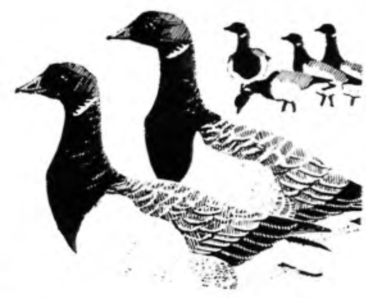
Post-hatching behaviour of Light-bellied Brent Geese *Branta bernicla hrota*



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Time budgets, spacing and antipredator behaviour of Light-bellied Brents were studied on an island in southeast Svalbard during the first three weeks of post-hatching. Male parents spent equal amounts of time on feeding and vigilance (33%), whereas females grazed more (46%) than they were vigilant (16%). For all geese more resting took place at night than around midday. Vigilance in the head up posture was less frequent during night than during day. At the time of loss of remiges non-breeder feeding activity declined from 60% to 35%; they flocked and began to follow families, even though attacked by male parents. When parents began moulting their remiges they became more gregarious and more tolerant towards non-breeders. Short distances between family members and between families, a high frequency of alert behaviour and effective antipredator responses including collective protection are suggested to account for the survival of all 90 goslings in the study area. We discuss how changes in the risk of predation of goslings and adults influence the extent of flocking.

The Svalbard population of the Light-bellied Brent Goose *Branta bernicla hrota* numbers 3000-5000 individuals and displays low and varying reproduction success (Madsen 1984, 1987 unpubl.). Until recently factors contributing to poor performance were unknown. In 1987 a study of the breeding ecology of the geese was conducted at the main breeding resort, Tusenøyane, in southeast Svalbard and it was shown that nest predation by Arctic Skuas *Stercorarius parasiticus* and polar bears *Ursus maritimus* was the major factor causing low hatching success (Madsen, Bregnballe & Mehlum 1989). In this paper we explore correlates between post-hatching behaviour, spacing and breeding success in the Light-bellied Brent on Tusenøyane, based on observations during the first three weeks after hatching in 1987. Special attention is paid to how the geese modify their behaviour and sociability to reduce the risk of predation on both the goslings and grown birds.

Study Area and Methods

The study was carried out on the 22 ha islet, Kalvøya (77°05'N, 22°00'E), in the Tusenøyane archipelago in southeast Svalbard. The archipelago is the major breeding area for the Svalbard population of the Light-bellied Brent (Madsen, Bregnballe & Mehlum 1989). Kalvøya was the brood-rearing area for seven Brent families and moulting area for 22 non-breeders or failed breeders (referred to as non-breeders). Potential avian predators were four breeding pairs of Glaucous Gull *Larus hyperboreus*, one pair of Arctic Skua and non-breeding individuals of three other species of skua which occasionally visited the area. Arctic foxes *Alopex lagopus* were absent.

In July 1987 daily temperatures ranged between -2° and 7°C; precipitation was low but the air was humid with fog c.20% of the time.

The vegetation in the brood rearing areas was dominated by mosses with protruding *Cochlearia officinalis, Saxifraga hyperborea* and *Carex* spp. at low frequencies. During the first three weeks of post-hatching mosses constituted the staple diet of parent Brent Geese but they selected *Cochlearia.* Goslings also took mosses but *Cochlearia* and *Saxifraga* dominated the diet (Madsen, Bregnballe & Mehlum 1989).

Observations were made through telescopes (20-60x) from the neighbouring island, Lurøya, from 7-27 July. Distance between the observer and the geese ranged from 600-900 m, and we observed no behavioural responses elicited by our presence. Behaviour and spacing were recorded by instantaneous scan sampling (Altmann

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1974) at intervals of 5 or 10 minutes, depending on the number of geese present. Observation periods varied between 1-10 hours, covering the whole diurnal cycle and attempting to spread observations evenly over the three weeks.

