J. Ornithol. 143, 33–42 (2002)

ISSN 0021-8375

How do Brent Geese (*Branta b. bernicla*) cope with evil? Complex relationships between predators and prey

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Summary

Actual predation is rarely observed in the field, and therefore the role of predators is often severely underestimated. Species are limited in their distribution, which is caused not only by predation but also by the anti-predator behaviour that prey-species have developed under the continuous selection pressure of predators. How finely tuned this behaviour can be, is illustrated in this paper by the way in which Dark-bellied Brent Geese play one predator against another. Snowy Owls keep Arctic Foxes at bay, and so in years when lemmings are abundant Brent Geese can safely nest in association with nesting Snowy Owls. However, this is dangerous in years when lemmings are scarce and Snowy Owls revert to a predatory species that can even take adult Brent Geese on the nest. Another, more common, nesting strategy of Brent Geese is to nest inside Herring Gull colonies on small islands. Herring gulls are not a threat to adult geese, but they can take goose eggs as well as taking a particularly high toll by preying on newly hatched goslings. On the other hand, Herring Gulls are probably useful to Brent Geese as indicators of places which will become fox-free islands after the ice break-up. Moreover the gulls provide additional protection against Snowy Owls as well as against other gulls. Furthermore, through fertilisation by their droppings, the gulls provide the nesting geese with high quality grass during the incubation period. Predator activity and abundance in the arctic is largely a factor of lemming abundance. This paper highlights the ideas we have developed about the impact of predators by comparing data on the breeding success of Brent Geese nesting in the same study area during two complete lemming cycles between 1990 and 1995.

Keywords: breeding success, predation, lemming cycle, Arctic Fox, Snowy Owl, Taimyr.

Zusammenfassung

Wie gehen Ringelgänse (*Branta b. bernicla*) mit Feinden um? Komplexe Räuber-Beute-Beziehungen

Prädation ist nur selten direkt beobachtbar und so schwer zu quantifizieren. Die Verteilung von Arten ist nicht nur durch Prädation bestimmt, vielmehr kann auch die Räubervermeidung eine Rolle spielen. Wie eng verzahnt dies sein kann, zeigt diese sechsjährige (1990–1995) Studie an Ringelgänsen auf der Taimyr-Halbinsel. In Jahren mit vielen Lemmingen brüten Ringelgänse gemeinsam mit Schneeeulen, die die Polarfüchse vom Brutplatz fern-

halten. In Jahren mit wenigen Lemmingen dagegen jagen die Schneeeulen Ringelgänse; sie werden vom „Beschützer" zum Räuber. Eine andere Strategie der Ringelgänse ist, auf kleinen Inseln innerhalb von Silbermöwenkolonien zu brüten. Silbermöwen können zwar erhebliche Prädation auf Eier und vor allem frisch geschlüpfte Ringelgänse ausüben. Der Vorteil für die Ringelgänse scheint aber darin zu liegen, dass die Silbermöwen zum einen anzeigen, dass die Inseln frei von Füchsen sind, und zum anderen schützen Silbermöwen vor Schneeeulen. Zudem profitieren die Ringelgänse von der Düngewirkung des Silbermöwenkotes auf die Vegetation. Innerhalb von Silbermöwenkolonien ist die Vegetation reicher als außerhalb. Um Prädation zu vermeiden, begrenzen die Ringelgänse also aktiv ihren Lebensraum. Der wirklich von Ringelgänsen benutzbare Teil der Arktis ist durch Prädatoren und Prädation vermeidendes Verhalten der Gänse eingeschränkt, wodurch die Populationsgröße limitiert ist.

Introduction

The arctic ecosystem is less complex than ecosystems in the temperate zone, not to mention ecosystems in the tropics. Yet the relationships between predators like Arctic Foxes (*Alopex lagopus*), Snowy Owls (*Nyctea scandiaca*), gulls (*Larus argentatus* and *Larus hyperboreus*) and their prey species such as lemmings (*Lemmus sibiricus* and *Dycrostonyx torquatus*), birds and birds' eggs are still far from simple. By studying the same colony of Dark-bellied Brent Geese (*Branta b. bernicla*, hereafter refered to as Brent Geese) for six years in a row, and comparing our data with occasional results obtained by others elsewhere on the Taimyr peninsula, we have discovered complicated relationships that all depend on the cyclicity in the abundance of lemmings.

