Breeding biology of dark-bellied brent geese *Branta b. bernicla* in Taimyr in 1990 in the absence of arctic foxes and under favourable weather conditions

BERNARD SPAANS, MARTIN STOCK, ANDREW ST.JOSEPH, HANS-HEINER BERGMANN and BARWOLT S. EBBINGE

Spaans, B., Stock, M., St.Joseph, A., Bergmann, H.-H. & Ebbinge, B. S. 1993: Breeding biology of dark-bellied brent geese *Branta b. bernicla* in Taimyr in 1990 in the absence of arctic foxes and under favourable weather conditions. *Polar Research 12(2)*, 117–130.

In combination with observations in spring staging and wintering grounds in western Europe, a detailed etho-ecological study of nesting dark-bellied brent geese *Branta b. bernicla* in western Taimyr, Krasnoyarsk, Russia, was made in 1990. Most brent geese arrived on the breeding grounds from 14–19 June and started nesting within a few days. In the study area 264 nests of breeding brent geese were found, mainly on islands but also along small rivers on the mainland. The mean clutch size was 3.0 and 80% of the eggs hatched. Time budget studies showed that incubating females spent on average 138 minutes per 24 hours on feeding. Despite favourable weather conditions and a low density of arctic foxes, only about one-third of the mature birds in the study area bred. In the autumn an intermediate breeding success of 20% juveniles was recorded in the wintering areas. This was probably due to the relatively poor condition in which the brent geese left their spring staging areas.

Bernard Spaans and Barwolt S. Ebbinge, Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 23, NL-6700 AA Wageningen, The Netherlands; Martin Stock, Nationalparkamt, Schleswig-Holsteinische Wattenmeer, Am Hafen 40 A, D-2253 Tönning, Germany; Andrew St. Joseph, Mellfarm, Pallesbury, Maldon, Essex CM9 8SS, England; Hans-Heiner Bergmann, Fachbereich Biologie Der Universität Osnabrück, Postfach 4469, D-4500 Osnabrück, Germany.

Introduction

The factors that determine the large variations in annual breeding success of the dark-bellied brent geese *Branta bernicla bernicla* are the subject of an ongoing debate (Summers & Underhill 1987, 1990; Ebbinge 1989, 1990). Factors assumed to be the most important are weather conditions in the arctic breeding area (Barry 1962; Boyd 1987), size of lipid and protein reserves upon arrival there (Ebbinge et al. 1982), and nest predation by arctic foxes *Alopex lagopus* (Roselaar 1979; Summers 1986; Dhondt 1987; Greenwood 1987; Owen 1987; Anthony et al. 1991). Nutrient reserves are stored in the Dutch, German and Danish Wadden Sea in the 5–6 weeks prior to spring migration (Ebbinge et al. 1982; St.Joseph 1982). Weather conditions during migration affect the final condition upon arrival (Ebbinge 1989). The number of arctic foxes and their predation pressure on arctic birds have been hypothesized to depend mainly on the abundance of lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus*. In particular in years after a lemming peak, the increased number of foxes are expected to terrorize the nests of arctic breeding birds due to scarcity of lemmings as their main prey.

The discussion about the relative importance of each of these factors, however, is hampered by the lack of knowledge about what is really happening in the breeding area of brent geese. The opportunity provided by E. E. Syroechkovskiy of the Laboratory of Evolutionary Animal Morphology and Ecology of the Russian Academy of Sciences to visit the Taimyr peninsula in 1990 and to start a detailed study on the breeding biology of brent geese gives new dimensions to this discussion.

This paper presents the results of our first Taimyr expedition in 1990 and data on body condition and reproductive success gathered in the wintering and spring staging areas in western Europe before and after the same breeding season. These data from the wintering areas, which have been gathered over several years, can now be viewed in perspective with data from Taimyr.

Our study on the breeding biology of brent geese in Taimyr focused on the following points: (1) the condition (body-mass) of the geese upon arrival; (2) the importance of body reserves during the breeding season; (3) the effect of potential predation on behaviour and breeding success of the geese; (4) the effect of lemming density on predation; and finally (5) how these factors are affected by the weather conditions.

We cannot presume to solve the riddle of the cyclic variations in annual breeding output of the brent goose on the basis of one season's work, but we feel that our first results can help to shape future work and therefore merit early consideration.

Study area

Habitat

The study was carried out in the coastal area north of the Piassina delta, about 200 km ENE of Dickson, Taimyr, USSR. The base camp was situated along the Lidia Bay, 74°07'N, 86°50'E (Fig. 1). This location was chosen in advance because of the presence of a small archipelago with the promising name 'Bird Islands'. We stayed in the study area from 1 June until 28 July 1990.

The coastal mainland consists of low, undulating tundra traversed by a number of small rivers of which the Lidia is the most important. The tundra vegetation is dominated by mosses, lichens, sedges and grasses. During snowmelt the rivers are wide, but after the snow disappears the water level declines and a lush vegetation of monocots develops on the banks alongside these rivers. This vegetation is dominated by *Dupontia psilosantha, Carex aquatilis, Arctophila fulva, Eriophorum scheuchzeri* and *Puccinellia spp.* Similar vegetation also occurs on the flat outer Beacon Islands (Fig. 1). In June the vegetation on these islands was dominated by mosses, but later in the season young monocots emerged. Island 1 was rather flat with mainly tundra vegetation comparable to the mainland. Islands 2, 3 and 4 were rocky with bare patches, some areas of tundra vegetation, and a richer grassy vegetation around colonies of the lesser black-backed gull *Larus fuscus taimyrensis* (Cramp & Simmons 1983). The large island Farwaternië was covered with tundra vegetation similar to that of the mainland.

Fig. 1. Upper: Location of the study area in Taimyr, Russia. Lower: the study area north of the Piassina-delta in Taimyr is indicated by grey. The Bird Islands are numbered.

