Breeding strategies of Dark-bellied Brent Geese *Branta b. bernicla* in a lemming-driven ecosystem in northern Siberia

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Abstract

Long-term studies (1990–2008) of Dark-bellied Brent Geese *Branta b. bernicla* breeding on the Taimyr Peninsula in the Russian high Arctic, revealed a three-year cycle in breeding success linked to Siberian Lemming *Lemmus sibiricus* and Collared Lemming *Dicrostonyx torquatus* dynamics. Peak lemming years provide abundant prey for Snowy Owls *Nyctea scandiaca*, Arctic Foxes *Vulpes lagopus* and Pomarine Skuas *Stercorarius pomarinus*, whose interactions coincidently facilitate Brent Goose nesting. Snowy Owls defend their own territories against Arctic Foxes, and Pomarine Skuas do the same against both Arctic Foxes and Snowy Owls, severely restricting foxes and owls from preying upon Brent Geese, their nests and their goslings. Brent clutch size varied from an average of five eggs in Snowy Owl territories, to four eggs in gull *Larus* sp. colonies in peak lemming years, and three eggs in gull colonies in non-lemming years. Following lemming crashes (for reasons not understood), predator abundance remains high and Brent completely fail to breed or skip reproduction, as foxes and owls switch to alternative prey and skuas are absent from the area. In the third year, with predator decline (through starvation or emigration) and lemming recovery, Brent Goose nesting success improves. A year later, the three-year cycle starts again. The key role of skuas in limiting the owls' ability to catch and carry larger prey, such as geese, creates fox-free areas where Brent are able to nest successfully,

confirming their previously overlooked role in the interspecific predator-prey interactions shaping Brent Goose reproductive success in the high Arctic. This review of papers and reports from the long-term studies describes how complex predator-prey and interspecific interactions determine the annual variation in breeding outcomes for Dark-bellied Brent Geese.

Key words: Arctic ecosystem, breeding success, Dark-bellied Brent Geese, interspecific interactions, lemmings, predation, protective nest association.

Dark-bellied Brent Geese *Branta b. bernicla* (hereafter Brent) breed largely on the Taimyr Peninsula (northern Siberia), winter along western European coasts and show boom-and-bust breeding cycles (Ogilvie & St. Joseph 1976). Up to 50% of the wintering flocks consist of young-of-the-year in some winters, whereas in others there are almost no young. Kees Roselaar (Roselaar 1979) and Ron Summers (Summers 1986) identified a typical three-year pulse in the proportion of young Brent in wintering flocks, which occurred in parallel with Curlew Sandpiper *Calidris ferruginea* breeding performance, and correlated with lemming abundance. Information from Russia (Kokorev & Kuksov 2002) showed that summers with abundant lemmings on the Taimyr Peninsula in Siberia (where both of these bird species primarily nest) coincided with good breeding seasons. In peak lemming years the breeding success of Brent and waders on the Taimyr Peninsula is almost always very high (Roselaar 1979; Summers & Underhill 1987; Greenwood 1987; Underhill 1987, 1988; Summers *et al.* 1998; Ebbinge 2014; Blomqvist *et al.* 2002).

The cycles of lemmings with Brent discerned the following basic pattern: a peak breeding year when lemming numbers also peak, followed by an almost complete failure to raise any goslings, and finally an unpredictable in-between-year, with sometimes fairly good breeding results. After which the cycle starts anew with a peak breeding year (the "Roselaar-Summers hypothesis"; Dhondt 1987). In the peak lemming year of 1991, Brent were found for the first time to nest within the territory of a Snowy Owl *Nyctea scandiaca* (Summers *et al.* 1994), which kept Arctic Foxes *Vulpes lagopus* at bay. At around the same time, Spaans *et al.* (1993) described how in 1990 the Brent nested on small islands within colonies of large gulls (predominantly Taimyr Gulls *Larus heuglini*, but also Glaucous Gulls *Larus hyperboreus*).

