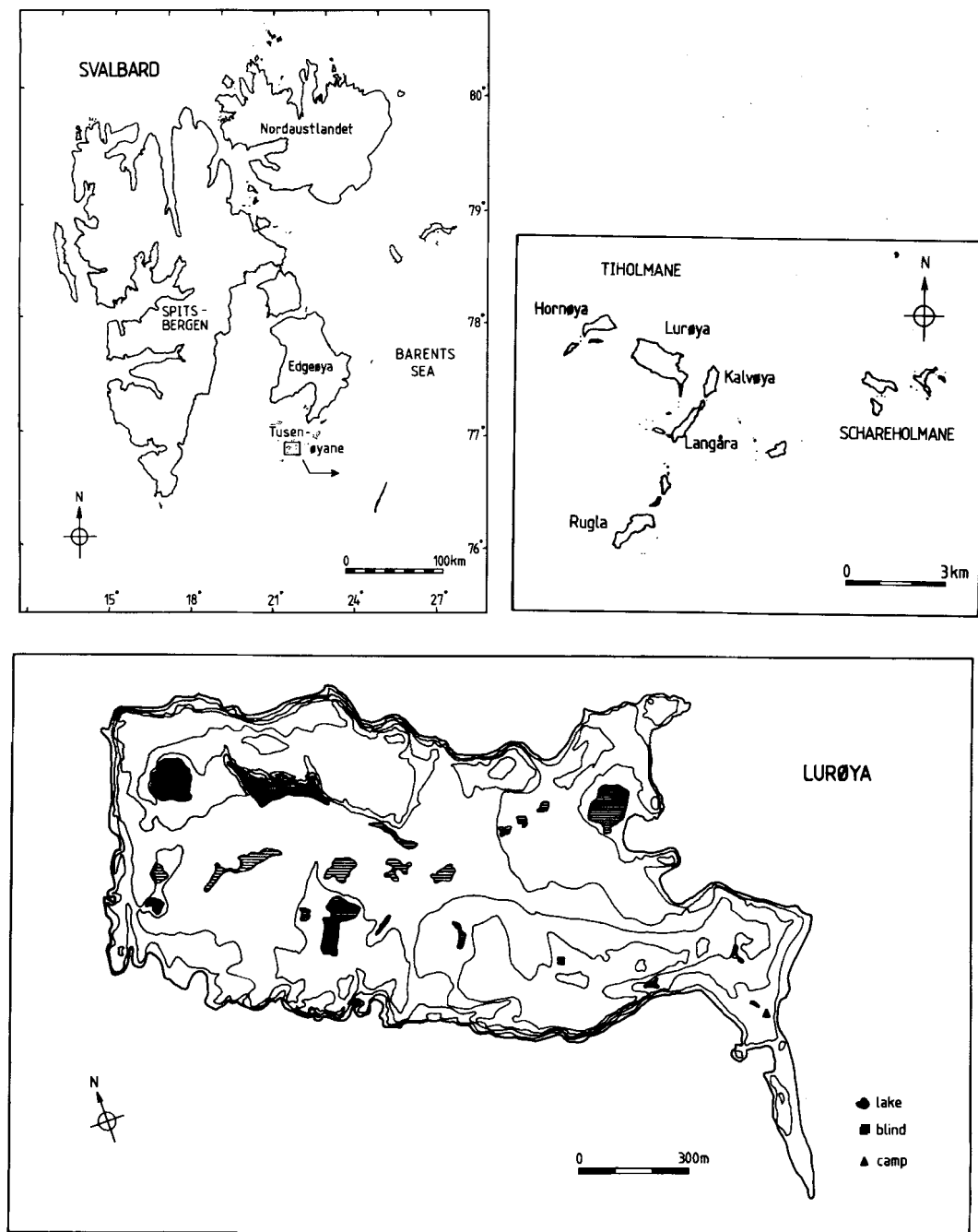


Fig. 1. Study area. On the map of Lurøya 2 m contour lines are shown.

present on the island on average every other day between 14 June and 12 July, and at least 11 different adult or subadult individuals were observed. After the disappearance of drift ice, no bears were recorded. Following their activity and

movements, it was our impression that the bears were not attracted to the island due to our presence, but went on land to rest or search for food (robbing eggs in birds nests). They stayed on the island for relatively short time. According to

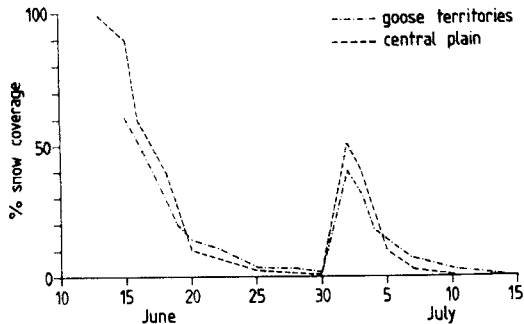


Fig. 2. Progression of snow clearance on Lurøya, expressed for 18 goose territories and the central plain, respectively (visual estimates).

Larsen (1986), polar bears meet on Tusenøyane because they follow the retreating drift ice on their spring migration towards northeastern Svalbard.

Methods

Nest records

Efforts were put into identifying all nesting pairs and their nests on Lurøya. As our movements were very restricted due to fear of disturbance, early records were made from the blind and a few observation points in the terrain. To record the fate of nests the attendance of pairs was controlled regularly. In the middle of the nesting period all known nests were visited once to record clutch sizes. It should be stressed that this action did not cause any egg losses to predators. At the time of hatching, nests were monitored intensively to record time of hatching and brood sizes. Start of incubation and start of egg-laying were extrapolated from hatching dates and known clutch sizes, using 24 days as standard incubation period (Barry 1962), and one day as interval between eggs laid.

After hatching, all nests were revisited and mapped on a sketch map (1:7,000), and inter-nest distances paced out. Territory borders were drawn from our knowledge of male movements.

Observations of territorial males and nests were also made on pairs nesting on the western slope of Kalvøya, approximately 600 m from our camp. From 22–30 July we visited the other islets of *Tiholmane* and *Schareholmane* by boat. On all islets we systematically searched for deserted

goose nests and counted the number of goose families and the number of non-breeding geese.

Activity budgets during nesting

Throughout the nesting period we recorded activity budgets of males, females and non-breeding birds, as well as territorial interactions and predator activity. Throughout the article adults without a nest are referred to as non-breeders, although they include failed breeders.

Observations were made from a blind on top of the southern ridge. A total of 15 nesting pairs was monitored, but never more than 11 pairs at a time. Due to nest predation, sample size decreased to six pairs in the second half of the nesting period. Distances between blind and nests ranged from 150 m to 800 m. All observations were carried out using telescopes (20–60x).

Observations were carried out from 14 June to 7 July. The nesting period was divided into 5-day periods. Within each period the 24 hrs were covered by observations at least once, and mostly 2–3 times. However, effective coverage was at times hindered by presence of polar bears at the blind or in the camp.

All territories under observation were scanned at intervals of 10 minutes, and the following parameters were recorded for male and female, respectively:

- 1) Activities, divided into grazing, resting (including females resting while incubating), preening, vigilance in head up posture and extreme head up posture, respectively (for definition, see Inglis 1977), agonistic encounters with head in forward position, flight, pursuit flight, and nest adjustment. Activities of non-breeding birds were recorded in the same way as for nesting geese. Duration of goose recesses from the nests was timed.

- 2) The male's distance from the nest, estimated to the nearest 10 m, and the same for the female when off the nest. When the female was off the nest, distance between the mates was also recorded. Estimated distances were corrected after hatching, when territory sizes were paced out.

- 3) The choice of feeding patch, estimated by the position of the feeding birds in relation to the nest.

- 4) The substrate of the feeding birds, roughly grouped into moss carpet, transition zone between moss carpet and fjellmark, and fjellmark.

Parameters 3) and 4) were only recorded in the second half of the nesting period. Between scans territories were surveyed for passing potential predators. In case of a passage the following were recorded: Activity of the predator, its estimated distance to the nest, activity of male, and if possible of female, before predator passage, and intensity of response. To quantify the response of nesting pairs to avian predators passing over the territory activities were given a 'vigilance score', related to the degree of vigilance:

| | |
|--------------------------------------|---|
| Graze, preen, rest | 0 |
| Vigilance in head up posture | 1 |
| Vigilance in extreme head up posture | 2 |
| Threat, standing | 3 |
| Threat, running towards predator | 4 |
| Pursuit flight towards predator | 5 |

Aggressive encounters between nesting pairs and non-breeders were recorded, including intensity and outcome (following method by Boyd 1953).