Weather conditions in 1990

Daily minimum and maximum temperatures were measured at the base-camp. Percentage snow-cover was measured by counting the number of steps with and without snow along a 2200 metre long tundra transect from the seashore to the top of a hill, north of the Lidia Bay. Temperature and snowmelt data from 1977 to 1990 collected by a station along the Piassina-river, ca. 40 km southeast of our camp, were made available to use by Y. Kokorev. Comparison of the mean maximum temperature over the previous 14 years with the minimum and maximum temperatures measured at our camp (Fig. 2) indicates that June and July 1990 were relatively warm. In our camp, the daily maximum temperature was on average
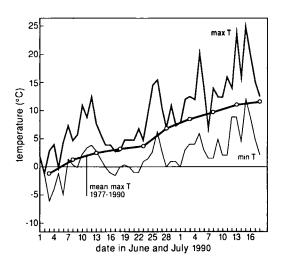
Fig. 2. Minimum and maximum temperature at the study area during the period of our stay. The average daily maximum temperature, per 5-day period, from 1977 to 1990 is also given, data from the Piassina weather-station ca. 40 km southeast of the study area.

Fig. 4. Duration of snow cover from 1977 to 1990. The number of days with snow cover after 1 June is measured on the same reference point. The average is shown with the horizontal line. The data are from the Piassina weather-station.

2° higher than at the weather station. The progress of snowmelt north of the Lidia Bay is shown in Fig. 3. In early July the area was almost snowfree. Snowmelt-data over the previous 14 years show that 1990 was a year with early snowmelt (Fig. 4). Until 10 June it was possible to reach the Bird Islands from the mainland over the frozen bay. Throughout the first week of July, islands 1 and 2 could still be reached after crossing a narrow channel by boat. From the second week of July, the islands were completely surrounded by water and could only be reached by boat.
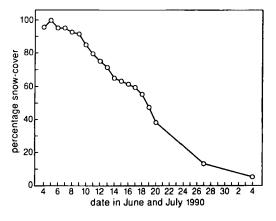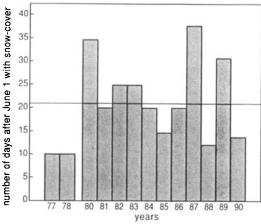

Fig. 3. Percentage of mainland-tundra covered with snow from 4 June to 4 July.

Predators

Lemmings and arctic foxes. – To establish the effect of predation on the behaviour and breeding success of the geese, counts were made of lemmings, arctic foxes and other potential predators. A population-dynamic study of lemmings was carried out by Russian biologists. Lemming density was measured by catching the animals both with live-traps and ordinary traps. During six weeks of continuous trapping with hundreds of traps less than twenty lemmings were caught, on average 0.25 lemmings/100 trap nights (Ryhlikova, 1993). On about 750 man-days spent in the tundra by the participants of our camp during June and July, only a few lemmings were observed. Snowy owls *Nyctea scandiaca*, roughlegged buzzards *Buteo lagopus* and pomarine skuas *Stercorarius pomarinus*, all lemming-predators, were seen migrating during the first half of June, but these predators disappeared almost completely from our study area, without making any attempt to breed. This is also an indication of a poor lemming year. Not a single arctic fox was observed and local hunters had not even tried to catch foxes the preceding winter because there were so few.

Other potential predators. – Lesser blackbacked gulls were common breeding birds in our study area (over 1200 pairs). These gulls were already present on the Bird Islands when we

arrived on 1 June. Glaucous gulls *Larus hyperboreus* were rare and only a few nests have been found. Long-tailed and arctic skuas *Stercorarius longicaudus* and *S. parasiticus* were also breeding in our study area but in small numbers.

Methods

In western Europe

On the Dutch island Terschelling brent geese were caught with cannon nets on 14 and 16 May 1990 to determine their body-mass just before their departure for the Arctic. Migration dates were recorded by several field workers in the Wadden Sea area in the second half of May (from 1976 to 1990). In autumn 1990 we recorded juvenile percentage and family-size in many staging sites along the coasts of the North Sea, to arrive at a reliable over-all population mean. In this way we accounted for the unequal distribution of families with juveniles over the wintering area (Lambeck 1990a, 1990b). Special attention was devoted to geese with engraved colour-rings to determine pair-bond and breeding success of birds marked in Taimyr.

In Taimyr

Brent geese were caught with cannon nets in our study area from 15 to 19 June 1990 to determine pre-breeding body-masses. We marked captured individuals with individually-coded colour rings, of which the inscriptions can be read by telescope at 300 m distance. We surveyed the entire study area for breeding geese; clutch-size and egg mass were determined in the first week of incubation. On seven different days we observed two breeding pairs on island 2 (called pair A and B) for 24 consecutive hours from a hide. On the mainland along the Lidia River we watched, also from a hide, five incubating females (called numbers 1 to 5) and only 1 male (the male of female 3). This male was chosen because both members of pair 3 were individually recognizable (marked with colour-rings in the Netherlands in May 1989). Along the Lidia River we observed on six days for 24 consecutive hours, but only male 3 was observed on one of these days. Due to the fact that incubation of the Lidia females started 5 days later than on the island, calendar days do not correspond when observations of both areas are

plotted against the start of incubation. During these 24-hour periods, activity of the geese was noted every 5 minutes. We also recorded starting-time and duration of feeding-recesses of the females, all interactions with potential predators, all intraspecific interactions and time and number of potential predators present near the nesting geese along the Lidia River. In addition, a scan of the activities of a flock of non-breeders (birds without a nest or territory, living in flocks) along the Lidia River was made every 15 minutes. Non-breeders did not occur on the Bird Islands.