Brent Geese usually nest on small islands close to the shore or in river deltas inside gull colonies, but in lemming peak years they can also be found nesting scattered on the tundra (Kokorev, pers. comm.). The breeding success of Brent Geese and of many wader species (Charadrii) nesting on the Taimyr Peninsula is highly correlated with lemming cycles (Roselaar 1979, Summers 1986, Summers & Underhill 1987, Greenwood 1987, Krebs 1993). The lemming cycle on the Taimyr Peninsula shows a marked periodicity of three years (Rykhlikova & Popov 2000). Brent Geese breed very well in lemming peak years, invariably fail to produce significant numbers of offspring in the year after a lemming peak, but in the third year of the lemming cycle the breeding success of Brent Geese is unpredictable.

Though many other factors, like body condition achieved on the spring staging areas and wind conditions during spring migration, have an impact on the breeding success of this high arctic migratory bird species (see Ebbinge 1989, Ebbinge & Spaans 1995, Ebbinge et al. 1999), none of them can explain the observed marked fluctuations in breeding success.

Summers & Underhill (1987) proposed the prey-switching hypothesis, which states that the assumed main predator for Brent Geese, the arctic fox (*Alopex lagopus*), concentrates on lemmings in lemming peak years, thus allowing waders and Brent Geese to nest safely in such years. After lemming densities have crashed in the following year, arctic foxes are assumed to turn to alternative prey items such as nesting birds and in particular their eggs, with a completely failed nesting season as a result, as indicated by surveys on the wintering grounds which show a complete lack of birds in first-winter plumage.

In this paper we present the main ideas we have developed about how lemmings and predators interact, and have an impact on the conditions in which Brent Geese nest, moult and raise goslings. This impact depends heavily on the phase of the lemming cycle.