Summers and Underhill (1987) interpreted Brent breeding cycles in the context of the "*prey-switching*" or "*alternative prey hypothesis*" of Hagen (1952), whereby Arctic Foxes and other predators switch between lemmings in peak years (when geese breed successfully) and avian eggs and pulli when lemmings are scarce. Their data confirmed that wader nesting success varied one hundred-fold between lemming peak (daily nest survival 0.20) and non-peak years (0.0022; Underhill *et al.* 1993). On Taimyr, numbers of Siberian Lemmings *Lemmus sibiricus* and Collared Lemmings *Dicrostonyx torquatus*

peak simultaneously, approximately every three years, before their numbers plummet the following year. In the year after peak years, fox numbers remain high, and it is rare to observe lemmings. Then follows a so-called "in-between-year" with few predators and still hardly any lemmings. In the next summer lemmings are again running all over the place after the snow melt.

Lemmings are prey for other predators which also take geese, their eggs and young, so the fluctuations in lemming numbers influence the dynamics of many tundra species, and the interactions between them are complex. Sites with high lemming densities in winter attract Snowy Owls and Arctic Foxes. Arctic Foxes reoccupy old dens and become territorial when lemmings are abundant, keeping other foxes at bay. In peak lemming years Arctic Foxes produce large litters and their numbers increase (Summers *et al.* 1998), but when the lemming density plummets during the following year, the highly abundant foxes are no longer territorial. As tundra nomads they do not reproduce themselves but shift to preying on nests of geese and waders, resulting in very poor breeding results for tundra-nesting birds (Underhill *et al.* 1993). Fox numbers then decline because of starvation or dispersal, resulting in the unpredictable in-between-year when there are few foxes but also few lemmings, until the next lemming peak when fox numbers increase again.

This paper reviews data collected during the late Prof. E.E. Syroechkovskiy's international expeditions to Taimyr in 1990–2008, some published in scientific journals (cited here), but mostly in the grey literature (*e.g.* expedition reports, also cited) and in Ebbinge *et al.* (2000). We consider three different behaviours used by the Brent to avoid predation by Arctic Foxes: (1) nesting on small islands between large gull nests (predominantly Taimyr Gulls but also Glaucous Gulls), (2) nesting within Snowy Owl territories, and (3) nesting scattered over the tundra in places where foxes are rare (Summers *et al.* 1994; Ebbinge *et al.* 2000; Ebbinge & Spaans 2002). In particular, we draw on data collected in two areas where the birds were studied over many consecutive years, enabling us to assess between-year variation in breeding success at the same sites: Lidia Bay and the Bird Islands and Beacon Islands in the Pyasina Delta (visited in 12 summers, in 1990–1995, 2002 and 2004–2008), and Medusa Bay, near Dikson on the Yennisey River estuary (visited in 13 summers, from 1994–2006 inclusive), supplemented by complementary data collected elsewhere on Taimyr (Fig. 1; Tables 1 and 2).

A major question addressed is why Snowy Owls, capable of killing adult Brent, permit them to nest within their territories.

Methods

Study area

The Taimyr Peninsula lies between the mouth of the Yennisey River near Dikson (in the west) and the mouth of the river Khatanga (in the east) in northern central Siberia (Fig. 1a,b). It consists of 400,000 km^2 of open tundra landscape, lakes and wetlands, divided by the River Pyasina and the Lower River Taimyr, both of which flow into the Kara Sea.