Nests with a known number of eggs were observed during hatching to determine the fraction of eggs that hatched. The size of each observed family was recorded immediately after hatching. Post-hatching behaviour of brent goose families was recorded to establish the effect of predation of goslings by gulls and skuas. We also counted the non-breeding birds on the islands where they were moulting.

Results

Body condition during spring staging and breeding success as measured in autumn

The breeding success measured in autumn flocks is plotted in Fig. 5 against the mean body-mass of adult female brent geese (caught during spring staging just before departure to the north of Siberia), together with comparable data from the other years (Ebbinge 1989; Ebbinge & Spaans 1992). Compared with other years, 1990 showed a relatively poor condition of the geese before departure and an intermediate breeding success of 20% juveniles in autumn. The mean number of juveniles per successful pair was 2.4 (N = 336).

In 1990 the geese left the Wadden Sea early (Fig. 6). Wind conditions during migration in the North Sea area and through the Baltic region were favourable with 57% of days with a tailwind blowing in the period 21–30 May in the Baltic (see Ebbinge 1989 for sources and methods of calculation).

Arrival and condition on the breeding grounds

We saw the first two brent geese on 10 June. Most migrating geese were observed from 14–19 June (Fig. 7). Between 15 and 19 June, nine brent geese were caught, weighed and individually marked
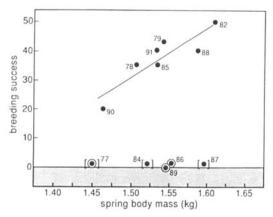
Fig. 5. Spring body-mass of female brent geese just before departure in the end of May from the Wadden Sea area and breeding success, expressed as percentage of juveniles, in the subsequent autumn and winter. Years that were unfavourable due to (head)wind during spring migration are given between brackets and unfavourable years due to high inferred fox predation on the breeding grounds are circled (data from Ebbinge 1989 and Ebbinge & Spaans 1992).

Fig. 7. Arrival of brent geese in Taimyr and timing of egg-laying, incubation and hatching. The left graph indicates the number of migrating brent geese per day in the Lidia Bay area, the right graph indicates the number of incubating females on island 1.

(Table 1). The mean weight of the females was only 40 g less than the weight of the females caught in the Wadden Sea (Fig. 5). Although the sample is very small, the small difference in mean body-mass indicates that the costs of migration were (partly) compensated on staging grounds between the Baltic region and Taimyr.
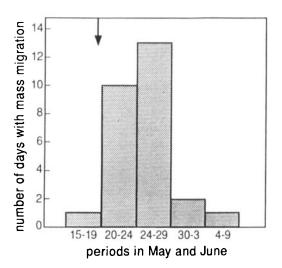

Fig. 6. Timing of departure from the spring staging area. Number of days with brent goose mass departure from the Dutch Wadden Sea in 5-day periods from 1976 to 1989. The arrow indicates the mass departure in 1990.
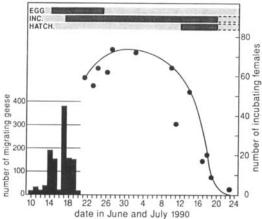
Distribution of breeding brent geese over the study area

A total of 264 nests of brent geese were found in the study area, 252 (= 96%) on the small off-shore Bird Islands and 12 nests on the mainland alongside small rivers (Fig. 8). The mean laying date of the first egg on a small colony along the Lidia River on the mainland was about one week later than the two inner Bird Islands. We do not have data on nest initiation on the outer islands. A review of the timing of migration, egg-laying, incubation and hatching is given in Fig. 7. Most of the geese started nesting within a few days after arrival.

A sketch of the distribution of vegetation types on island 2 with the position of 16 brent goose nests is given in Fig. 9. In contrast to the vegetation the nests seemed to be rather evenly dispersed and the mean density was 2,8 nests/ha. The highest density was measured on island 1: 3,9 nests/ha.

Mean clutch-size was 3.0 ± 1.2, (N = 72) and ranged from 1 to 6 eggs per nest. Mean egg-weight was 79.5 ± 7.5 g, (n = 94 eggs), range 64 to 98 g, fresh weight i.e. measured at clutch completion ($\pm$ standard deviation).

We could not relocate any of the 11 individually marked geese caught in June as a breeding bird in our study area but they could have been missed.

Table 1. Pre-breeding body-mass of 9 brent geese caught between 15 and 19 June. The pair-bond and the net breeding success have been determined in the subsequent autumn and winter in western Europe.

Codes	Male body-mass	Female body-mass	Observed in w. Europe	Number of juv.
RPGA × RPGC	1510	1610	+	5
RPGK × RPGH	1490	1380	+	0
RPGF		1400	+	?
RPGJ	1380		−	−
RPGN		1560	+	1
RPGP	1590		+	?
RPGT		1530	+	?
Mean body-mass	1484	1496		

Breeding behaviour

Only the female incubated, leaving the nest regularly to feed while the male stayed near the nest. Around the nest, the males defended a territory.

We were able to precisely estimate the length of the incubation period for one pair which was 24.5 days (measured from clutch completion to hatch of last gosling).

The total time off the nest (recess time) per 24 hour period is plotted for the two island females and the five Lidia females in Fig. 10. When a female left the nest, she carefully covered the eggs with down, and frantically started to feed, usually within her territory, but sometimes on another island. On average, 90% of the time females spent off their nest was used for feeding. While the female was off, the male usually stayed close by to defend the nest against gulls or skuas. All females left their nests more often as the breeding season progressed, varying from once per 24 hours in the beginning to up to 16 times per 24 hours at the end (Fig. 11). The average recess frequency was 11 per day for the Lidia females and 9 per day for the island females. Although there was some variation in the length of a feeding recess per female during the incubation, the increasing number of feeding recesses was the main reason for the increasing total time off the nest per 24 hours. However, there were striking differences between females: the mean duration over all observation days of an individual feeding recess of the Lidia females ranged from 10.9 (female 4) to 15.4 minutes (female 2), with a mean of 12.9 minutes, while this was 16.7 for the island female A and 27.3 minutes for the island female B. The large differences in total time off the nest are thus due to a longer mean recess duration on the island. Average recess frequency for all females was 10.6 per day with a mean recess duration of 15.5 minutes.