Feeding bout length, pecking rate (measured as the time it takes to make 25 pecks) and walking rate (time to make 10 steps) were timed on stop-watch for males, females and non-breeders.

Nominal variables (time budgets, activities) were analysed by chi-square statistics, firstly by comparing whole time budgets (number of scans) with as many degrees of freedom as possible, secondly by comparing single activities. Trends in nominal data (diurnal changes, changes during the period) were tested by chi-square statistics and Spearman rank correlation analysis.

Post-hatching observations

Families were kept under observation during the period 6 to 27 July, and brood sizes were recorded at regular intervals. Stage of moult was recorded by observations of missing remiges or escape behaviour.

Analysis of diet

Food selection by the geese was assessed by direct observation of food plants and plant parts ingested, and by examination of droppings. Droppings were collected from territories and from sites grazed by non-breeding Brent Geese and Barnacle Geese. After hatch dropping samples of parent geese and goslings were separated (droppings distinguished by size differences). Samples

were preserved in 70% ethanol for later analysis. In the laboratory the composition of the diet was determined by microscopical identification of epidermal fragments, following a point-quadrat sampling procedure (for method see Owen 1975). The point quadrat method will bias the diet composition in favour of mosses, as mosses fragment much more than epidermis of vascular plants during gut passage (Derksen et al. 1982). To adjust for this, only moss fragments of at least 20 cells were included in the counts.

Vegetation analyses

Species composition of vegetation zones was described by pin-point analyses. Along a main transect 10 secondary transects were laid at 1 m intervals. Secondary transects were 2 m long with hit points at 10 cm intervals, i.e. totalling 210 hit points per main transect.

To estimate goose exploitation rates of *Cochlearia* plants, density of plants was assessed in areas grazed by nesting pairs. Along transects plants were counted in 20 × 20 cm² plots, and grazing intensity of individual plants recorded, either by the proportion of the rosette removed, or by the number of plants, including roots, removed. The latter was detectable by holes in the moss carpet, where the geese had been probing for whole plants, usually leaving part of the root behind. Sampling was carried out in the second half of the nesting period and immediately after hatching.

Results

The Tiholmane-Schareholmane goose populations

Brent Goose. – Nest surveys on the islands revealed a total of at least 98 pairs of Brent attempting to nest (including three disturbed by us; Table 3). Largest numbers were found on Lurøya, followed by Kalvøya. 23 families and 120 non-breeding birds were recorded on the islands. A crude estimate of hatching success is given by the ratio of the number of families and the number of nests, being 0.24 (excluding the three disturbed nests). Of course, some nests have probably escaped our attention, although we believe to have located the majority. On the other hand, the recorded number of families is in the lower

end. Therefore, the estimate of hatching success appears realistic.

Barnacle Goose. – On Lurøya single pairs were observed in the second half of June but numbers varied much between days (up to 12). 1–2 pairs were often observed on the northwestern ridge from 18–29 June, possibly nest prospecting. They were, however, driven off by territorial Brent males (see p. 12).

On the adjacent Hornøya up to 28 Barnacle Geese were seen in the second half of June. In early July a flock of 26–28 geese built up on Lurøya-Kalvøya, and from 10–12 July this flock, now counting 22 birds, started to shed remiges.

23 July Hornøya was surveyed, and a nesting colony of Barnacle Geese was found on the south-eastern slope, where the geese had been seen in June. Eight females were still incubating, and another nine predated/deserted nests were found.

Clutch sizes were: 4 nests with 2 eggs, 3 with 4 eggs, and 1 with 5 eggs, averaging 3.1 eggs per female. Nests were placed on rocky outcrops on a moss carpet. Inter-nest distance ranged between 15 and 25 m. We found no families. 29 July Hornøya was revisited, and three families with newly hatched goslings were observed. Four females were still incubating. Hence, egg-laying seems to have commenced during the first days of July.

Nesting Brent Geese on Lurøya and Kalvøya

Nest sites and territories. – We estimated that there were 38 nesting pairs on Lurøya in mid June. Unfortunately, three nests were disturbed and predated by Arctic Skuas as we pitched camp and put up the blind, and these have been omitted from the analysis. 29 nests were localized during the nesting period, and another six territorial pairs were identified, of which we found nests of

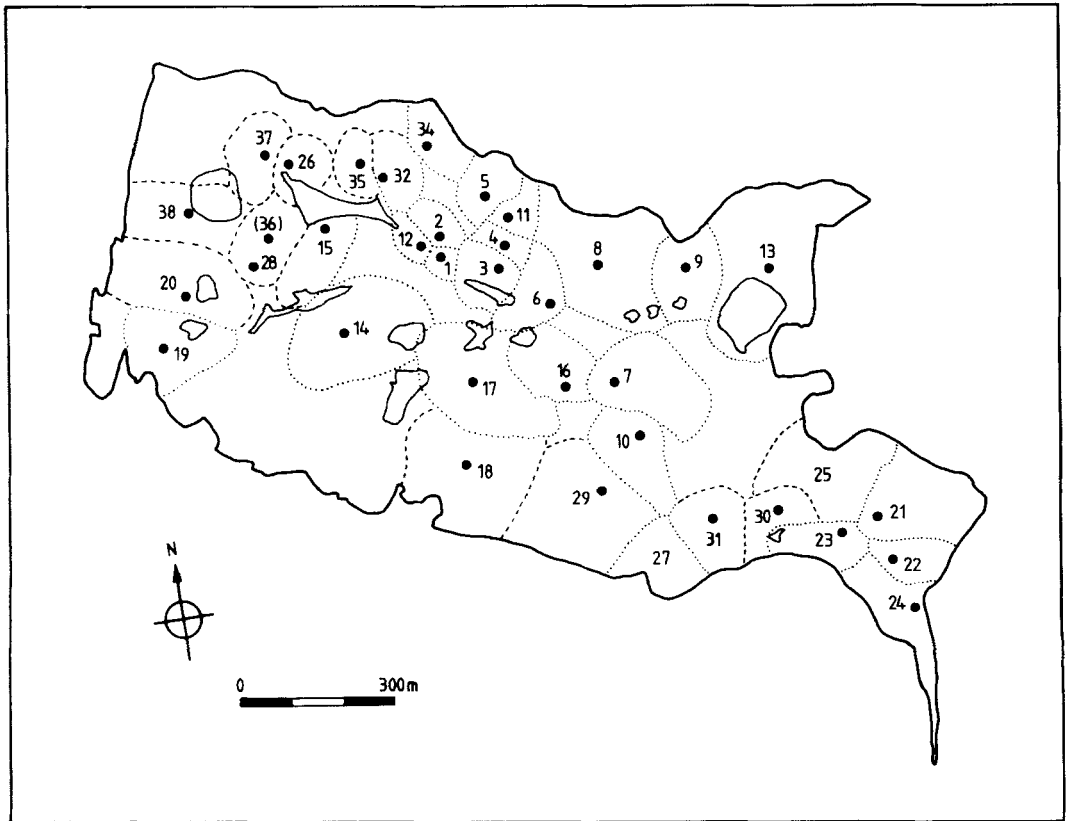


Fig. 3. Distribution of territories and nests on Lurøya in mid June. Stippling indicates that territory boundaries are not exactly known. Nest no. 2, 7, 15, 16, 17, 18, 19, 20, 21 and 32 were successful.

Table 1. Breeding phenology of Brent Geese on Lurøya and Kalvøya, 1987.

| | Median date | Range | N |
|---------------------|-------------|------------|----|
| Start of egg-laying | 10 June | 8–21 June | 17 |
| Start of incubation | 15 June | 11–25 June | 17 |
| Hatching | 7 July | 4–18 July | 17 |

the four after hatch. The distribution of nests and territories is shown in Fig. 3. Highest densities were found on snow-free ridges. Most nests were placed on elevated points in the terrain like hummocks, between rocks on gravel heaps, often quite unsheltered from the wind.

In mid June inter-nest distance (nearest neighbour distance) ranged from 38 m to 253 m, with an average of 120 ± 9.6 S.E. ($n = 34$). For 25 territories there was sufficient documentation of territory borders. Territory size ranged from 0.3 ha to 6.1 ha, with an average of $2.0 \text{ ha} \pm 0.3$ S.E. Later during nesting, when many nests had been lost due to predation – and the territories subsequently abandoned (see below) – the neighbouring pairs took over the area. In one case a male took over the neighbouring territory the day after it had been abandoned, expanding its territory from 2.8 ha to 4.8 ha. Another territory was expanded from 0.7 ha to 2.1 ha.