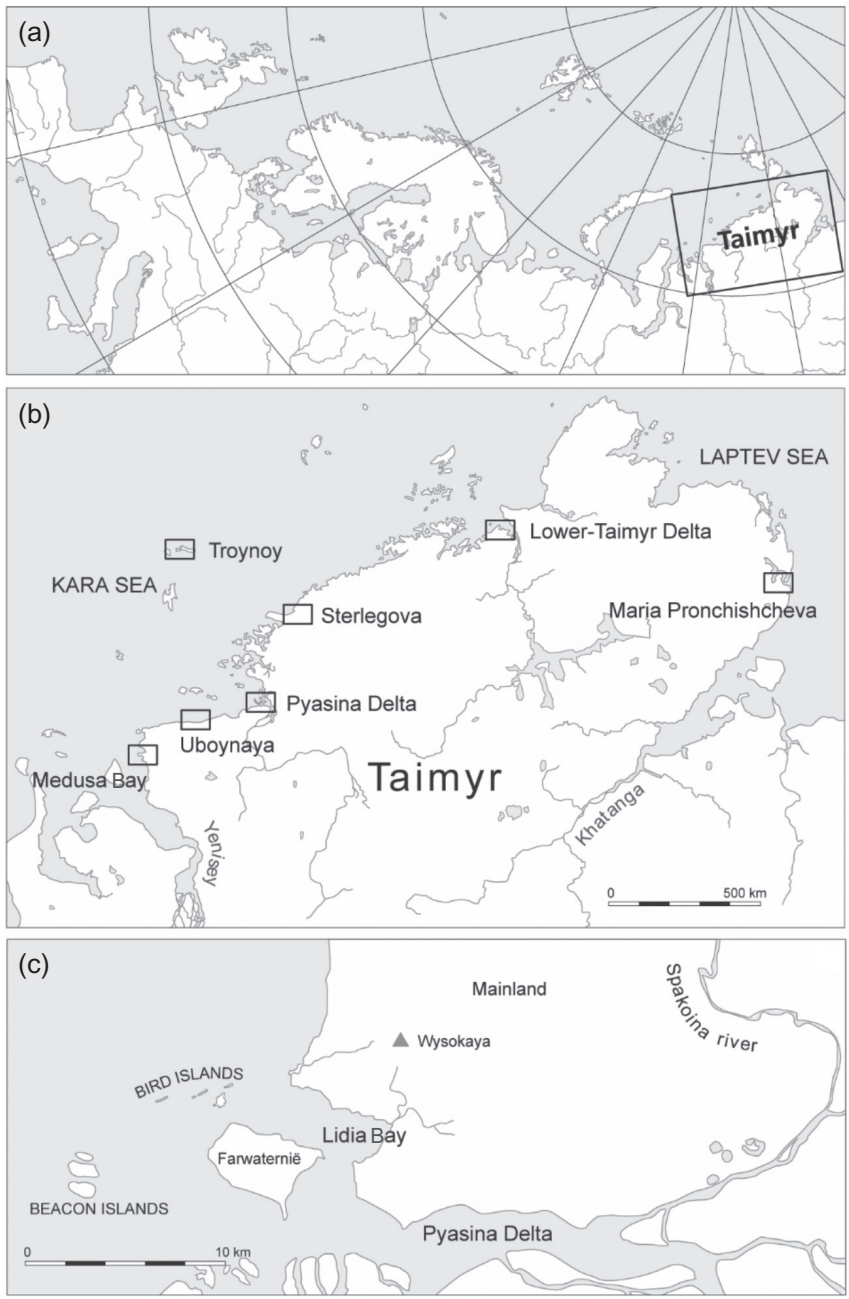

Figure 1. Map of the study area showing: (a) location of the Taimyr Peninsula in the Russian Arctic, (b) research locations on the Taimyr Peninsula, and (c) a detailed view of the Pyasina Delta.

Table 1. Number of Brent Goose nests located at the different research locations on the Taimyr Peninsula from 1990–2008. Grey bars indicate peak lemming years, with Snowy Owls nesting. In some years, when not all of the Beacon Islands and Bird Islands could be visited, the estimated number is given in brackets, with the minimum number of nests actually counted being given before the brackets. * indicates not near a Snowy Owl; ** indicates nesting near a Snowy Owl. Brent Goose breeding success is shown as the percentage of first-winter birds (excluding second year birds) recorded in flocks on the wintering grounds in western Europe (also in Fig. 3)