Males have more time for feeding than the incubating females. The percentage of time spent on feeding during the incubation period of both island males, the male of Lidia female 3 and the non-breeding birds present in the Lidia valley decreased in the course of the time (Fig. 12). Both island males spent more time on feeding (40.4% on average) than the Lidia male 3 (31.0%) but the non-breeding geese spent the least time on feeding.

Most of the feeding of the incubation females took place in the afternoon and the least in the early morning (Fig. 13). The males showed an opposite pattern: there was a tendency to feed more during midnight (Fig. 14).
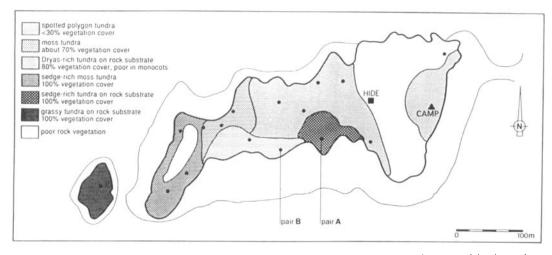

Fig. 8. Number of nesting brent geese in the study area. The black square indicates the location of the base-camp. Island 2 was the main observation island.

Fig. 9. Map of island 2. Vegetation-types are indicated as well as the location of the brent goose nests, the camp and the observation hide. Pairs A and B were studied in detail.

Intraspecific interactions

The breeding area, especially on the island, was divided into territories. Male A had a relatively good territory (100% vegetation cover) while male B had a poor territory (<30% vegetation cover, Fig. 9). Male B in fact hardly defended his territory which was only used for feeding by himself. His female almost always left the island to feed somewhere else. Female A, however, was always feeding within her own territory which had to be heavily defended by male A, who engaged in frequent conflicts with the neighbouring males (Fig. 15). The number of conflicts showed a marked decrease in the week before hatching.

Interactions with potential predators

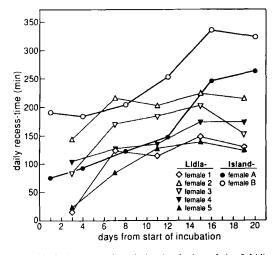On the island the most numerous potential pred-

Fig. 10. Daily recess time during incubation of the 5 Lidia females (1 to 5) and the two island females (A and B). Females were non-stop observed during 24-hours periods.
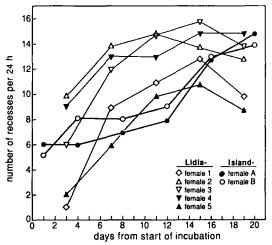

Fig. 11. Daily number of recesses during incubation. Same females as in Fig. 10.
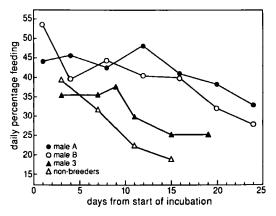
Fig. 12. Daily percentage of total time spent on feeding by male brent geese during the incubation period. Male A and B have territories on island 2 and male 3 in the Lidia valley. The non-breeders were also observed in the Lidia valley, on the same dates as male 3.

Fig. 14. Diurnal variation in feeding of males during the incubation period. The percentage of total daily feeding-time of the 2 island males A and B is given per 4 hour periods.

ators were the lesser black-backed gulls. Pomarine skuas and long-tailed skuas were sometimes seen flying over but did not seem to pay any attention to the breeding geese. Sometimes the threat of the male was enough to keep a gull at a distance but very often a pursuit-flight followed. Male B had more interactions with the lesser black-backed gulls during the incubation period than male A (Fig. 16) which may be explained by the closer proximity of pair B to a gull-colony. Although there is no general trend in time, there was a striking similarity in the interactions of the two males. Apparently there were days on which

lesser black-backed gulls assailed the geese and days on which they did not. The only successful gull action that we observed on the island was a gull that managed to remove the down cover of a goose nest while the female was absent, but the male chased the gull away before it could take an egg. On other islands we saw egg-predation by the lesser black-backed gull and the arctic skua but in all cases disturbance of the geese by our presence was probably the prime cause of this predation. On the mainland no lesser black-backed gulls bred and although they regularly flew over the valley they left the geese undisturbed most of the time. The actions of male 3 were mainly directed to the pair of arctic skuas breeding
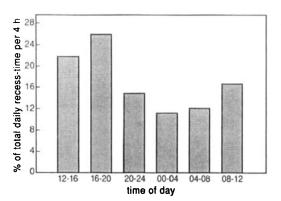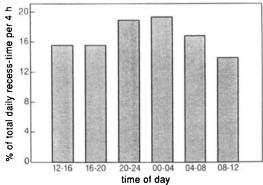

Fig. 13. Diurnal variation in feeding of females during incubation. In this figure the percentage of total daily recess time for all females is given per 4 hour periods.
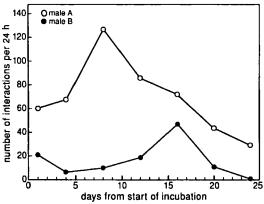

Fig. 15. Intraspecific interactions of males during incubation. The total number of interactions per 24 hours is given for the island males A and B.

in this area (Fig. 16). Like the lesser black-backed gulls on the island, the skuas did not seem to be very successful in taking eggs in the Lidia valley. The number of gulls and skuas present near nests in the Lidia valley decreased during the incubation period (Fig. 17). It is likely that other more profitable food, for example from marine sources, became available for these birds in the course of the season.