Breeding phenology. – Data on timing of breeding are presented in Table 1 and hatching dates shown in Fig. 4. Included are data from six nesting pairs on the adjacent island Kalvøya. For 12 nests we know the time of hatching, and for five families

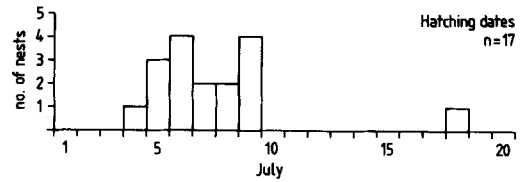


Fig. 4. Hatching dates as observed in 12 nests, extrapolated from age of newly hatched young in five broods.

we extrapolated hatching date based on gosling size (only when 0–4 days of age). Extrapolation of the date of laying of the first egg indicates that the timing was very synchronous, with 10 June as median date. First hatching date was 4 July, median date 7 July.

Nest success. – Clutch size was recorded in the middle of the nesting period for 12 nests: 5 nests had 3 eggs, 3 had 4 eggs, and 5 had 5 eggs, averaging 4.0 eggs per female. For the purpose of calculating the total nesting success on the island we made the assumption that the remaining 23 nests which were not visited contained four eggs on average.

Of the 35 nests at the start of incubation only 10 hatched eggs (28.6%, Table 2), and of an estimated 140 eggs at start, 36 hatched (25.7%). The majority of losses was attributed to predation (62% of all eggs), polar bears and Arctic Skuas taking an almost equal share of the eggs. Glaucous Gulls, which are known to be heavy predators on Brent Goose and Barnacle Goose eggs in western Spitsbergen (Nyholm 1965; Prop et al. 1980, 1984), showed astonishingly little interest in the goose nests, seldom crossing the island or search-

Table 2. Goose populations on Tiholmane and Schareholmane, summer 1987.

| | Brent Goose | | | Barnacle Goose | | |
|--------------------|-------------|-----------------|--------------|----------------|------------------|--------------|
| | Nests | Families | Non-breeders | Nests | Families | Non-breeders |
| Lurøya | 38 | 11 | 12 | | | |
| Kalvøya | 11 | 7 | 22 | | | 21 |
| Langåra | 5 | 1 | 2 | | | 18 |
| Islet W of Langåra | 1 | | | | | |
| Rugla | 10 | | 45 | | | |
| Islet N of Rugla | 2 | | | | | |
| Islet E of Kalvøya | 11 | 2 | 25 | | | |
| Hornøya | 4 | | | 17 | 4–7 | 6 |
| N Schareholme | 10 | 2 | 18 | | | |
| W Schareholme | 4 | | | | | |
| E Schareholme | 2 | | | | | |
| Total | 98 | 23/ 69 pulli | 124 | 17 | 4–7 11+ pulli | 45 |

Table 3. Estimated hatching and nesting success of Brent Goose nests on Lurøya, summer 1987. Notes: 1. Number of eggs has been estimated from a mean clutch size of 4.0 eggs in nests in the middle of the incubation period. 2. Excluding nests disturbed by observers.

| | Nests | Eggs |
|---|-------|------|
| Start of incubation period ¹ | 38 | 152 |
| Disturbed by observers | 3 | 12 |
| Predated by polar bears | 12 | 48 |
| Predated by Arctic Skuas | 9 | 39 |
| Deserted following snow storm | 4 | 11 |
| Hatching failure | | 6 |
| Hatched | 10 | 36 |
| % hatching ² | 28.6 | 25.7 |

ing for nests. They appeared almost exclusively to be feeding in the drift ice.

By themselves the Arctic Skuas did not seem to pose a severe threat to the goose nests during incubation. Males responded vigorously towards passing skuas (see p. 19), and we only observed one nest which was partially predated by an Arctic Skua during a goose recess. However, skuas were immediately present in case of disturbance and effectively utilized the situation as described below.

On three occasions we observed polar bears searching for goose and Eider Duck nests on Lurøya. One case deserves a more detailed description as it illustrates how skuas took advantage of the presence of the bear. 16 June a female polar bear and a cub of the year traversed the northwestern ridge. The adult bear walked, seemingly at random, back and forth along the snow free rocky outcrops where several goose nests were situated. Two types of goose reactions were recorded. Some geese left their nests at long distance, others stayed on the nest. The bear only found the nests by flushing the geese, usually at a distance of 5–10 m. During its 50 minutes stay on the slope, the bear emptied four goose nests. However, another four geese which left their nests at long distance lost their eggs to 2–3 skuas which were constantly patrolling the slope while the bears were there.

Thus, although skuas took 39 eggs in total, we estimate that 36 were taken in connection with polar bear presence, eggs which would not have been predated otherwise. Thus, in total 84 eggs (60% of all eggs) were lost due to the presence of bears.

For six nests predated by bears and 12 nests not predated by bears, respectively, we have data

on territory size of the nesting pairs and snow coverage in the territories in mid June, when most bear predation took place. There was no significant difference in territory size of pairs suffering from predation and of pairs whose nests were not subjected to bear predation (mean size 1.41 ha and 1.82 ha, respectively, Mann-Whitney U-test, $U = 42$, $P > 0.1$). For pairs suffering from bear predation there was a significantly higher degree of snow coverage in the territories than for pairs which did not have their nests predated (mean coverage 62% and 39%, respectively, $U = 13$, $P < 0.05$).

Following the snow storm on 1–2 July, four females deserted their nests. One incubating female was completely covered by a 30 cm deep snow leigh.

On Kalvøya six nests and one territory were localized when observed from Lurøya. Two nests were predated (predator unknown), one nest abandoned following the snow storm, and one territory abandoned, probably due to predation of the nest. A total of seven goslings hatched from the remaining three nests. Assuming that there was a total of 28 eggs at the start of incubation, 25% of the eggs hatched. On Hornøya 3–4 territorial males were observed during early incubation. By the end of June none of them could be found, despite intensive observation from Lurøya.

Post-hatching losses. – From hatching onwards to 30 July brood sizes were regularly observed on Lurøya and Kalvøya. 10 July three families with newly hatched goslings swam from Langåra to Lurøya and on to Kalvøya. Apart from this observation it was our impression that there was only a minor exchange of families between the islands. Hence, the seen broods were most probably the same throughout July. The number of broods counted during July was stable, and mean brood size was 3.00 ($n = 23$). During July, there was no decrease in brood sizes.

Moult. – Non-breeding Brent Geese started moult of remiges around 13 July and three days later all had lost flight ability. The first parents started moult around 15 July, and 22 July the majority was flightless.

Behaviour during nesting

Behaviour of the female. – Nesting females spent

Table 4. Overall diurnal time budgets (in %) of nesting male and female and non-breeding Brent Geese during the incubation period. For male and female time budgets are specified for situations 1) where the female is on the nest, 2) where the female is off the nest, 3) where eggs are hatching. Note 1: Includes females resting while incubating.

| Activity | Graze | Rest ¹ | Preen | Vigilance Head up | Vigilance Extreme head up | Threat Head forward | Running attack | Flight | Pursuit flight | Nest adjust | No. of scans |
|------------------------------|-------|-------------------|-------|----------------------|---------------------------------|---------------------------|-------------------|--------|-------------------|----------------|-----------------|
| <i>Male during nesting</i> | | | | | | | | | | | |
| Overall | 31.1 | 15.4 | 3.8 | 25.9 | 18.4 | 0.6 | 1.8 | 1.3 | 1.7 | 0 | 3,873 |
| Female off nest | 10.6 | 0.5 | 0.8 | 10.1 | 69.3 | 1.0 | 3.1 | 1.8 | 2.8 | 0 | 387 |
| Female on nest | 33.8 | 16.3 | 3.9 | 29.4 | 11.6 | 0.5 | 1.7 | 1.1 | 1.7 | 0 | 3,486 |
| <i>Male at hatching</i> | | | | | | | | | | | |
| Overall | 6.1 | 15.7 | 1.7 | 45.2 | 26.1 | 3.5 | 1.7 | 0 | 0 | 0 | 115 |
| <i>Female during nesting</i> | | | | | | | | | | | |
| Overall | 6.4 | 83.8 | 7.7 | 0.2 | 0 | 0 | 0 | 0.2 | 0 | 1.7 | 5,201 |
| Female off nest | 85.0 | 0 | 10.2 | 2.0 | 0.3 | 0 | 0.3 | 2.2 | 0 | 0 | 388 |
| Female on nest | 0 | 90.5 | 7.5 | 0.1 | 0 | 0 | 0 | 0 | 0 | 1.9 | 4,813 |
| <i>Female at hatching</i> | | | | | | | | | | | |
| Overall | 1.3 | 84.9 | 7.9 | 2.0 | 0 | 0 | 0.6 | 0.6 | 0 | 3.3 | 152 |
| <i>Non-breeding geese</i> | | | | | | | | | | | |
| Overall | 53.3 | 23.5 | 8.8 | 9.4 | 0.5 | 0.5 | 3.1 | 3.1 | 0 | 0 | 2,647 |

the majority of their time incubating and the remaining time was spent preening, grazing and nest adjusting, including egg rolling (Table 4). The females were never seen in pursuit flight, and they were rarely vigilant. The most frequent activity of incubating females was resting, followed by preening, which was most frequent shortly after nest recesses. There was no significant difference in the overall time budget during the 24 hrs (chi-square = 4.34, df = 10, $P > 0.05$), or during the incubation period (chi-square = 11.1, df = 8, $P > 0.05$).