Behaviour was classified according to the position of the head and neck (Lazarus & Inglis 1978), and named according to its main function: graze, preen, threat, rest (head low or on back, only occurring when sitting), vigilance in head up (common in all locomotory states), vigilance in extreme head up (occurring mostly when standing and walking). For goslings only the main activity of the brood was recorded; rest includes being brooded as well as sitting without being brooded.

Spacing of families was recorded by: distance between the most distant gosling and the nearest of its parents; distance between male and female; distance from the middle of the family to the nearest member of another family as well as to the nearest non-breeder. The distance between mates of non-breeders was recorded as long as pairs could be distinguished (until 9 July). Distances were estimated to the nearest meter from 0 to 15 m and rounded to the nearest whole 10 m from 15 to c.120 m.

When potential predators approached, or intra- or intergroup interactions appeared during scans, as many aspects of behavioural reactions as possible were recorded. Adults were sexed by neck and body size. The stage of wing-moult in adults was ascertained by observing the remiges when wings were spread. Gosling age was either known from observation of hatching date or estimated from gosling size and feather development. On Lurøya brood sizes in 11 families were checked regularly and some observations were made on behaviour. There appeared to be no interchange of families between the islands.

Differences in time budgets were tested using chi-square statistics. The criteria for chi-square tests (observed frequencies must be independent) are not strictly fulfilled because data were collected from the small number of geese and individuals tended to synchronise behaviourally. Differences in distances were tested using the Kolmogorov-Smirnov two sample test, referred to as the K-S test.

Results

Time of hatching and moult

Most observations (90%) were from six families hatching 4-9 July, so the most-studied goslings were 18-24 days old when observations stopped. The brood sizes of all seven families were 1, 1, 2, 2, 4, 4, and 4, respectively. After hatching the families left the nest within 8-36 hours (n = 4). Two families returned the following night to brood the goslings in the nest. In the following analysis we have only described the behaviour after final nest departure. For statistics regarding hatching success in the study area, see Madsen, Bregnballe & Mehlum (1989).

The first three weeks of the post-hatching season were divided into three 7-day periods, roughly corresponding with the state of wing-moult.

I) 7-13 July: both non-breeders and parents were able to fly.

II) 14-20 July: non-breeders lost their ability to fly, e.g. on 16 July only two of 22 were able to fly.

III) 21-27 July: parents lost their remiges; on 24 July most parents were unable to fly.

Time budgets

Parents, non-breeders and goslings differed in

Table 1. Overall time budget (%) for male and female parent, gosling and non-breeding Brent Geese during the first three weeks of post-hatching. n is the total number of behavioural records. Females v males: total time budget χ^2 = 237, df = 5, P<0.001; each behaviour df = 1, P<0.001 for all except preen P>0.9. Females v non-breeding geese: total time budget χ^2 = 34.4, df = 5, P<0.001; each behaviour df = 1, P<0.001 for graze and preen, df = 1, P>0.1-0.9 for others. Males v non-breeding geese: total time budget χ^2 = 427, df = 5, P<0.001; each behaviour df = 1, P<0.001 for all. Goslings v female and goslings v males, df = 1, P<0.001 for all.

	Graze	Rest	Preen	Vigilance head up	Vigilance extreme head up	Threat	n
Female parents	46.1	34.0	2.1	15.0	1.2	1.6	1698
Male parents	33.3	27.3	1.8	21.2	11.7	4.7	1677
Goslings	54.9	41.4	-	3.7	-	-	1613
Non-breeders	40.0	35.7	4.7	16.8	0.9	1.0	3257