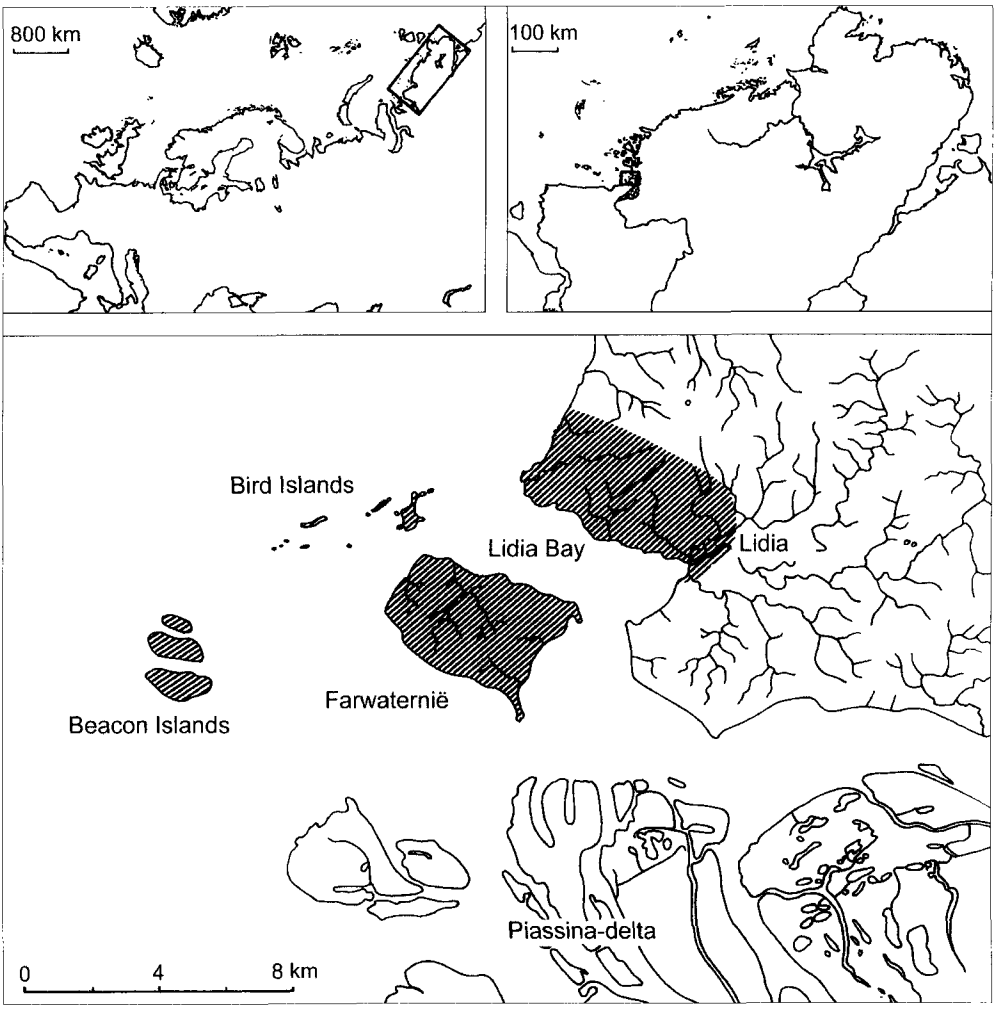

Fig. 1. Study area (hatched) along Lidia Bay and the Bird and Beacon Islands in western Taimyr. The two maps on top indicate the location of this area on a larger scale.
Abb. 1. Untersuchungsgebiet (gestrichelt) entlang der Lidia Bucht und der Vogel- und Bakeninseln auf der westlichen Taimyr. Die beide oberen Karten zeigen die Lage in einem größeren Maßstab.

Study area and methodology

In 1990 we started a six-year programme studying the factors that determine the breeding success of Brent Geese. We decided to restrict our study to a single locality over a period covering two complete lemming cycles, and chose Lidia Bay (74.07 North; 86.50 East) in the Pyasina delta as a focal area. The study area (Fig. 1) encompasses a total area of 36 km^2 of which 10 km^2 consists of tundra vegetation with many small streams, easily accessible to Arctic Foxes after mid June when most of the ice has melted. Out in the bay are 4 smaller islands with rocky outcrops (the Bird Islands), and further out three quite large flat islands (the Beacon Islands) with many shallow lakes with a total area of 1 km^2. For a more detailed description see Spaans et al. (1993).

Table 1. Nest predation by Arctic Foxes around Lidia Bay and Bird Islands (n. a. = not applicable).
Tab. 1. Prädation von Nestern durch Polarfüchse am Festland um Lidia Bucht und auf den Vogelinseln (n. a. = nicht vorhanden).

		On mainland Auf dem Festland		On gull islands Auf den Möweninseln		
Year Jahr	Lemming index	Goose nests Gänsenester	Predation	Goose nests	Predation	Fox index
1990	0.3	12	0 %	252	0 %	0
1991	10.4	9	100 %	291	0 %	1
1992	1.2	0	n. a.	15	7 %	39
1993	1.7	15	20 %	251	0 %	0
1994	10.0	6	67 %	243	0 %	0
1995	0.4	0	n. a.	381	0 %	0

An international team with Dutch, Russian, English, German and Polish biologists annually surveyed the entire study area for nesting Brent from 1990 to 1995 (see Fig. 1, and Spaans et al. 1993). All nests were counted and from a sub-sample clutch sizes were established in the first week of July, when all geese were incubating. This means that the clutch size does not reflect the total number of eggs laid per goose, but the net result of eggs laid minus eggs lost through predation. After the eggs had hatched (usually around 20–25 July), all nests were revisited to establish the proportion of eggs that had hatched successfully. The total number of surviving goslings in the moulting flocks was used to estimate gosling survival. Direct observations on goose families departing from the Bird Islands provided extra information on the extent of gosling predation by gulls. Also the number of gull nests on each island were counted annually, as well as the number of nesting and non-nesting Snowy Owls. All fox dens throughout the whole study area were examined as to the presence of foxes, and fox visits to the main Bird Island were registered as an index of fox presence during the first ten days after arrival of the first Brent Geese (usually 10–20 June; Spaans et al. 1998).