Overall time budgets during nesting and at hatching were not significantly different (Table 4, chi-square = 3.24, df = 5, $P > 0.1$). Hatching was defined as the period from the first sight of a pullus in the nest to the first movement of the family away from the nest (range 8 to c. 36 hrs).

When the females left their nest they covered the eggs with down. The females spent 85.0% of their recess time grazing and 10.2% preening (Table 4). After a grazing break the females sometimes flew back to the nest to preen before resuming incubation. There was no significant change in recess time spent grazing (chi-square = 5.35, df = 5, $P > 0.10$). In the five most studied females (each scanned more than 700 times) there was no significant individual difference in recess time spent feeding (chi-square = 2.63, df = 4, $P > 0.10$).

Nest attentiveness of all females was 90.9% for the whole incubation period (calculated as mean of total attentiveness in five 5-day periods, 895 hrs monitored, 3-14 females were followed in each 5-day period). Two females monitored from start of incubation to hatching were attentive to their nests for 91.4% of the time (176 and 194 hrs monitored, respectively, the number of monitored hours evenly distributed throughout the incubation period).

Generally, nest attentiveness decreased during incubation, although the pattern of change differed between individual females (Fig. 5). In the days after the snow storm (1-2 July) two of the five females shown in Fig. 5 stopped incubation, one of which had already decreased attentiveness to 76% of the time on the day before the snow storm. Two females observed during 24 hrs before hatching were very attentive to their nests, viz. 97% and 100% of the time, respectively.

The decrease in nest attentiveness during the incubation period primarily resulted from females increasing the number of recesses per day,

whereas the length of recesses did not change significantly (Fig. 5). The average recess frequency for all females was 6.7 per day ($n = 234$, calculated as mean of the frequency in each 5-day

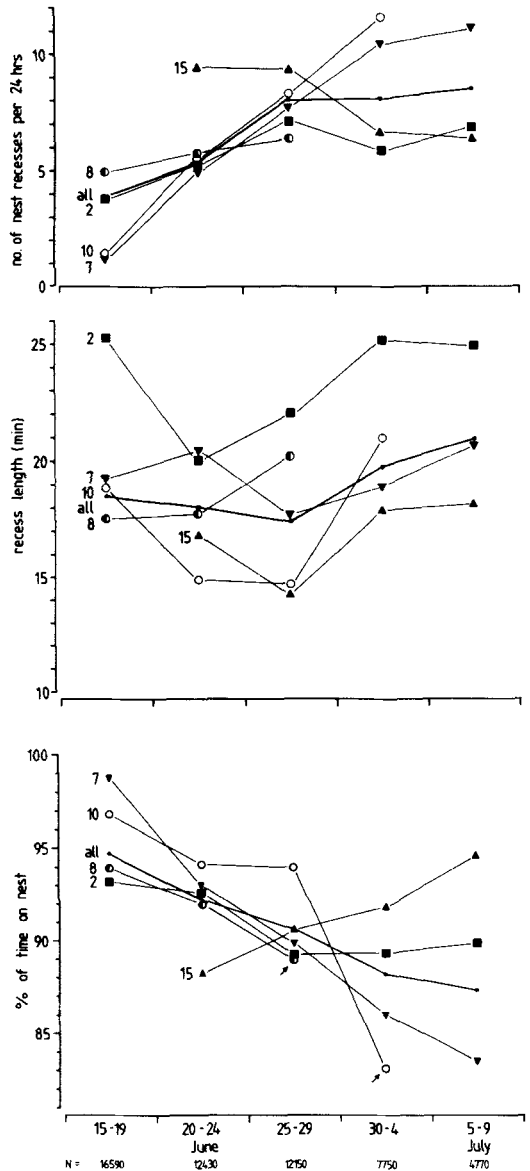


Fig. 5. Change in nest attentiveness, recess frequency and recess length in five individual Brent Goose females, and average for all females under observation (n varying from 3 to 14). Arrows indicate that females deserted the nest before hatching. Figures denote which territory females came from. N is the total number of observation minutes. The decrease in average nest attentiveness during incubation is significant ($r_s = 1.00$, $P = 0.01$), and so is the increase in recesses per 24 hrs ($r_s = 0.90$, $P = 0.05$), whereas there is no significant development in recess length.

period). Mean recess length was $19.2 \text{ min} \pm 0.42 \text{ S.E.}$ ($n = 218$, range 5–50 min). 93% of all recesses lasted 12–30 min.

Females were least attentive to their nests during mid-day (89.1%, 08–16 hrs), more attentive in the evening (93.4%, 16–24 hrs), and most attentive during night (95.1%, 00–08 hrs). This diurnal change in attentiveness was a result of more frequent and longer recesses during daytime than at night (Fig. 6).

Behaviour of the male. – The three most frequent activities, calculated for the whole nesting period, were vigilance, feeding, and resting (Table 4). Vigilance postures extreme head up and head up were displayed in almost equal proportions of the time.

When females left the nest to feed males increased vigilance from 41% to 79% (Table 4). The increase was brought about by more frequent use of the extreme head up posture (chi-square = 812, $df = 1$, $P < 0.001$), whereas the use of the head up posture decreased (chi-square = 64.9, $df = 1$, $P < 0.001$). As a result of increased

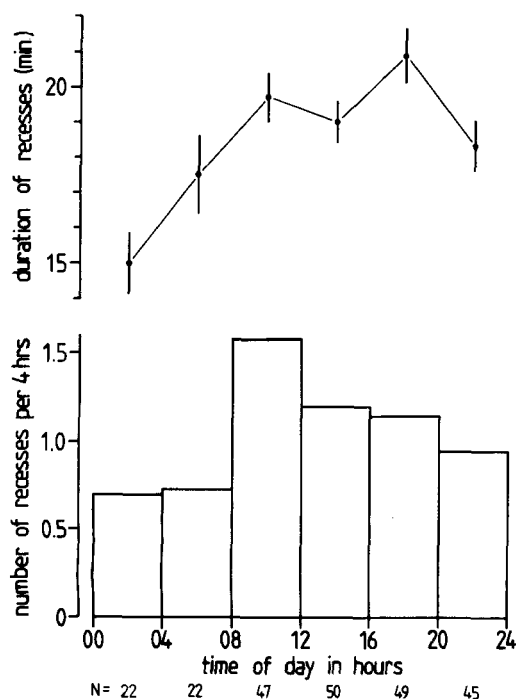


Fig. 6. Diurnal variation in mean duration of female nest recesses and mean number of recesses per four hours. N is the number of recesses, vertical bars are 95% confidence limits.

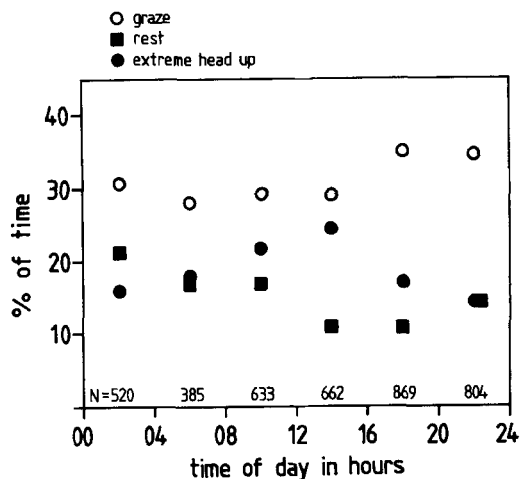


Fig. 7. Diurnal variation in grazing, vigilance in extreme head up posture and resting by territorial Brent male during nesting. N is number of scans.

vigilance, frequency of feeding decreased (chi-square = 84.3, $df = 1$, $P < 0.001$).