After hatching

The two studied island pairs hatched their eggs on average 5 days earlier than the five studied females in the Lidia valley. On island 2 the first goslings hatched on 12 July and the last on 16 July. Within a few days after hatching the families left the islands. They presumably swam to the river mouths on the mainland where the food situation was more attractive. The mean observed brood size (island and river-breeders) was 2.4 (N = 34) while clutch size was 3.0 (N = 76), thus 80% of the eggs hatched. Both island pairs studied (A and B) were less successful: only one out of the three eggs hatched in each case. The parents were capable of defending their goslings against the lesser black-backed gulls. Only two times did we witness a gull taking a gosling, both times while the family was swimming in the water under windy conditions.

The Lidia breeders stayed in the nesting area after hatching. The banks of a small lake, about
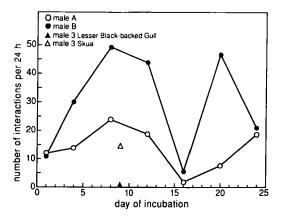

Fig. 17. Presence of avian potential predators at the Lidia brent geese colony. The number of times per 24 hours one or more lesser black-backed gulls and (arctic) skuas were present is given.

1 km west of the nesting site along the Lidia River became one of their preferred feeding sites. The percentage of eggs hatched was 89% (16 goslings from 18 eggs in nest 1 to 5). We observed the families for more than one week. During the week only one gosling was lost. After a week's time the goslings had grown so much that predation by gulls or skuas did not seem likely.

We were able to determine the breeding results of two individually marked breeding pairs soon after hatching: Lidia pair 3 had one gosling (from one egg) and the pair OFYA and OFYF had also 1 gosling (number of eggs unknown).

Because we left the area on 28 July, we do not have data about the gosling survival of the local population studied. The large number of moulting non-breeders on the Beacon Islands (Fig. 1) at the end of July, about 1200, suggested that there were many non-breeding birds in 1990. Assuming that the study area is representative for the entire breeding population, 264 breeding pairs with 2.4 juveniles per pair and 1200 non-breeding birds gives a juvenile percentage of:

$$\frac{2.4 \times 264}{(2.4 \times 264) + (2 \times 264) + 1200} = 27\%.$$

Due to losses during growth and migration, juvenile percentage in winter area should be less than this value.

Observations of marked individuals in the winter area

Geese with known pre-breeding weights. – No less

Fig. 16. Interactions of male brent geese with (avian) potential predators. The total number of interactions per 24 hours with lesser black-backed gulls is given for the island males A and B and for Lidia male 3 the number of interactions with arctic skuas is also given.
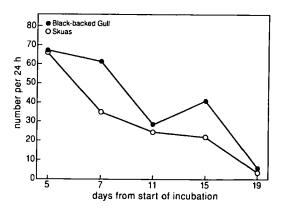
than 8 of the 9 geese caught in spring in Taimyr were seen by different observers in the subsequent autumn and winter in western Europe. As juveniles stay with their parents during the first winter it was possible to determine the family size of two ringed pairs and one ringed female: the pair RPGC and RPGA was accompanied by five full grown juveniles (Ameland, Netherlands), the pair RPGH and RPGK had no juveniles (southeast England) and the female RPGN was seen with an unringed male and 1 juvenile (Texel, Netherlands) (Table 1).

Geese with unknown pre-breeding weight but with known breeding results soon after hatching. – Both pairs of this category were seen again. Lidia pair 3 was seen with one full-grown juvenile (coast of Groningen, Netherland) and pair OFYA and OFYF had one juvenile as well (Schiermonnikoog, Netherlands). This means that both pairs raised their single gosling successfully because both were seen with only one gosling soon after hatching in Taimyr.

Discussion

The late arrival of brent geese in Taimyr (Fig. 7), compared with the departure from the spring staging areas (Fig. 6), means that there must be staging areas along the northern coast of Russia. No staging areas are known in the Baltic (Kumari 1979; Lampio 1979). Given the fact that in Taimyr almost all vegetation was covered with snow at the beginning of June, it is likely that the staging areas are situated far more to the southwest where snowmelt starts earlier. Kistchinski & Vronski (1979) suggest that spring migration between the White Sea and Taimyr is a non-stop migration, and the dates on which migration is seen along the north Russian coast correspond with our arrival dates in Taimyr. This means that the White Sea is most likely the intermediate staging area. Given the early departure from the Wadden Sea, the geese must have spent almost three weeks on these staging grounds in 1990. This period is long enough to replenish the body reserves used during the first part of the migration (Ebbinge & Spaans, 1992).

The mean female body-mass at arrival in Taimyr was 1496 g (Table 1). This body-mass is about 250 g heavier than lowest mean Wadden Sea body-mass (first half of April) and about 140 g

heavier than mean winter body-mass (Ebbinge et al. 1982), so it is clear that the geese at arrival in 1990 did have reserves. However, it is likely that in years when departure weights in the Wadden Sea are higher and weather during migration is comparable, the body condition on arrival in Taimyr will improve. Since the departure weights were low in 1990 (Fig. 5), 1496 g will probably be a rather poor pre-breeding condition.

Brent geese started breeding very soon after arriving in Taimyr (Fig. 7). These observations are in sharp contrast to findings in Raveling (1978), Fox & Madsen (1981), Ely & Raveling (1984) and Gauthier & Choinière (1990) where species such as the cackling goose *Branta canadensis minima*, the two subspecies of the whitefronted goose *Anser albifrons* and the greater snow goose *Anser caerulescens* atlantica spend 10 to 20 days on the breeding grounds before egg-laying starts. As with the brent geese in our study, however, Ross geese *Anser rossii* and lesser snow geese *Anser c. caerulescens* start to lay eggs within 3–5 days after arrival (Raveling 1978).