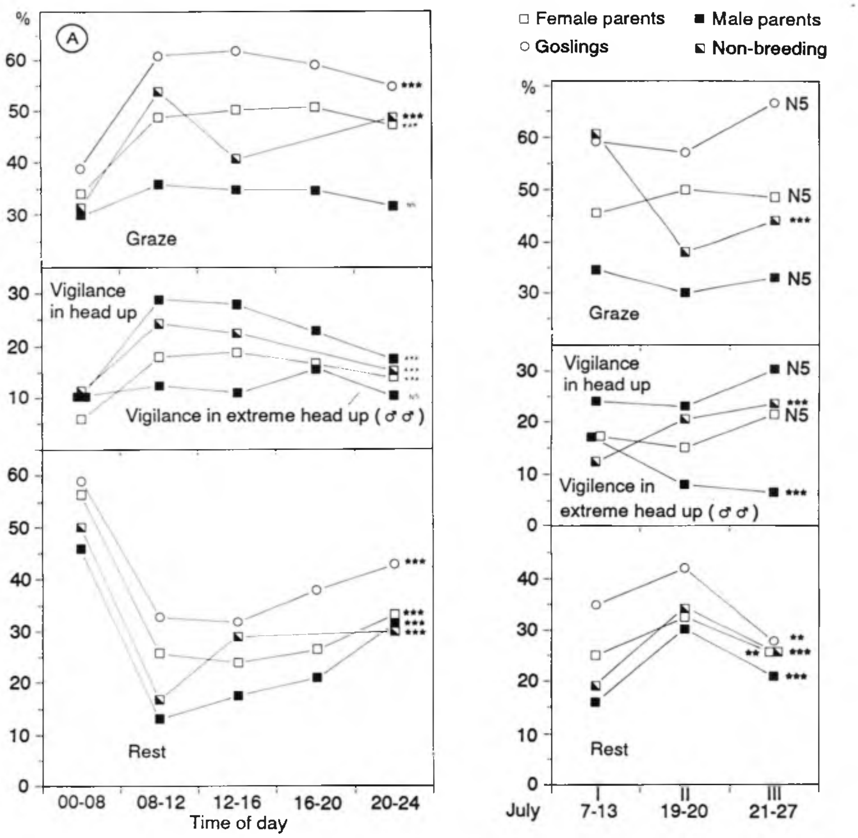

Figure 1. Variation during 24 h (A) and during the post-hatching period (B) of the most common behaviour classes for male and female parents, goslings and non-breeding Brent Geese. Behaviour for each category of individuals was 230-1200 times within each of the five diurnal periods (A) and 240-800 times between 08.00 and 24.00 h within each of the three 7 day periods (B). Tests of total time budgets for each category of individuals A: females $\chi^2 = 128$, df = 12, $P<0.001$; males $\chi^2 = 160$, df = $P<0.001$; goslings $\chi^2 = 69$, df = 4, $P<0.001$; non-breeders $\chi^2 = 232$, df = 12, $P<0.001$. B: females, total time budget $\chi^2 = 52$, df = 6, $P<0.001$; males $\chi^2 = 63$, df = 8, $P<0.001$; goslings $\chi^2 = 23.5$, df = 6, $P<0.05$; non-breeders $\chi^2 = 99$, df = 8, $P<0.001$. Significance levels of each behaviour shown by * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$.

the amount of time devoted to most behaviour classes (Table 1). Female parents grazed and rested more than male parents. Males were more vigilant than females, especially in the extreme head up posture, and they devoted more time to threatening. Before parents started moulting the frequency of extreme head up was lower in male parents when the family grazed less than 15 m from nearest other family compared to grazing farther away (21.7% of the time extreme head up when more than 25 m to nearest family (n = 106); 21.4% for 15-25 m (n = 70) and 9.4% for less than 15 m (n = 134); $\chi^2 = 8.4$, df = 2, $P<0.05$).

Brood size had no apparent effect on how male parents and goslings allocated time to the various classes of behaviour in the total time budget (males $\chi^2 = 12.8$, df = 10, $P>0.2$; gos-

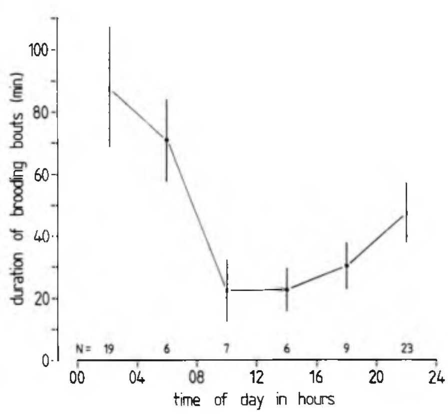

Figure 2. Diurnal variation in duration of mean brooding bouts in minutes. N is sample size, vertical bars are 95% confidence limits. Result of t-test for 00.00-08.00 v 08.00-24.00 h is t = 36.1, df = 68, $P<0.001$.