Among the most frequent activities there was diurnal variation in vigilance in extreme head up posture and resting (Fig. 7; chi-square = 34.4, $df = 5$, $P < 0.001$, and chi-square = 43.6, $df = 5$, $P < 0.001$, respectively), whereas there was no significant change in the frequency of grazing and vigilance in head up posture. Vigilance in extreme head up posture peaked during daytime and reached a lowpoint at night; resting showed the opposite pattern.

Over the nesting period the only significant change in time allocation was vigilance in extreme head up posture which increased (chi-square = 22.6, $df = 4$, $P < 0.001$).

At hatching male time devoted to feeding decreased compared to the nesting period (chi-square = 33.0, $df = 1$, $P < 0.001$), whereas vigilance in extreme head up and head up postures increased (chi-square = 5.94, $df = 1$, $P < 0.05$, and chi-square = 23.5, $df = 1$, $P < 0.001$, respectively).

Response to avian predators. – When potential avian predators were absent from the territories and the females were on the nest, males attended an 'average' vigilant score (see 'Methods') equivalent to the head up posture (Fig. 8A). When a skua or a Glaucous Gull flew over the territory or landed in it, males responded by increased

vigilance or direct pursuit flight for the predator. In 41.6% of observed predator passages ($n = 202$) males responded by chasing the predator in accelerating flight. Predators were mostly chased to the territory border, but sometimes also into neighbouring territories, releasing pursuit of predator and intruding male by the territory holding male. During the nesting period, intensity of response to predators did not change significantly (chi-square = 9.93, $df = 6$, $P > 0.05$).

In nesting females vigilance levels were zero according to the 'vigilance score'. When predators intruded the territory, females usually did not respond at all, and were never observed to increase vigilance. In a few instances they stretched head and neck along the ground.

At hatching the males' intensity of response to predators decreased significantly compared to nesting (Fig. 8A; chi-square = 8.05, $df = 1$, $P < 0.01$). The 'average' response was vigilance in extreme head up posture compared to walk/run head forward during nesting; at hatching no males were observed chasing predators.

During female nest recesses the vigilance level

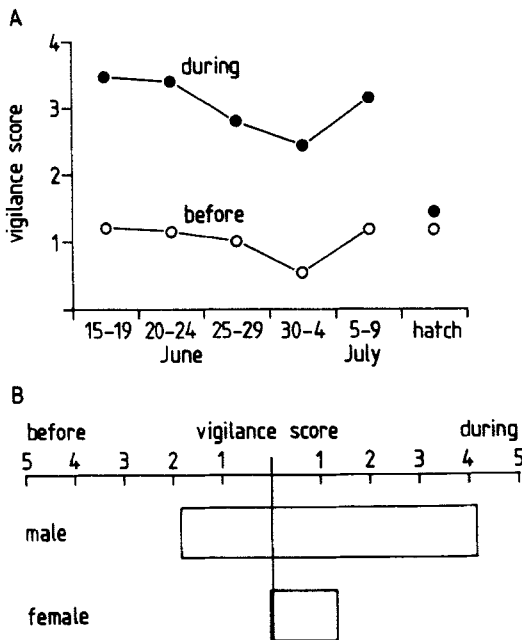


Fig. 8. Vigilance in nesting Brent Geese expressed by a 'vigilance score' (see 'Methods'). A: Change in average vigilance of males prior to and during avian predator passage, while the female is on the nest. B: Response to avian predators by male and female, when the female is off the nest.

of the male increased to an 'average' equivalent to vigilance in extreme head up posture (Fig. 8B). When predators intruded the territory, males responded vigorously, in 44.7% of the instances ($n = 38$) by pursuit flight, in 7.9% of the instances by flying to the nest to guard it. During recesses, females performed non-vigilant activities. When predators approached, 'average' vigilance level in females increased (Fig. 8B), but in 71.4% of the instances ($n = 42$) females continued the non-vigilant behaviour. In 21.4% of the instances females stopped the former activity and flew back to the nest. Females were never seen chasing predators.

Intra- and interspecific interactions. – During the nest phase territorial males were frequently involved in intra-specific interaction with intruding non-breeders or neighbouring males. 74 encounters were recorded; 63% involved a pursuit flight by the male, which sometimes ended in fights with direct bodily contact. In the remaining 37% of the encounters males walked or ran head forward towards the intruder(s). In all encounters with non-breeders ($n = 42$) territory holding males defeated the intruders. In 92% of encounters with intruding territorial males ($n = 32$) the territory holding bird won; in the remaining 8% the territory holding male had to retreat to the centre of the territory. However, none of the encounters resulted in males being replaced.

A total of 10 encounters was recorded between territorial Brent males and pairs of Barnacle Geese. In five situations the male responded by pursuit flight upon intrusion, in the other five by threat postures. In eight situations the males chased the Barnacle Geese out of the territory; in two situations the male eventually accepted the presence of Barnacle Geese in the territory.

Spacing in territory. – During nesting, males usually stayed 20–80 m away from the nest. In two territories followed over most of the nesting period until hatching males remained at distance until shortly before hatching (Fig. 9). Only on the day of hatching, or the day before, the males came close to the nest. The drop in distance observed on 3 July for the two males was probably related to increased snow cover following the snow storm on 1–2 July.

During recesses from the nest, females usually stayed in the territories to feed and preen. When the female flew from the nest, the male normally

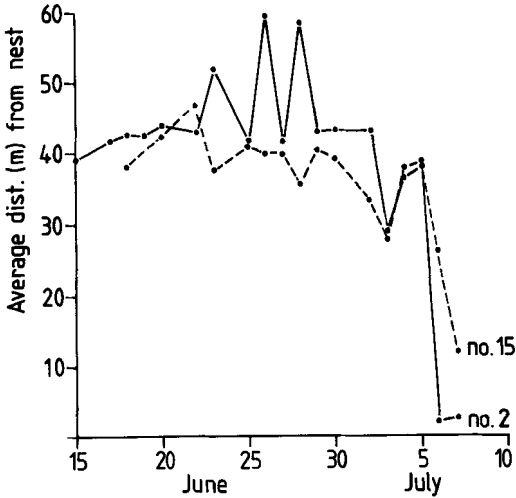


Fig. 9. Daily mean distance to nest for two territorial Brent males. In both hatching took place 7 July.

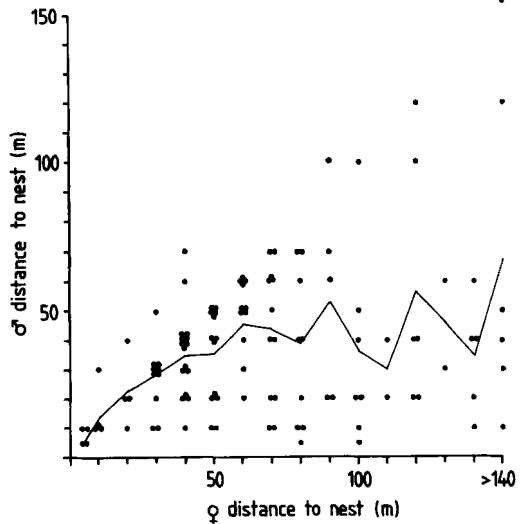


Fig. 10. Relationship between male and female distance to the nest during female nest recesses (data from six territories during second half of incubation). Line shows average male distance; $r_s = 0.299$, $n = 116$, $P < 0.05$.

left its position to follow its mate. One male (territory no. 15) usually flew to one position from where both nest and female could be monitored. Average distance between the sexes varied between 13 and 18 m in four pairs; in another pair (territory no. 2) the average distance was 45 m. In situations where a female walked to the borders of the territory, and in the second half of incubation sometimes also outside the territory, the male usually remained closer to the nest (Fig. 10). The correlation between male and female distance to the nest indicates that males actually followed females, and did not just keep a constant distance to the nest. From the first to the second half of incubation the average male-female distance increased significantly from 10 m to 28 m ($t = 4.30$, $P < 0.001$).