Most brent geese bred on small off-shore islands but some were breeding on the mainland along rivers. If there had been arctic foxes, the island birds would have had a safer location than the birds on the mainland, although most of the islands would have been easily accessible to foxes over the still frozen sea during the first two weeks of incubation. The developing vegetation in the river valleys and on the outer islands seemed to be much more attractive to geese than the vegetation on the inner islands, where nest density was highest (Fig. 8). The fact that the majority of the geese did not choose to breed in the best feeding-areas may be the result of a difference in potential predation pressure and/or difference in availability of the nest-sites soon after the arrival of the geese. The melting snow in spring may flood river-valleys and the low-lying outer islands to a large extent in the second half of June. Because of the very short summer season at this latitude (74°N), delayed nesting causes problems at the end of the season when goslings must be able to fly before changing weather conditions make feeding impossible.

Due to large territories around the nest where the females feed during incubation, nest density is low (maximum 3.9 nests/ha) compared for instance to the barnacle geese *Branta leucopsis* on Svalbard where nest density on breeding islands has been reported to be 84.7 nests/ha on

average (Prop et al. 1984). Here the geese breed in colonies on islands and fly to the mainland for feeding. Madsen et al. (1989), however, found a breeding density of only 0.5 nests/ha for light-bellied brent geese *Branta bernicla hrota* on the Tusenøyane islands, Svalbard.

The time a female spends off her nest will depend on her body reserves and the quality and quantity of the food she is able to gather during the feeding recesses. Concerning the food, the river-valley birds had a better local food supply than the island birds. This might explain part of the differences in recess time (Fig. 10). On the island female A fed in her own territory whereas female B, who had a poorer territory (Fig. 9), in most cases flew to the mainland or other adjacent islands to feed, resulting in longer nest recesses (27 minutes). This illustrates the importance of a territory with sufficient food. Madsen et al. (1989) found for the light-bellied brents on Svalbard an average recess frequency of 6.7 per 24 hours and a mean recess length of 19.2 min. This means that on Svalbard the females spent on average less time off their nest (129 min per day) than the dark-bellied brents in our situation (10.6 recesses of 15.5 min per day = 165 min). This difference can be the result of a difference in digestibility of the food. Madsen et al. report that the food of the brent on Svalbard partly consists of mosses. We seldom saw the geese eating mosses in our area. The nest attentiveness of the female black brant *Branta bernicla nigricans* reported by Thompson & Raveling (1987) is about the same as for the dark-bellied but the feeding time per day is shorter, caused by the low percentage of feeding during recesses (64%, based on 3 recesses). The longest feeding time (239 minutes per day) is reported for the light-bellied brents in Canada (Afton & Paulus 1993). The mean daily feeding time for our island female B however was 238 minutes. In the latter case only one out of the three eggs hatched so 238 minutes might be too long but the example shows that such a long feeding time was also possible in our situation. Brent geese are less attentive to their nests than other goose species (Prop et al. 1984; Afton & Paulus 1993). The females apparently do not have sufficient body reserves to fast during incubation. The dependence on local food during incubation makes brent geese very vulnerable for bad weather conditions during this period (Barry 1962). The effect of not being able to feed sufficiently during incubation was observed by Mad-

sen et al. (1989): four female light-bellied brents deserted their nests 19 days after the start of incubation within 32 hours after a snow storm.

Predation of eggs is more likely to occur when the recesses are long (Inglis 1977; Prop et al. 1984; Raveling 1989; Thompson & Raveling 1987). We never observed that a male sat on the nest while the female was feeding as is described for whistling swans *Cygnus c. columbianus* (Hawkins 1986).

The preference of the females to feed during mid-day, the warmest part of the day (Fig. 13), may be determined by the fact that the eggs will cool less at that time when the nest is left for longer periods. This diurnal rhythm has also been found in light-bellied brent geese (Madsen et al. 1989) and in other goose species (Prop et al. 1980; Aldrich & Raveling 1983; Thompson & Raveling 1987). The abundant presence of down in the nests of brents clearly is an adaptation to their low nest-attentiveness. Thompson & Raveling (1988) showed that eggs in black brant nests cooled less than those in the nests of the more attentive emperor and cackling goose.

Some males spent a considerable amount of time in defending their territory against neighbouring males (Fig. 15). As the territory of male B was probably not attractive for the neighbours, male B had less conflicts than male A. The decrease in the number of conflicts between the males in the week before hatching could be the result of an improving food situation at that time; intrusion pressure decreased and defending every square metre of the territory became less important.

Spring was early in 1990 (Fig. 2) and the decreasing time spent on feeding by the males and non-breeders during the incubation time indicates that the food situation was improving during the course of the incubation period (Fig. 12). The difference in male feeding time between the island and the Lidia colony might result from the poorer food situation on the island. Because the males of breeding pairs had to defend and guard their families after hatching, it was necessary that they had reserves for this period. This might explain the difference in feeding time between breeding and non-breeding birds. The average feeding percentage of non-breeders observed by Madsen et al. (1989) during the incubation period was 53.3%; in the Lidia situation it was only 28.0%.

The overall picture of decreasing feeding time, resulting in low feeding percentages (Fig. 12), will

be indicative for a favourable food situation in the course of the season. During spring staging it is not unusual that brent geese spend over 89% of the daytime on feeding (Prop & Deerenberg 1991), this means about 16 hours feeding per day. In order to achieve the same feeding time in the 24 hours daylight in Taimyr, on average 67% of the time should be spent feeding.