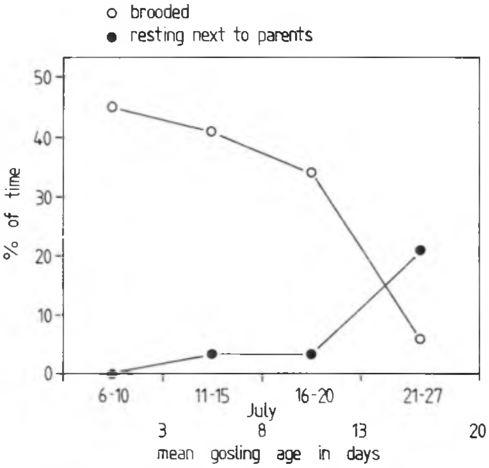

Figure 3. Variation in time Brent goslings devoted to brooding and resting next to parent without being brooded, respectively, during the post-hatching period.

lings χ^2 1.8, df = 4, P>0.8). In females the total time budget differed somewhat between families but with no trend in relation to the number of young in the family (across different brood sizes, χ^2 = 14.2, df = 6, P<0.05), indicating that individual differences in behaviour may have had a prominent effect.

Compared to male parents, non-breeders spent more time grazing and resting but less time in vigilance in extreme head up and in head up (the frequency of vigilance in head up was only higher in male parents when the geese were sitting).

Grazing and vigilance was lowest during the night, except for male parents which both grazed and kept vigil in extreme head up with the same intensity throughout the 24 h (Fig. 1 A). More time was spent resting during the night than during daytime. Goslings were mostly brooded in the evening and at night and brooding bouts were longer during the night (Fig. 2). Resting without being brooded was seen only between 10.00 and 14.30 h (n = 23).

Behaviour changed during the three-week period (Fig. 1 B). In the first week non-breeders spent considerably more time feeding than parents. In the second week grazing in non-breeders had declined markedly and vigilance in head up posture increased. This change coincided with