In these six consecutive years lemming abundance was studied by means of standard trapping methods (Rykhlikova & Popov 2000). The abundance of lemmings is calculated as an index which expresses the number of trapped lemmings per 100 trapping days. One trapping day represents one trap open and able to make a catch for a period of 24 hours. Each year the study team was present before the arrival of the first Brent Geese in early June. In 1990 and 1992 it left the study area was as early as July, but in 1991, 1993, 1994 and 1995 the study team remained in the area till mid-August in order to study the distribution of moulting Brent Geese and to catch them for ringing. During these surveys a wider area up to 30 km to the north of the Bird Islands was surveyed, and moulting Brent Geese and their goslings were caught and marked with colour-rings in 1991, 1993, 1994 and 1995.

Within the frame-work of the Great International Arctic Expedition, however, many other sites on the Taimyr Peninsula were visited by research teams, and their results, too, contributed greatly to the ideas we were able to develop about the key factors that influence Brent Goose breeding success.

Table 2. Clutch size of Brent Goose nests on Bird Islands and gosling predation by gulls.
Tab. 2. Gelegegröße von Ringelgänsen auf den Vogelinseln und Prädation von Küken durch Möwen.

Year Jahr	Lemming index	Number of goose nests Anzahl Nester	mean clutch size mittlere Gelegegröße	Gosling predation by gulls Prädation von Küken durch Möwen
1990	0.3	252	3.0 (n = 72)	some
1991	10.4	291	3.8 (n = 130)	70 %
1992	1.2	15	?	n. a. (fox year)
1993	1.7	251	2.9 (n = 129)	90 %
1994	10.0	243	3.8 (n = 101)	80 %
1995	0.4	381	2.8 (n = 245)	99 %

Results

Lemmings

Two species of lemmings occurred in our study area: *Lemmus sibiricus* and *Dicrostonyx torquatus*. During peak years especially the former was extremely abundant. As can be seen in Tables 1 and 2 the lemming density followed a clear-cut three-year cycle, being more than ten times as abundant in the peak years 1991 and 1994.

Arctic Foxes

The fox dens in our study area were not occupied in 1990, and in that summer we did not observe a single Arctic Fox. In 1993, despite the low numbers of lemmings one fox den was still occupied in which cubs were successfully raised. In the lemming peak years 1991 and 1994 at least two fox dens within our study area were occupied by foxes with young.

In 1992 none of the fox dens was occupied, but many wandering foxes were observed in our study area, and even on the Bird Islands we sometimes observed up to three different foxes visiting on one day. This is the only year in which foxes visited these islands after the first geese had arrived (Spaans et al. 1998).

In 1995 we expected large numbers of foxes again, because of the lemming peak in the preceding year. However, many foxes had succumbed in the winter of 1994–95, and after the thaw many starved foxes were found in our study area. Only a few wandering foxes were observed in late July and August, but none of the dens was occupied.

Snowy Owls

In 1990 only 1 Snowy Owl was observed in the first week of June. Similarly in 1993 Snowy Owls were hardly ever observed in our study area.

In the two lemming years Snowy Owls nested within the study area on the mainland tundra and on the large island of Farwaternie. In 1991 1 pair successfully raised chicks and in 1994 6 pairs nested successfully. In the two years (1992 and 1995) following a lemming peak year, Snowy Owls were seen very regularly (in 1992 up to 30 individuals; and in 1995 up to 6 individuals), but did not nest. However, in 1995 several unsuccessful attacks by Snowy Owls on goose families were observed, and such attacks may well be the main reason why eventually all Brent Goose families returned to the Bird Islands with their goslings.

Herring Gulls

On the Bird Islands 3,000 pairs of Herring Gulls and about 10 pairs of Glaucous Gulls nested every year. In 1992, the only year that foxes regularly visited these islands, it was clear that the gulls were incapable of defend-

ing their nests against them. However, they still laid eggs, which were then taken and cached by foxes.