Because of the absence of arctic foxes, lesser black-backed gulls and skuas were the only potential predators. Madsen et al. (1989) observed a heavy egg-predation by arctic skuas on Svalbard, but in 92% of the cases predation took place during disturbance of the brent goose colony by polar bears *Ursus maritimus*. Although egg and gosling predation by avian predators was also a constant danger for the geese in Taimyr, they were well able to defend their clutch and young goslings. Therefore predation must be considered as a factor of only minor importance in 1990 in our situation. The observations of the two marked pairs, each with one full-grown juvenile in western Europe while both pairs had only one gosling after hatching in Taimyr, are an indication that gosling surviving was indeed high in 1990.

We observed a large number of non-breeders in our study area (1200). These birds started moulting already during the hatching period. Because we never observed complete nest failure, we suspect that most of these birds did not even attempt to breed. This means that 69% of the local population failed to produce eggs.

Combining the Taimyr and western Europe data

The estimated dark-bellied brent geese population size in January 1990 was 220,000 birds (St. Joseph 1991). Because virtually no dark-bellied brent nested successfully in 1989, there were no yearlings in the population in 1990. Therefore 100% of the birds of the population were theoretically capable of breeding. This means that there were 110,000 potential breeding pairs in the summer of 1990, mortality during spring and spring-migration not taken into account. In autumn 1990 the percentage of juveniles was 20% and the mean number of juveniles per pair was 2.4. This means that in every 100 brents there were $100 - 20 = 80$ adults (or 40 pairs) of which $20/2.4 = 8.33$ were successful pairs. So the percentage successful parents was $8.3/40 = 20.8\%$. The total number of pairs that brought one or more juveniles to the

wintering-grounds was $0.208 \times 110,000 =$ about 23,000 pairs.

There has been discussion about the occurrence of a density-dependent reduction in the proportion of successful breeding pairs in good breeding seasons (30% juveniles or more) (Ebbinge 1985; Summers & Underhill 1991), but 23,000 successful pairs comprise only a fraction of the predicted number of successful pairs in a good breeding season (according to Summers & Underhill, without density-dependent reduction, it is 44% of the predicted number, and according to Ebbinge it is about 60% when density-dependent reduction occurs). Thus relatively few pairs managed to raise juveniles successfully in 1990.

In Taimyr snowmelt was early (Fig. 4), the mean temperature in June and July was high (Fig. 2), arctic foxes were absent, predation by birds (gulls and skuas) was probably of little importance and the food-rich riverbanks could easily hold more breeding pairs. If predation and/or weather-conditions would be the most important factors determining the breeding success (Barry 1962; Roselaar 1979; Summers 1986; Boyd 1987; Dhondt 1987; Greenwood 1987; Owen 1987), 1990 should have been a very good breeding year. The fact that population-breeding success was only moderate indicates that another factor played an important role in 1990. It seems plausible that this was the poor pre-breeding condition of the geese (Fig. 5). Although mean condition is poor, there are always, due to the variation in the body-mass, individuals with a condition better than average (Table 1). If only females in better condition have sufficient reserves to start breeding, we can explain the intermediate breeding success on population scale. Under this hypothesis the intermediate breeding success is not the result of many breeding pairs that were moderately successful but of a relatively small number successful breeding pairs and many pairs that did not lay eggs at all. In that case breeding birds were pairs in relatively good condition. The fact that the local breeding birds in our study seemed to have been successful is in agreement with this explanation. Also, the observations of the marked geese with known pre-breeding weight in western Europe, where the heaviest female (1610 g) had five, an intermediate female (1560 g) had one, and the lightest female (1380 g) had no juveniles, correspond with this hypothesis.

Ecology in Moscow, who organized and gave us the opportunity to participate in the international exhibition to the Taimyr Peninsula. N. Vronski, A. Abolitz, G. Boere, P. Prokosch and J. Veen played important roles in the organisation of the expedition and co-operation with the Russians. J. Koenes and his carpenters, Zoological Laboratory of the University of Groningen, prepared a pre-fabricated observation hut suitable for arctic conditions. We are also grateful to the many people who assisted in collecting data presented in this paper. The catching of geese in spring on Terschelling has been carried out by J. Burgers and G. Müskens. In Taimyr, V. Grabowski, Y. Kokorev, A. Ivanov-Smolenski and A. Moroz helped with the observations. M. Ryhlikova collected data on the occurrence of lemmings. H. Schmauder was important as an interpreter and A. Grosheva prepared excellent meals. The figures have been prepared by D. Visser. Comments by R. H. Drent, J. Tinbergen and two anonymous referees greatly improved this paper.

References

Afton, A. D. & Paulus, S. L. 1993: Incubation and Brood Care. Pp 62-108 in Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L. (eds.): Ecology and Management of Breeding Waterfowl. Univ. of Minnesota Press, Minneapolis.

Aldrich, W. & Raveling, D. G. 1983: Effects of experience and body weight on incubation behavior of Canada Geese. *Auk* 100, 670-679.

Anthony, R. M., Flint, P. L. & Sedinger, J. S. 1991: Arctic fox removal improves nest success of Black Brant. *Wildl. Soc. Bull.* 19, 176-184.

Barry, T. W. 1962: Effect of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26,. 19-26.

Boyd, H. 1987: Do June temperatures affect the breeding success of Dark-bellied Brent Geese? *Bird Study* 34, 115-159.

Cramp, S. & Simmons, K. E. L. (eds) 1983: Handbook of the Birds of Europe, the Middle East and North Africa, Vol 3. Oxford University Press, Oxford.

Dhont, A. A. 1987: Cycles of lemmings and Brent Geese *Branta b. bernicla*: a comment on the hypothesis of Roselaar and Summers. *Bird Study* 34, 151-154.

Ebbinge, B. S. 1985: Factors determining the population size of Arctic-breeding geese, wintering in western Europe. *Ardea* 73, 121-128.

Ebbinge, B. S. 1989: A multifactorial explanation for variation in breeding performance of Brent Geese. *Ibis* 131, 196-204.