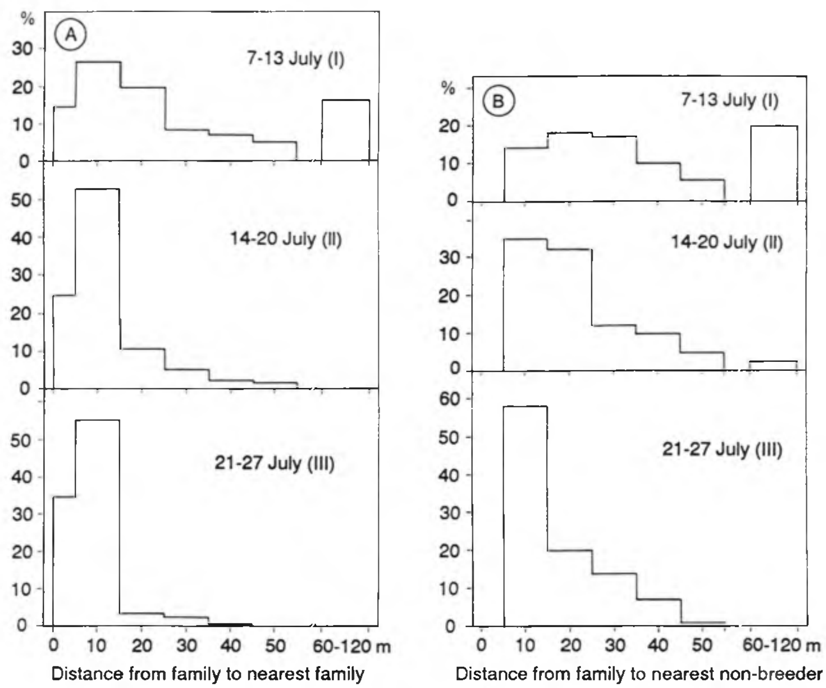

Figure 4. Spacing pattern in active (not sitting) adult Brent Geese during the first three weeks of post-hatching. A: distance from the middle of each family to the nearest member of another family (mean values/sample sizes are: 26.5 m/201, 18.8 m/221 and 9.2 m/121 in periods I, II and III, respectively). B: distance from the middle of each family to the nearest non-breeder (mean values/sample sizes are: 43.0 m/208, 22.5 m/112 and 17.7 m/92). Kolmogorov-Smirnov test with df = 2: (A) I v II χ^2 = 39.7, P<0.001; (A) II v III χ^2 = 6.8, P<0.05; (B) I v II χ^2 = 28.3, P<0.001; (B) II v III χ^2 = 7.2, P<0.05.

the loss of remiges and more walking and running to keep close to the families. In male and female parents the frequency of vigilance in head up increased from period I and II to III but the change was not statistically significant (neither when I and II were analysed separately nor combined v III). Over the period, male parent frequency of vigilance in extreme head up decreased. The increase in time spent resting from first to second week in all geese coincided with reduced spacing; in the third week the flock preferred to rest on a plateau which was not visible from the observation post. Females stopped brooding their goslings when they were about two weeks old, after which goslings rested next to their parents (Fig. 3).

Spacing and social behaviour

Within the families mates walked less than 3.5 m apart for 87% of the time when active, i.e. both parents not sitting (n = 974). When passive, i.e. both parents were sitting, they were less than 1.5 m from each other for 83% of the time (n = 706). Mates with four goslings kept a larger distance between each other when active than mates with one gosling (K-S test, n = 517 and n = 257, χ^2 = 14.6, df = 2, P<0.001). Male-to-female distance was intermediate in the families with two goslings but not significantly different from the one or four gosling families (K-S test, not significant). Mate distance when active did not change significantly with time (K-S test, not significant).

Maximum adult-gosling distance was significantly shorter in families with one gosling than in families with two or four goslings (mean was 1.3 m, 1.8 m and 2.1 m, respectively; K-S test, 1 v 2, n = 228 and n = 157, χ^2 = 25.5, df = 2, P<0.001; 1 v 4, n = 536, χ^2 = 92.4, df = 2, P<0.001; 2 v 4 χ^2 = 6.7, df = 2, P<0.05). Adult-gosling distance increased from the first to the second week in families with four goslings (mean was 1.8 m and 2.3 m, respectively; K-S test, n = 246 and n = 196, χ^2 = 25.1, df = 2, P<0.001) but the change was not significant in families with one or two goslings. There was no significant increase in parent-gosling distance from second to third week (K-S test, not significant). Brood-mixing, where non-related goslings grazed among each other, was seen several times but only in three cases did a gosling follow the wrong family when separating and then for less than 10 minutes.

Spacing between families ranged from totally separate to company of two families for short periods during the first days after nest departure (Fig. 4 A). Three occasions of strong agonistic encounters between families were observed in the first days of brood rearing. At the end of the first week and during the second week families were seen in one or two flocks varying in density (from loose to dense). During the last week resting and grazing almost exclusively took place in one dense flock (Fig. 4 A). Thus, mutual distances between families decreased during the first three weeks of the post-hatching period (Fig. 4 A). On Lurøya a similar pattern was observed: the families were totally separated in the first two to three days after hatching; later a loose flock was established, and after moulting had started all eleven families stayed together in one dense flock and usually close to a lake.