Feeding zones of males and females were mapped for three territories, where geese were sufficiently visible from the blind (Fig. 11). Although sample size for females is small, it is representative for most of the nesting period. In one of the territories (no. 7) there was a high degree of overlap in zones used by both sexes, whereas in the two other territories (nos. 2 and 15) feeding zones were highly segregated. In territory no. 15 the female foraged mainly in one marsh zone, where the male seldom came to feed, possibly because the nest was not visible from there. In territory no. 2 the female fed outside the territory for most of the time, whereas the male only fed within the territory.

Feeding efficiency. – Feeding bout length in females during nest recesses was five times longer when the male stood near (< 40 m) the grazing female, than when the male stood far away (> 40 m). Mean was $30.9 \text{ sec} \pm 2.5 \text{ S.E.}$ ($n = 82$) vs $6.1 \text{ sec} \pm 0.3 \text{ S.E.}$ ($n = 162$), $t = 9.87$, $P < 0.001$. When females were alone, feeding bout lengths were similar to those of males. Mean for males was $5.8 \text{ sec} \pm 1.5$ ($n = 230$; $t = 0.87$, $P > 0.5$). Females grazed and walked at an accelerated rate compared to males: Average pecking speed (time for 50 pecks) for males was $25.0 \text{ sec} \pm 2.7 \text{ S.E.}$ ($n = 23$) and for females $13.3 \text{ sec} \pm 0.7 \text{ S.E.}$ ($n = 52$) ($t = 4.12$, $P < 0.001$); walking speed (time for 10 steps) for males was $20.0 \text{ sec} \pm 2.2 \text{ S.E.}$ ($n = 36$) and for females $8.9 \text{ sec} \pm 0.6 \text{ S.E.}$ ($n = 184$, $t = 4.86$, $P < 0.001$).

Non-breeders increased their feeding bout length when they changed from grazing in pairs (mean was $5.1 \text{ sec} \pm 0.2 \text{ S.E.}$ ($n = 161$)) to grazing in loose flocks ($20.6 \text{ sec} \pm 2.9 \text{ S.E.}$ ($n = 72$), $t = 5.33$, $P < 0.001$). Non-breeders grazed with the same pecking speed as territorial males (mean for non-breeders was $23.0 \text{ sec} \pm 1.5 \text{ S.E.}$ ($n = 64$, $t = 0.67$, $P > 0.5$)), but walked at a speed in-between females and males ($12.4 \text{ sec} \pm 0.5 \text{ S.E.}$ ($n = 103$)).

Time budget of non-breeding geese. – Most non-breeding geese were paired and aggregated in

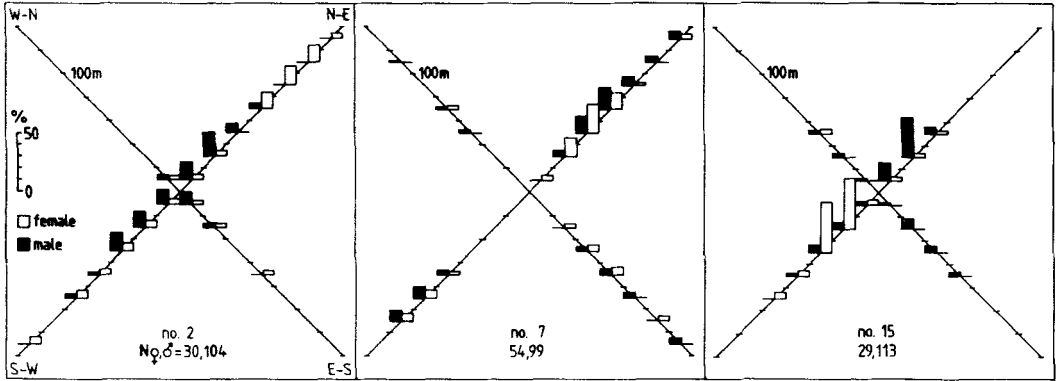


Fig. 11. Feeding zones by males and females in three territories, expressed by proportion of feeding time spent in relation to distance and direction to the nest.

small, loose flocks during the nesting period. Single yearlings occurred among them.

Non-breeders spent 53% of the time feeding (Table 4); other frequent activities were resting, preening and vigilance in head up posture. Vigilance in extreme head up posture was almost non-existent among non-breeders.

Feeding activity varied through the 24 hrs; it was highest in daytime (08–20 hrs) with 56.6% and lowest at night with 49.7% (chi-square = 16.6, df = 5, $P < 0.01$), whereas resting showed the opposite pattern with 18.4% at day and 28.1% at night (chi-square = 50.7, df = 5, $P < 0.001$).

Diet and exploitation of vegetation

Diet during nesting and post-hatching. – In the nesting period droppings were collected from territorial males (two samples), nesting female (one sample) and non-breeding pairs (three samples). Unlike nesting Barnacle females nesting Brent Geese do not defaecate on the fringe of the nests but only during nest recesses, which made it difficult to collect droppings from the females.

Due to the low diversity of plants on Lurøya, the composition of the diet was restricted as well (Table 5). The diet varied from site to site, reflecting differences in feeding habitats. Mosses constituted a staple part of the diet, but the geese selected *Cochlearia*, *Saxifraga* spp. and *Carex* (Fig. 12). On some occasions geese were observed picking flowering buds of *Saxifraga*.

During post-hatching, paired samples of droppings of parents and goslings were collected on three occasions on Lurøya, and on one occasion on Kalvøya (Table 5). Mosses constituted the

staple diet of parents, but they were still selecting *Cochlearia*. In one sample from 27 July mosses made up 99% of the diet (95% of the gosling diet).

In two of the gosling dropping samples there was a striking difference compared to the parents. 10 July the 1–4 day old goslings selected *Cochlearia*, *Saxifraga hyperborea* and *Carex* and took almost no moss, whereas the parents had eaten far more moss and accordingly less *Saxifraga* and *Carex* (Table 5). 22 July 16 day old goslings on Kalvøya selected *Saxifraga hyperborea* and took less moss than the parents did. On the other two dates (12 July and 27 July) parent and gosling diets were more alike.

In three samples of Barnacle Goose droppings (two of non-breeding pairs, one of nesting female) mosses were the most frequent food plants. Judging from the few samples, it seems that food selection of Brent Goose and Barnacle Goose did not differ to a large degree.

Exploitation of Cochlearia. – During the nesting period, Brent Geese heavily exploited the *Coch-*

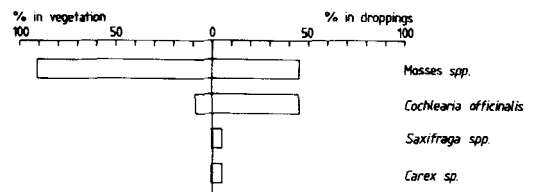


Fig. 12. Food selection by pairs of Brent Geese 22 June 1987 in a marsh zone on Lurøya, expressed by frequency of plant species in droppings and vegetation prior to goose grazing.

Table 5. Diet of geese on Tiholmane, summer 1987, expressed in frequency (%) of plant species in droppings. * indicates that samples are paired (parent and gosling droppings from same site). Note 1: droppings from the same territory. M(male), F(female), P(parents), G(goslings), N(on-breeders)

| Date | Locality | Brent Goose | | | | | | | | | | Barnacle Goose | | | | | |
|------------------------------------|----------|-------------|----|----------------|----------------|----|----|--------|----|----|--------|----------------|----|--------|----|----|---|
| | | M | M | M ¹ | F ¹ | P* | G* | Lurøya | P* | G* | Lurøya | P* | G* | Lurøya | N | N | F |
| Moss spp. | 71 | 52 | 27 | 27 | 49 | 38 | 3 | 40 | 42 | 99 | 95 | 72 | 43 | 56 | 94 | 82 | |
| <i>Cochlearia officinalis</i> | 23 | 12 | 19 | 21 | 47 | 58 | 48 | 14 | 1 | 2 | 1 | 10 | 1 | 10 | 1 | | |
| <i>Saxifraga hyperborea</i> | | 2 | 16 | 10 | 5 | 17 | 12 | 29 | 1 | 1 | 9 | 44 | 18 | 1 | 4 | | |
| <i>S. caespitosa/oppositifolia</i> | | 33 | 4 | 38 | 4 | 10 | 1 | 12 | 1 | 1 | 19 | 12 | 12 | 12 | 14 | | |
| <i>Carex</i> sp. | 6 | 1 | 4 | 16 | 16 | 21 | 21 | 3 | 1 | 1 | 19 | 12 | 4 | 4 | | | |