This observation showed that gulls can only nest successfully when they do so out of reach of Arctic Foxes. The breaking up of the ice (or the absence of foxes as in 1990) is therefore an essential prerequisite for the successful nesting of gulls. All gull colonies are situated on islands that are, in most years, inaccessibe to foxes.

In all years gulls were already present on their breeding islands on 1 June, well before the first Brent Geese arrived. Thus, by joining these gull colonies, Brent Geese, too, select fox-free areas. Only when foxes are very abundant and hungry, or when the ice breaks up very late, is there a risk that such islands may be visited by foxes.

Brent Geese nested successfully as little as one metre away from a gull's nest, and so obtained protection against other gulls through the efforts of the nest owner to drive them away from its own nest. Most predation on goose eggs by gulls seemed to take place around the perimeter of the colony, where many gulls were present, but very few of them defending territory against other gulls. As soon as the goslings had hatched, the parent geese tried to lead their goslings away from the gull islands and then, in particular on windy days, many goslings fell victim to gulls. On a calm day, however, many goose families successfully swam to the mainland, covering a distance of about 5–10 km.

Brent Geese

One of our first remarkable findings was that in the two lemming peak years (1991 and 1994) in areas outside our study area, where in other years hardly any Brent Geese were found nesting, Brent Geese successfully nested inside the territories of Snowy Owls (Underhill et al. 1993; Summers et al. 1994). Presumably Snowy Owls keep Arctic Foxes out of their territories and thus create 'safe havens' for Brent Geese to nest in. This conflicts with the simple prey-switching hypothesis, because Snowy Owls are known to nest only when lemming abundance is high, and the prey-switching hypothesis predicts that foxes will not be interested in other prey-items when lemmings are abundant. So, why then do Brent Geese nest near Snowy Owls in lemming peak years? Within our study area, aside from small numbers on the mainland tundra, Brent Geese nested on the Bird Islands (gull islands) where 3,000 pairs of Herring Gulls also nested (See Table 1).

Only in 1992 and 1995 were no Brent Goose nests found on the mainland. These two years were years following a lemming peak year. In both years there were considerably higher numbers of non-nesting Snowy Owls (10–30 individuals) in the study area than in other years.

In 1992 there were also very many Arctic Foxes, even on the gull islands (see fox index in Table 1). This fox index indicates the number of visiting foxes on the Big Bird Island during the first 10 days of nest initiation (10–20 June).

In 1995, fox numbers were extremely low despite the lemming peak in 1994. The local trapper had caught many foxes in the previous autumn, but apparently hardly any foxes had survived the winter.

The highest numbers of Brent Goose nests on the mainland was found in the years 1990 and 1993 when both predator numbers and lemming numbers were low, the so-called in-between years when lemming numbers are starting to build up again.

During the two lemming peak years, 1991 and 1994, Brent Geese also nested on the mainland, but despite the abundance of lemmings, most nests were still robbed by Arctic Foxes (see Table 1). Thus, even in lemming peak years Brent Goose nests are not safe from Arctic Fox predation on the mainland.

Within the study area in all six years the vast majority of Brent Goose nests were found on the Bird and Beacon Islands. The only exception was 1992, the year with many foxes,

Table 3. Distribution of moulting Brent Geese in Lidia Bay in relation to lemming cycles.
Tab. 3. Verteilung von mausernden Ringelgänsen um die Lidia Bucht in Beziehung zum Lemming-Zyklus.

Peak years Jahre mit Lemminghoch		Low years Jahre mit Lemmingtief		In-between years Zwischenjahre	
1991	Dispersed zerstreut	1992	?	1990	?
1994	Dispersed	1995	only on islands nur auf den inseln	1993	Dispersed

which also regularly visited these islands during the time of nest initiation. For that reason most Brent Geese left the islands after two weeks without being able to lay any eggs (Spaans et al. 1998). The regular visits of foxes to the islands disturbed the geese, which then gave up defending their nesting territories. In the end only 15 pairs of Brent Geese managed to lay eggs, whereas in other years more than 250 nests were established.