Prior to moulting non-breeding males and females kept a longer distance from each other than female and male parents (male-to-female distance in parents v male-to-female distance in non-breeders: when active mean distance was 2.3 m and 5.5 m, respectively; K-S test, χ^2 = 185, df = 2, P<0.001; when passive mean distance was 1.2 m and 1.9 m; χ^2 = 113, df = 2, P<0.001). Until 9 July, non-breeding pairs grazed in unstable and loose flocks after which they became more gregarious and, from about 14 July, they all grazed and rested in one flock. A similar change in spacing occurred in Lurøya.

The distance between families and non-breeders declined through the study period both when active (Fig. 4 B) and when passive (K-S test, I v II, n = 133 and n = 180, χ^2 = 27.4, df = 2, P<0.001; II v III, n = 40, χ^2 = 18.5, df = 2, P<0.001). Thus, pairs of non-breeders grazed and rested independently of the families when the goslings were only a few days old. Within the first week non-breeders began to follow one or more of the families and grazed and rested close to these (less than 20 m distant). The families often avoided the proximity of non-breeders by walking or running from them, alternatively the male parents attacked the non-breeders, often so vigorously that both female and goslings were left 30-50 m behind. In the second and especially in the third week parents tolerated grazing and resting non-breeders within closer ranges. Thus, the distance triggering attacks from male parents dropped from a mean of 18.6 m in the first period to 12.7 m in the second period (K-S test, n = 23 and n = 26, χ^2 = 8.1, df = 2, P<0.05); furthermore, after 22 July attacks were not observed. On Lurøya the non-breeders grazed independently of families until 16 July; from then on they were always seen together with families.

Responses to predators

Only Arctic Skuas approached the families regularly and mostly during afternoon and evening; thus 19 of 21 observations were made between 12 and 22 hours. Reactions to approaching skuas included: increased vigilance (observed 5 times); vigilance and threat (4); vigilance, threat and goslings seeking protection (1); vigilance, threat, goslings seeking protection and families running to nearest other family (6) and, all families crowded and parents jointly defended related as well as unrelated goslings (1). The sequence of events of this collective protection was as follows: parents ran to the centre of the loose flock, all goslings huddled and formed one group, parents encircled the goslings with wings raised and necks stretched towards the avian predator. On Lurøya we twice observed such collective protection of goslings against skuas. There was no trend over time in the vigour of response nor in the frequency of attacks.

When the non-breeders lost their ability to fly they responded to attacks and mobbing by Arctic Skuas by crowding, followed by running in a dense flock up to the family flock ($n = 5$). The escape pattern of the moulting Brent Geese differed markedly from that of a flock of 21 non-breeding Barnacle Geese *Branta leucopsis* which also grazed on Kalvøya. The Brent Geese always ran up the slopes towards the middle of the island, whereas the Barnacle Geese always escaped to the sea. Throughout the moult the Barnacle Geese stayed close to the water and never moved more than 70-100 m inland.

Discussion

The overall time budgets in the Light-bellied Brent families resemble those found in other goose species: guarding of the family was primarily provided by the male allowing the female to spend time feeding (Ebbinge & Ebbinge-Dallmeijer 1977, Lazarus & Inglis 1978, Prop *et al.* 1980, Madsen 1981, Lessells 1987). The Brent females increased the time spent grazing from 6% during the nesting phase to about 46% after hatching, whereas the males grazed for about one third throughout (Madsen, Bregnballe & Mehlum 1989). This suggests that the share of duties provided a balance in energetics between the mates over the breeding cycle.

Skuas regularly attacked the families but with little success. Thus, all 90 goslings on Kalvøya and Lurøya survived the first three weeks of the fledging period. This strongly indicates that the risk of gosling predation was minimised as a result of parental behaviour.