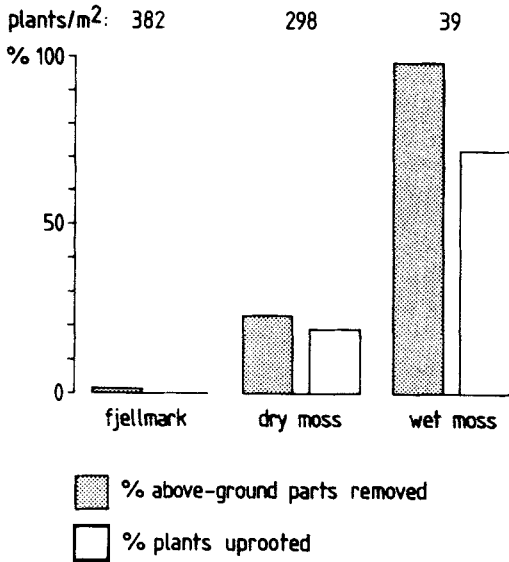


Fig. 13. Exploitation rates of *Cochlearia officinalis* in three vegetation zones by a pair of Brent Geese during incubation. Above the histograms is shown the number of plants per m² prior to grazing. In each vegetation zone between 30 and 45 plots were analysed.

learia plants on the wet moss carpet. Plants were uprooted, and nearly 100% of the rosettes were removed (Fig. 13). In the dry moss exploitation rates were only about 20% of the rosettes, and only 20% of the plants were uprooted; in the fjellmark exploitation was negligible.

In late July exploitation rate of *Cochlearia* at a moulting site of 10 family parties of Brent Geese was estimated two days after the families had abandoned the site and moved on to another. The density of plants was 188 plants per m². 95% of the plants had been grazed, and 34% of the rosette leaves had been removed. The remaining leaves were sitting low in the moss, and appeared to be inaccessible to the geese.

Discussion

Goose populations in southeastern Svalbard: possible implications of predation and interspecific competition

With an estimated number of around 1,000 potential breeding pairs in the population of Svalbard Brent Geese (Madsen unpublished) the Ti-

holmane-Schareholmane archipelago held approximately 10% of the breeding pairs in 1987. From surveillance in 1985 (Persen 1986) it seems that the majority of the population breeds on Tusenøyane, though some pairs also nest in western Spitsbergen (Prestrud & Børset 1984; Black & Owen 1984).

In the Tiholmane-Schareholmane archipelago we documented that the nest success of the Brent Geese was only about 25%. On Lurøya eggs were primarily lost due to predation by polar bears, directly and indirectly accounting for the loss of 60% of all eggs at start (indirectly by giving the skuas a chance of egg predation). From the other islets the breeding results indicate that bears had also been ravaging there. As we arrived at the start of incubation we do not know predation rates in the egg laying phase, and the total predation pressure may thus have been underestimated.

Predation pressure exerted by the bears, together with observations of several bears, presumably searching for nests on the islands, indicate that the polar bear is not an accidental predator on goose nests. There are reasons to believe that polar bears occur all over, with similar behaviour in the entire Tusenøyane archipelago, and therefore pose a severe threat to the breeding output of the major part of the Brent Goose population in years when drift ice is present during incubation. The relationship between drift ice (and ultimately bear predation) and breeding success of Brent Geese will be dealt with in a later report (Madsen & Mehlum unpublished).

Although we only have few data it was indicated that bear predation of nests was related to snow coverage: nests in territories with high coverage suffered more from predation than nests in territories with less snow. This suggests that bear predation of eggs will be highest in years with drift ice in the sea around Tusenøyane combined with late snow melt. More generally, extensive snow coverage is known to have severe impact on reproduction in arctic nesting geese (e.g. Boyd 1982; Prop et al. 1984). The causal factors are thought to be that snow prohibits nest-initiation and covers food supplies (see Boer & Drent in press). The present study indicates that extensive snow coverage can also facilitate the predator's search for nests. A similar finding was made by Meltofte (1985), studying breeding waders and impact of arctic fox predation on nesting success in Northeast Greenland. However, for Svalbard Brent Geese we need more field observations

to tell how general and critical predation is to breeding output of the population.

In North American literature there exists, to our knowledge, only few descriptions of bears as predators on goose nests. Barry (1964) noted that in 23 observed instances in the Anderson River Delta, Arctic Canada, polar bears did not bother nesting Black Brant *Branta bernicla nigricans* even though the bears passed nearby, whereas Brown Bears *Ursus arctos* occasionally damaged goose colonies. Trainer (1959, in Cornely et al. 1985) reported that in the Copper River Delta, Alaska, brown bears occasionally ate eggs, goslings and adults of Dusky Canada Goose *Branta canadensis occidentalis*. At La Pérouse Bay, Hudson Bay in Arctic Canada, Abraham et al. (1977) observed a Black Bear *Ursus americanus* eating Snow Goose eggs; polar bears which are numerous in Hudson Bay normally arrive only after the hatching of the snow geese, but do occasionally eat eggs (F. Cooke pers. comm.).

The observations of bear predation from Tusenøyane thus seem to be extreme. However, that they are not exceptional is indicated by the report from one of the first biological expeditions to Tusenøyane, viz. the German Expedition to the Arctic Ocean in 1898 (Römer & Schaudinn 1900). The authors described the polar bear as a competitor of the Norwegian egg collectors, plundering and destroying many nests (presumably mostly Eider nests). In the stomach of a killed bear they found a 'colossal scrambled egg'.

Owen & Norderhaug (1977) and Persen (1986) have suggested that due to the increase in the Svalbard population of Barnacle Goose, the Brent and Barnacle Goose may get into competition for suitable nest sites on the small islands around Svalbard. Suitable fox-free nesting sites are limited. It has been suggested that some of the islands off western Spitsbergen are fully occupied by Barnacle Geese and that the capacity of the foraging habitat has been reached (Prop et al. 1984).

The breeding range of the Barnacle Goose has expanded, now including Tusenøyane. In 1969 no Barnacle Geese were observed (Norderhaug 1974), but in 1985 Persen (1986) found Barnacle Geese breeding on some of Tusenøyane, even outnumbering Brent Geese on certain islands.

Our observations showed that interspecific aggressions were regular, and of the same high intensity as intraspecific aggressions between Brent Geese. On Lurøya nest prospecting pairs

of Barnacle Geese were mostly expelled from the Brent Goose territories, even though the latter species is smaller. The success of the Brent ganders could be related to heightened fighting motivation as territory holding birds (Lamprecht 1986). However, in situations where the two species establish territories at the same time, the physically larger Barnacle Goose must be expected to be able to displace the Brent Goose.

Exploitative competition is likely to occur because exploitation rates of food plants are, at least in some habitats, high, and low vegetative diversity seems to give rise to large overlap in the diets of the two species. It still needs to be quantified how critical the situation is.

Interspecific competition between nesting goose species has received little attention. Mickelson (1975) reported that in the Yukon-Kuskokwim Delta, Alaska goose species partly segregate with regard to choice of nesting habitat, but that some competition for nest sites exists between Cackling Canada Geese *Branta canadensis minima*, Emperor Geese *Anser canagicus*, and Black Brant. The consequences for the populations seem, however, not to be serious. Fabricius et al. (1974) studied the interspecific relationship of nesting Greylag Geese *Anser anser* and Canada Geese on islets off the coast of south-eastern Sweden. Interspecific aggressions were observed; nevertheless both species bred successfully and showed numerical increase in the area. The question is, however, how the situation will develop, if carrying capacity of the islands is reached.

The consequences of the co-occurrence of Barnacle Goose and Brent Goose on Tusenøyane are still unclear. Looking at the population balance between the two species in a historical perspective, there is reason to fear that a continued increase of the Barnacle Goose population may be fatal to the small population of Brent. It seems that the Brent were driven away from western Spitsbergen in the beginning of this century due to egg and down collection (e.g. Gordon 1922), combined with the population crash following the disappearance of the eelgrass food stock in the wintering quarters. At that time the population of Barnacle Goose was very small, counting only a few hundred individuals. Barnacle Geese did apparently not breed on islands, but were scattered over steep cliffs and slopes in valleys (Jourdain 1922). Due to protective measures, first in the Scottish wintering quarters, followed up by

creation of bird sanctuaries in western Spitsbergen, the population rapidly increased and dispersed over the former nesting grounds of the Brent (Owen & Norderhaug 1977). In 1972 Brent Goose shooting was banned in Denmark. The population of Light-bellied Brent recovered from 2,000 to 4,000 individuals in the following decade, and has fluctuated between 3,000 and 4,000 since then (Madsen 1987, unpublished).