A very remarkable year was 1995 when many more nests (381) were established on the islands as opposed to 243–291 in the other successful years. Possibly in this particular year it was very difficult for Brent Geese to find alternative safe nesting sites elsewhere. Because of the lemming peak in the previous year many Snowy Owls roamed around without nesting, and their presence may have forced more geese than in the 5 preceding years to nest on the islands. Occasional observations of a Snowy Owl trying to visit these islands invariably resulted in a mass attack of the nesting gulls, effectively chasing the owl away from the islands.

Annual mean values for the clutch sizes in Brent Goose nests are given in Table 2.

It is striking that in the lemming peak years 1991 and 1994 the clutches contain on average almost one egg extra. The most numerous egg predator, the Herring Gull, nested earlier in these years, and all Herring Gulls fed almost exclusively on lemmings in the early part of the season. This most probably resulted in a marked reduction of egg predation by these gulls. In the other seasons clutch sizes are most likely reduced by partial predation of clutches.

The proportion of goslings taken by gulls on and around the islands, usually in the first week after hatching, was high in all years. In 1995 it was extremely high because the geese did not disperse from the islands to moult and raise their goslings elsewhere (Table 3).

Discussion

Life-time reproduction by long-lived birds is highest when adult birds make the best trade-off between their own survival and that of their eggs or offspring. Sacrificing some eggs or young, or even a complete brood by nesting within a gull colony offering the prospect of more successful breeding seasons in the future, can result in a greater lifetime reproductive success for an adult bird than risking its own life by nesting elsewhere.

The fact that in our study area the majority of Brent Geese nested in Herring Gull colonies on small islands could thus be explained by a lower mortality risk for nesting adult geese, which compensates for the often high mortality of goslings through predation by gulls. Foxes are usually cut off from the gull-islands, while Snowy Owls, which are capable of taking adult geese on the nest, have great difficulty penetrating the gull colonies because they are vigorously attacked by the gulls. We think that the presence of Snowy Owls was the

main reason why the geese did not disperse from the islands in 1995 as they did in the other years (1991, 1993 and 1994), when we stayed long enough to observe this dispersal. The failure to disperse from the Bird Islands meant that the concentration of moulting birds was much higher than in other years, and food shortage coupled with the heavy predation through gulls is probably the main reason why almost all goslings perished in that year.

The gulls are no threat to the adult geese themselves, and what is more the gull droppings stimulate good quality grass for the nesting geese to feed on during the time of incubation. However, gulls can and do take eggs, particularly when there are no lemmings to serve as alternative food. Geese fiercely defend their eggs against gulls, and since handling the eggs for consumption takes some time, the gulls are exposed for a considerable length of time to counter-attacks, often only swallowing half the contents of an egg, and run a serious risk of incurring injuries from the geese. This probably explains why egg-predation is relatively rare.

Newly hatched goslings, however, are easy for gulls to pick up swiftly, and can later be swallowed whole without persistent counter-attacks by the parent geese. They are thus a much more profitable prey item for gulls. Therefore, in the first few days after hatching, and in particular in windy conditions, a large proportion of the goslings are taken in these gull-island-colonies, and most goose families leave these islands during the first week after hatching to raise their goslings at a safe distance along the riverbanks on the mainland.

A second nesting strategy is to breed inside the territories of Snowy Owls, but this strategy is only an option once every three years when lemming abundance is great and Snowy Owls nest. It is likely that this strategy eliminates egg-predation altogether, and that predation on goslings after hatching is also minimal, though there are some reports of Snowy Owls taking small goslings (K. Günther, pers. comm.). On the negative side, there is some risk of adult geese being taken by the Snowy Owls (Spaans & Cottaar, unpubl.), but so far this has only been documented in non-lemming years when Snowy Owls do not nest themselves. When lemmings are abundant it is probably more economical for the Snowy Owls to feed solely on lemmings and spare the effort of catching an adult goose. For the geese, of course, there is the problem of assessing how Snowy Owls will behave in any particular year. When there are many lemmings, Snowy Owls are already nesting when the geese arrive between 10–15 June. Maybe nesting Snowy Owls present no obvious threat to geese, whereas non-nesting Snowy Owls, which are much more on the wing, do.