The frequency of vigilance in extreme head up was low in non-breeders and high in male parents. The time spent in the posture by males decreased from the first to the second week and remained low after loss of remiges. This supports the suggestion by Lazarus & Inglis (1978) that the posture is an investment in parental care (see Lazarus & Inglis (1978) for functional interpretation of the posture); in the present study it cannot be ruled out, however, that the decrease in frequency was partly due to a simultaneous decrease in inter-family distance and hence share of vigilance between males. The frequency of extreme head up in male parents was low compared to studies of other goose species (Lazarus & Inglis 1978, Madsen 1981, Lessells 1987). In the other studies, arctic foxes were present and the difference may indicate that the use of the posture is adjusted to the predator environment (predators presence and encounter rates), which has been indicated by studies of Pellis & Pellis (1982) and Giroux, Bédard & Bédard (1986). Species-specific differences and other area-specific variables, e.g. escape possibilities, can probably also account for the amount of time allocated to vigilance.

What are the possible advantages of flocking and what are the reasons behind the observed changes in spacing over time from totally separated families to loose flocks and from loose flocks to one dense flock? Here, we address five parental considerations which must be balanced: (1) imprinting, (2) feeding efficiency, (3) sharing of parental investment with other parents, (4) reducing risk of gosling predation, (5) reducing risk of predation of oneself.

It might be expected that families would flock immediately after hatching when the risk of losing goslings to avian predators is highest (MacInnes 1962, Mickelson 1975). However, in contradiction to this, we observed parental aggression directed against other families and long inter-family distances during the first days of brood rearing. A possible explanation is that avoidance of other families enhances bond-binding and imprinting of goslings to their own parents, reducing the risk of permanent brood-mixing after crowding of families.

The families avoided and vigorously attacked the non-breeding geese, possibly because their proximity interfered with feeding efficiency which is highly desirable for females and goslings (Lazarus & Inglis 1978). On the other hand, these attacks were incompatible with ensuring a low risk of gosling predation because during attacks vigilance decreased and distance from goslings to parents increased. A possible reason why the distance to non-breeders triggering attacks decreased was that the loss of remiges reduced male parents' ability to attack and at the same time protect goslings.

It has been suggested that one advantage of flocking is that individuals can share vigilance and thereby increase the time available for other activities, e.g. foraging (e.g. Lazarus & Inglis 1978, Fox & Madsen 1981). Our observation that the frequency of vigilance in extreme head up by male parents is lower when families are close together supports this.

Following the first days of brood-rearing, one of the parental benefits of flocking was that it enabled them to reduce the risk of gosling predation through collective defence. The phenomenon of group defence might be explained as an adaptation by a small goose species to improve protection.

Thus, reducing the risk of gosling predation and sharing of vigilance explains the amalgamation of families but does not provide sufficient explanation for why the families flocked even more densely with time. Because both presumably the risk of avian predation of goslings decreased with growth in goslings and dense flocking was probably incompatible with high feeding efficiently it could therefore be expected that the demand for flocking would decrease with time.

However, during moult running to the sea or inland becomes the only way that adults can escape from predators and therefore it would be expected that the demand for early detection of predators would increase in all adults at the time of moult. The non-breeding Brent seemingly met this demand by increasing overall vigilance through following families, lowering nearest neighbour distance combined with increasing vigilance in the head up posture. Therefore we find it reasonable to conclude that the further increase in the proximity of families occurred because parents became more vulnerable to predation by the larger skua species or by arctic foxes. Arctic foxes were not present in 1987 but in 1989 they were found to be numerous on the islands (Madsen, Bregnballe & Hastrup in prep.).

In the above discussion we have implicitly suggested that parental behaviour during the post-hatching period has evolved through selection for behaviour which adds positively to lifetime reproductive success of the individual. Thus, we argue that the observed time budgets and changes in behaviour and spacing reflect different parental considerations, viz ultimately securing own, mate and gosling survival - demands which may at times override and possibly even contradict each other.

Fridtjof Mehlum and Norsk Polarinstitutt are thanked for invaluable support making the study possible. We thank J.M. Black, J. Lazarus and an anonymous referee for comments on the manuscript.

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*Communication no. 233 from the Division of Wildlife Ecology, National Environmental Research Institute.

Figure 5. Brent Geese families in Svalbard, summer 1987. *Photographed by J. Madsen*