Ebbinge, B. S. 1990: Reply by Barwold S. Ebbinge. *Ibis* 132, 481-482.

Ebbinge, B. S. & Spaans, B. 1992: The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding of Dark-bellied Brent Geese *Branta b. bernicla* in the high arctic. In: Ebbinge, B. S. 1992: Population limitation in Arctic-Breeding Geese. Ph.D. dissertation, University of Groningen. Pp 144-155.

Ebbinge, B., St.Joseph, A., Prokosch, P. & Spaans, B. 1982: The importance of spring staging areas for arctic-breeding geese, wintering in western Europe. *Aquila* 89, 249-258.

Ely, C. R. & Raveling, D. G. 1984: Breeding biology of Pacific White-fronted Geese. *J. Wildl. Manage.* 48(3), 823-837.

Fox, A. D. & Madsen, J. 1981: The pre-nesting behaviour of the Greenland White-fronted Goose. *Wildfowl* 32, 48-54.

Gauthier, G. & Choinière, L. 1990: Energy reserves and reproductive performance in Greater Snow Geese. Acta XX Congressus internationalis Ornithologici (Supplement). P. 425.

Greenwood, J. J. D. 1987: Three-year cycles of lemmings and Arctic geese explained. *Nature 328*, 577.

Hawkins, L. L. 1986: Nesting behaviour of male and female Whistling Swans and implications of male incubation. *Wildfowl 37*, 5-27.

Inglis, I. R. 1977: The breeding behaviour of the Pink-footed Goose: behavioral correlates of nesting success. *Anim. Behav. 27*, 747-764.

Kistchinski, A. A. & Vronski, N. V. 1979: Migrations of Brant. In: Migrations of birds of Eastern Europe and Northern Asia, Ciconiiformes-Anseriformes. Publishing house Nauka, Moscow. Pp 188-194.

Kumari, E. E. 1979: Status of *Branta bernicla bernicla* on passage in Baltic USSR. In Smart, M. (ed): Proceedings of the First Technical Meeting on Western Palearctic Migratory Bird Management, Paris 1977. Slimbridge: International Waterfowl Research Bureau.

Lambeck, R. H. D. 1990a: The applicability of age ratio and brood size counts in population dynamic studies of the Brent Goose *Branta b. bernicla*. *Ardea 78(3)*, 414-425.

Lambeck, R. H. D. 1990b: Differences in migratory pattern and habitat choice between social classes of the Brent Goose *Branta b. bernicla*. *Ardea 78(3)*, 426-440.

Lampio, T. 1979: Status of *Branta bernicla bernicla* in Finland. In Smart, M. (ed), Proceedings of the First Technical Meeting on Western Palearctic Migratory Bird Management, Paris 1977. Slimbridge: International Waterfowl Research Bureau.

Madsen, J., Bregnballe, T. & Mehlum, F. 1989: Study of the breeding ecology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota*. *Polar Res. 7*, 1-21.

Owen, M. 1987: Brent Goose *Branta b. bernicla* breeding and lemmings – a re-examination. *Bird Study 34*, 147-149.

Prop, J. & Deerenberg, C. 1991: Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia 87*, 19-28.

Prop, J., van Eerden, M. R., Daan, S., Drent, R. H., Tinbergen, J. M., St.Joseph, A. M. 1980: Ecology of the Barnacle Goose *Branta leucopsis* during the breeding season: preliminary results from expeditions to Spitsbergen in 1977 and 1978. Pp. 50-112 in Proc. Norwegian-Netherlands Symp. Svalbard. Arctic Centre, Groningen.

Prop, J., van Eerden, M. R. & Drent, R. H. 1984: Reproductive success of Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. Nor. Polarinst. *Skr. 181*, 87-117.

Raveling, D. G. 1978: The timing of egg laying by northern geese. *Auk 95*, 294-303.

Raveling, D. G. 1989: Nest-predation rates in relation to colony size of Black Brant. *J. Wildl. Manage. 53(1)*, 87-90.

Roselaar, C. S. 1979: Fluctuaties in aantallen Krombekstrandlopers *Calidris ferruginea*. *Watervogels 4*, 202-210.

Ryhlikova, M. E. 1993: Lemmings in the West Taimyr Arctic: Population density, distribution of territories and relation with other animals. Bericht über die Deutsch-Russischen Biologen-Expeditionen nach Taimyr in den Jahren 1989, 1990 und 1991. WWF-Deutschland, Husum.

St.Joseph, A. K. M. 1982: Review of the status of *Branta bernicla bernicla*. In Scott, D. A. & Smart, M. (eds), Proceedings of the Second Technical Meeting on Western Palearctic Migratory Bird Management, Paris 1979. Slimbridge: International Waterfowl Research Bureau.

St. Joseph, A. K. M. 1991: Status of the Brent Goose *Branta bernicla*, 1986–89, Dark-bellied Brent. *IWRB Goose Research Group Bulletin. 1*, 4–5.

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. & Underhill, L. G. 1987: Factors related to breeding production of Brent Geese and waders on the Taimyr Peninsula. *Bird Study 34*, 161–171.

Summers, R. W. & Underhill, L. G. 1990: Multivariate analyses of breeding performance in Dark-bellied Brent Geese *Branta b. bernicla*; comment. *Ibis 132*, 477–481.

Summers, R. W. & Underhill, L. G. 1991: The growth of the population of Dark-bellied Brent Geese *Branta b. bernicla* between 1955 and 1988. *J. Appl. Ecol. 28*, 584–585.

Thompson, S. C. & Raveling, D. G. 1987: Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. *Auk 104*, 707–716.

Thompson, S. C. & Raveling, D. G. 1988: Nest insulation and incubation constancy of arctic geese. *Wildfowl 39*, 124–132.