In several ways the situation of the Brent Goose may be critical. Firstly, it seems that some of the islands off western Spitsbergen are 'saturated' with Barnacle Geese. A continued population increase will probably lead to further expansion, and could ultimately lead to increased inter-specific competition. Secondly, due to a high predation pressure/low recruitment, the scope of an increase in the Brent Goose population is small. Thirdly, the Brent Geese will have difficulties finding alternative suitable nesting grounds to those on Tusenøyane. They can probably not return to western Spitsbergen, and due to the presence of arctic foxes, they can probably not breed successfully on the mainland of Svalbard. Thus, the Brent Geese may be 'ecologically trapped' on Tusenøyane. These points are, admittedly, not based on much hard data, and further studies of the breeding ecology of the two species may, hopefully, reveal a less pessimistic picture.

Why did the Barnacle Geese breed so late?

The Barnacle Geese started egg-laying in early July, three weeks later than the Brent on Lurøya, and despite their presence on the nesting ground from at least mid June. The late nesting seems to have been detrimental to at least some of the parents. Two parents from different pairs were marked with plastic leg bands from the Wildfowl Trust ringing scheme. On the wintering ground in Caelaverock in Scotland, about 95% of all individuals with rings are identified each winter (Owen 1984). The two parents did not appear the following winter, indicating that they died before arrival to Scotland (M. Owen pers. comm.).

Why did the geese start so late, when there was no physical obstruction, e.g. snow cover, in June? One possibility is that nesting was postponed due to predation. The nesting geese were vulnerable to polar bear predation because they nested in a relatively dense colony, and bears were observed around the colony site in mid June. However, the mechanism by which the delay happened is

obscure. One possibility is that the females replaced clutches. Barnacle females can, if eggs are removed during the early stage of incubation and provided that food is plentiful, start re-nesting after approximately two weeks (Mitchell et al. 1988). However, re-nesting has never been observed among geese nesting in the Arctic, where food is normally scarce in early incubation (M. Owen pers. comm.). If the geese were in good condition on arrival they may, on the other hand, possibly have produced eggs from their body reserves.

Behaviour of nesting females

Nest attentiveness in the studied Light-bellied Brent Geese was similar to what Thompson (in Thompson & Raveling 1987) found for Black Brant. Thus, percentage time spent incubating, mean recess length and mean number of recesses per day were almost equal in the two subspecies of Brent Goose. Light-bellied Brent Geese were less attentive to their nests and grazed for a higher percentage of recess time than other goose species, except for Barnacle Geese breeding in western Spitsbergen (Stroud 1982; Prop et al. 1984; Thompson & Raveling 1987). This suggests that the Light-bellied Brent arrives at the arctic nesting grounds with a lower level of reserves relative to body size than other goose species, and therefore depends more on local food sources for egg production and energy consumption during incubation than most other arctic breeding geese (Ankney 1984).

Four females deserted their nests about 19 days after the start of incubation. All four left their nests within 32 hrs after a snow storm. One female showed clear signs of exhaustion during the last 20 hrs before desertion, and increased the frequency of recesses and the time off the nest. The observations indicate that some of the females' reserves were too low towards the end of incubation to meet energy demands for constant incubation. Furthermore, inattentiveness increased during the incubation period in four of five females, indicating that the females were dependent on local food supplies as a supplement to stored body reserves.

Decreased attentiveness during incubation has also been found for other goose species (e.g. Inglis 1977; Stroud 1982; Prop et al. 1984). Furthermore it is indicated that female geese which are least attentive to their nests suffer the greatest

rate of clutch losses to predation (Harvey 1971; Inglis 1977; Raveling & Lumsden 1977; Prop et al. 1984). In concordance with this, one Brent female which took longer recesses than all other females, lost two out of five eggs to an Arctic Skua. However, as suggested below, another possible reason for this predation was not directly the long recesses, but inefficiency in male guarding.

The females took the fewest and shortest recesses during night when ambient temperatures were lowest and egg cooling rates would be highest. A similar diurnal rhythm has been found in other goose species (Prop et al. 1980; Aldrich & Raveling 1983; Thompson & Raveling 1987).

Territorial behaviour: Role of the male

Several hypotheses have been put forward regarding functional aspects of territoriality in geese, and accordingly, the role of males in the pre-nesting and nesting period. According to four more recent hypotheses, the territory provides 1) a defence of the incubating female from attacks performed by neighbouring males (Ross' Goose *Anser rossii*, Ryder 1975), 2) an area around the nest in which the female and male can feed without interference from other geese (Pink-footed Goose *Anser brachyrhynchus*, Inglis 1977), 3) a defence of the female from rape attempts by neighbouring males (Snow Goose, Mineau & Cooke 1979), or 4) a defence of the nest against being taken over by prospecting pairs (Barnacle Goose, Owen & Wells 1979).

We did not make observations which can throw light over hypotheses 1, 3 or 4, possibly because we first arrived at the start of incubation. At the time of nest building and egg-laying suitable nest sites on Lurøya were limited due to extensive snow cover. Intrusions by other Brent Geese or Barnacle Geese can be interpreted as attempts to take over nests, but during the nesting period no fights around the nests were observed.

The territory was important for Brent Geese as an exclusive feeding area for the nesting pair. Both male and female spent proportionally much time foraging compared to other species, viz. 31% and 10%, respectively (see Thompson & Raveling 1987 for females of other species; Barnacle males c. 21%, Dittami et al. 1977; White-fronted males c. 25%, Stroud 1982; Pink-footed males c. 20% (not including night time), Inglis 1977). Female feeding breaks may well

be, as indicated above, of vital importance for successful breeding. In all but one pair feeding took place inside the territory, and the first analyses of exploitation of *Cochlearia* indicated that in the wet moss zones the available plants were heavily exploited by the nesting pairs.

As soon as nesting pairs abandoned territories following nest losses, neighbouring males quickly took over the area. One reason for this behaviour may be that the available feeding area increased. Females also soon responded by using the new zone for feeding during nest recesses. Owen & Wells (1979) and Owen (1980) argue that the larger the territory the better, because time spent in territorial fights, which are energy-demanding, will decrease. This appears, however, not logical concerning Brent Geese, as males expanded their territories until they met the borders of a new male. As a result the number of neighbours thus remained constant, but the travel distances to the border increased, i.e. territorial defence became even more energy-demanding.

The function of the territories for geese may well vary between species, and furthermore in relation to nesting densities, predator abundance, food supplies, and not least the need for females to feed during nesting.

One role of the male during nesting is to exclude other geese from the defended area. Two other important roles are to detect, deter and chase off predators, and to attend the female during feeding bouts to allow her a maximum food intake in the shortest possible time (Ankney 1977; Raveling 1981; Fox & Madsen 1981). Our observations support that Brent ganders take part in all three roles. During female nest recesses male presence highly enhanced female feeding efficiency. It seems, however, that during some recesses males were sometimes brought into conflicting situations. Thus, when females walked to distant parts of the territory, or even outside it, males remained at some distance inside the territory, but stood out of sight of the nest. In one such case (territory no. 2) a skua utilized the situation and took two eggs in the nest, before the geese reacted by flying back to defend it.

Exploitation of food supplies

Our observations indicated that exploitation rates of *Cochlearia* were high in the wet moss carpet, which was the predominant feeding habitat during nesting and post-hatching. The high proportion

of moss in the diet may have resulted from depletion of dicotyledones. The proportion of moss was high compared to other studies of goose diets on breeding grounds (Prop et al. 1980; Madsen & Fox 1981; Sedinger & Raveling 1984, but see Derksen et al. 1982 about moulting geese). Generally, geese select food plants with the highest nutrient contents (Prop et al. 1980; Sedinger & Raveling 1984; Madsen & Mortensen 1987). Mosses are known to be less nutritious than monocotyledones and dicotyledones, and appear to be bulk food in lack of more nutritious food plants. Although goslings appeared to have a more diverse diet than adult Brent Geese, moss was still an important ingredient. Implications for the growth of goslings and energy budgets of adults remain unsolved and should be addressed in future studies.

In some territories we observed that male and female feeding patches were segregated. We suggest that this was because males – due to predator scanning duties – normally positioned themselves with sight to the nests. Hence marsh zones, which were out of sight of the nests, were almost not exploited by the males, and here females could achieve the highest intake rate during nest recesses.

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