Analogous to their behaviour on gull islands, the goose families vacate the Snowy Owl territories after hatching to raise their goslings elsewhere. Hence, in lemming peak years this second breeding strategy seems to be the more profitable for Brent Geese, but one drawback might be the fact that each year the geese have to spend time searching for suitable localities with nesting Snowy Owls, whereas the gull colonies are at predictable sites that can be found every year by the geese using local knowledge collected in previous seasons. In these gull colonies the goose eggs hatch 1–2 weeks earlier than those of Brent Geese nesting in Snowy Owl territories. In the high arctic such a difference in timing may be of great importance, particularly in years with an early onset of frost.

A third strategy is to nest more or less isolated along small rivers on the mainland tundra, which is a very profitable strategy in years without foxes (1990 in our study area). Whenever foxes are present, however, even in lemming peak years, such nests rarely survive the egg stage.

In our study area all three strategy options were open to the geese, but only strategies 1 (nesting on gull islands) and 3 (nesting alone on the mainland tundra) were employed. Even in 1994 when 6 pairs of Snowy Owls were nesting within our study area, hardly any of the

Snowy Owl territories (strategy 2) were occupied by Brent Geese to nest. The only exception was a Brent Goose nesting 120 metres away from a Snowy Owl nest on the large island of Farwaternie. Strategy 3 was employed by only 4 % of the Brent Geese nesting in our study area in 4 out of the 6 seasons, and proved successful only in 1990, when there were no foxes at all in our study area, whereas strategy 1 was used by 96 % of the birds in 5 out of the 6 seasons.

In only one season, 1992, were none of these strategies used, with virtually no Brent Geese making any attempt to nest. This was a result of direct disturbance by foxes, which were extremely abundant that season, forcing the majority of the geese to abandon their nesting territories in the early stage of nest initiation before they could lay any eggs (Spaans et al. 1998).

The impact of predators on goose numbers is likely to become more obvious now that so many goose populations have increased in numbers, and the nesting habitat which is safe from predators is becoming filled to capacity. Density dependent effects may therefore become more evident as these safe nesting sites become overcrowded and more geese are forced to nest in places that are more accessible to predators.

Future studies and analyses will have to show how representative our study area actually is for Brent Geese by assessing the relative success of each of the strategies as well as the importance of each strategy for the Brent Goose population as a whole. Such studies will have to cover simultaneously several areas along the entire coastline of the Taimyr Peninsula. In addition, it will be important to find out whether individual geese always adhere to the same strategy, or whether they are capable of selecting and following the most profitable strategy for a particular year, which depends strongly on the abundance of both lemmings and predators.

Predator influence on the breeding success of a prey species is thus more far-reaching than one would imagine by simply measuring nest or offspring survival. Behavioural adaptations of the prey species itself minimise predation risks, but are at the same time quite likely to impose much narrower restrictions on its distribution than they would otherwise have incurred. We have deliberately applied the anthropomorphic term 'evil' to this baleful influence that predators exercise on the population distribution of their prey, because by trying to avoid predation adult Brent Geese seem to impose much more severe restrictions upon the area that they and their offspring actually use than may be strictly necessary. Such a mechanism will have a profound density dependent regulatory effect. Knowledge about such relationships in these virtually pristine high arctic ecosystems, will help us to understand the natural ways in which population sizes are controlled. This basic insight in turn is indispensable for sound international nature management, and is equally applicable to areas of the world in which man is a much more dominant factor.

Acknowledgements

We are extremely grateful to Prof E. E. Syroechkovskiy and his team for all their help in organising the international arctic expeditions in which we were able to participate. Dr G. C. Boere and Dr P. Prokosch were also extremely helpful in paving the way for our team and ourselves to work for six consecutive summers in Lidia Bay in western Taimyr.

The resident hunter Yuri Ostrovskiy, the helicopter crews from Dixon, the director of the Great Arctic Reserve, V. Badukin, Aleksandr Yunak, Andrey Moroz, Maksim Sinitsin, Nikita Vronski, Aleksandr Abolits were all very co-operative. The technical staff of Alterra, Willem van der Veer, Kees van 't Hoff and Frans van den Eijnden all helped in carefully preparing our expeditions and also assisted in the field.

In particular we would like to mention Marina Rykhlikova, Yakov Kokorev, Vasily Grabovskiy, Andrey Moroz, Igor Popov, Gerard Müskens, Jaap Mulder, Jouke Prop, John Quinn, Andrew StJoseph, Wojciech Kania, Przemek Chylarecki, Martin Stock, Hans-Heiner Bergmann, Tijs Tinbergen, Jan Musch, Harry Blijleven and many other camp members who contributed to the success of our research project. Last but not least our thanks are due to our cooks, Alla Grosheva, Anna Voronina, Katja Bourskaya, Natasha Vasukova, Lena Deriougina and Andrey Rey, who

did everything they could to make our stay in the tundra as comfortable and pleasant as possible.

Barbara Ganter's critical review of this paper greatly improved its structure and Doug Taylor kindly corrected the English text.

References

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

Ebbinge, B. S. & Spaans, B. (1995): The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. Journal of Avian Biology 26: 105–113.

Ebbinge, B. S., Berrevoets, C., Clausen, P., Ganter, B., Günther, K., Koffijberg, K., Mahéo, R., Rowcliffe, M., StJoseph, A. K. M., Südbeck, P. & Syroechkovskiy, E. E. (1999): Dark-bellied Brent Goose *Branta bernicla bernicla*. In : Madsen, J., Cracknell, G. & Fox, A. D. (Eds.): Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publ. 48: 284–297.

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

Krebs, C. J. (1993): Are lemmings large *Microtus* or small reindeer? A review of lemming cycles after 25 years and recommendations for future work. In: Stenseth, N. C. & Ims, R. A. (Eds.): The Biology of Lemmings: 247–260. London.

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

Rykhlikova, M. E. & I. Yu., Popov (2000): Population dynamics and habitat selection of lemmings in arctic tundra of north-western Taimyr. In: Ebbinge, B. S., Mazourov, Y. L. & Tomkovich, P. S. (Eds.): Heritage of the Russian Arctic: Research, Conservation, and International Co-operation. Proceedings of the Willem Barents Memorial Arctic Conservation Symposium held in Moscow, Russia 10–14 March 1998: 544–553. Moscow.

Spaans, B., Blijleven, J., Popov, I., Rykhlikova, M. E. & Ebbinge, B. S. (1998): Dark-bellied Brent Geese *Branta bernicla bernicla* forgo breeding when Arctic Foxes *Alopex lagopus* are present during nest initiation. Ardea 86: 11–20.

Spaans, B., Stock, M., St. Joseph, A. K. M., Bergmann, H.-H. & Ebbinge, B. S. (1993): Breeding Biology of Dark-Bellied Brent Geese *Branta bernicla bernicla* in Taimyr in 1990 in the Absence of Arctic Foxes and Under Favorable Weather Conditions. Polar Research 12: 117–130.

Summers, R. W. (1986): Breeding production of Dark-bellied Brent Geese *Branta 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 *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. Bird Study 34: 161–171.

Summers, R. W., Underhill, L. G., SyroechkovskiJr., E. E., Lappo, H. G., Prys-Jones, R. P. & Karpov, V. (1994): The breeding biology of Dark-bellied Brent Geese *Branta b.bernicla* and King Eiders *Somateria spectabilis* on the northeastern Taimyr Peninsula, especially in relation to Snowy Owl *Nyctea scandiaca* nests. Wildfowl 45: 110–118.

Underhill, L. G., Prys-Jones, R. P., Syroechkovski Jr., E. E., Groen, N. M., Karpov, V., Lappo, H. G., van Roomen, M. W. J., Rybkin, A., Schekkerman, H. & Summers, R. W. (1993): Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchischeva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. Ibis 135: 277–292.

Accepted: 01 July 2001