Year	Gull islands		Near Snowy Owls			Tundra		Remote offshore island	Brent Goose breeding success
	Bird Islands (Pyasina)	Oleni Islands (Medusa)	Maria Pronchishcheva Lake	Medusa Bay	Uboynaya	Mainland tundra (Pyasina)	Mainland tundra (Sterlegova)	Troynoy	
1990	252					12	34		26%
1991	288		16			9*	4		38%
1992	15		1			0		0	0.1%
1993	255					15			26%
1994	240			46	> 5	6*	4	950	8%
1995	390			0		0		400	0.5%
1996				47					14%
1997		8		0					12%
1998				0					1%
1999		7		125					25%
2000		0		0					2%
2001		> 1		0					10%
2002	> 132 (270)	35		64	26	0			9%
2003				0					12%
2004	736	51		26		0			16%
2005	> 242 (325)			38		25**			33%
2006	151					0			3%
2007	> 292 (301)					3			12%
2008	129					0			2%

Table 2. Numbers of Snowy Owl pairs nesting in the various study sites each year. Grey bars = peak lemming years; blank cells = no data for the site in that year. Brent breeding success is the percentage of juveniles recorded in wintering flocks in western Europe (excluding second year birds).

Year	No. Snowy Owl pairs				Brent Goose breeding success
	Maria Pronchishcheva Lake	Medusa Bay	Uboynaya	Mainland tundra (Pyasina)	
1990				0	26.4%
1991	10			2	37.8%
1992	0			0	0.1%
1993				0	25.5%
1994		13	20	6	8.4%
1995		0		0	0.5%
1996		4			13.7%
1997		0			12.4%
1998		0			1.2%
1999		8			25.4%
2000		0			2.1%
2001		0			9.6%
2002		9	4	0	9.2%
2003		0			12.4%
2004		1 (6)		0	16.1%
2005		22		14	32.5%
2006		0		0	3.2%
2007				0	12.2%
2008				0	1.5%

During the 1990–2008 study period, data were not only collected at the two main study sites which were visited many times: (1) the Pyasina Delta (12 summers, focussing on Bird Islands and Beacon Islands (Spaans *et al.* 1998), as well as on the mainland along Lidia Bay and the River Spakoina), and (2) Medusa Bay near Dikson (13 summers, both on mainland tundra and the Oleni Islands), but with information also collected at four additional sites. From Maria Pronchishcheva Lake (two summers;

Underhill *et al.* 1993), the Uboynaya River (two summers; Mork *et al.* 1994), Sterlegova (three summers) and the remote offshore island of Troynoy (two summers) (Fig. 1b).

Field surveys

The Taimyr international expeditions primarily focussed on the breeding success of Brent and waders *Limicolae* sp., but the abundance of other bird species, lemmings and Arctic Foxes were also monitored. The wader data have been published elsewhere (see Ebbinge *et al.* 2000), but while intensively searching for Brent and wader nests we also registered nests of other bird species, including Pomarine Skuas *Stercorarius pomarinus* and Greater White-fronted Geese *Anser albifrons*. Conspicuous nests of Snowy Owls and Arctic Fox dens were easy to find over even wider areas. At most of the field camps, *c.* 10 people searched for nests over many hours, from 1 June until early August. Such searches occasionally led to unexpected "lucky encounters" (see Results) – observations which helped to understand the choices that the geese make in selecting nest sites, moulting sites and where goslings are raised until fledged.

We collected nest data for Brent adopting all three breeding behaviours. For those nesting in gull colonies, data were collected from 1990–1995, in 2002, and from 2004–2008 (total = 12 seasons), on the Bird Islands and Beacon Islands in the Pyasina Delta. The Bird Islands consist of 13 separate rocky islands, which in mid June could be reached by small boats after ice melt (Spaans *et al.* 1998). In the delta, further out to the southwest, there are the larger Beacon Islands, which are flat, sandy and harbour more gulls, though at lower nesting densities. A permanent hut was constructed on the main Bird Island (dubbed "Big Bird Island") in 1990, from which nesting Brent and gulls could be observed continuously without disturbance. Data on numbers of nesting Brent and gulls (including clutch sizes) were gathered on each of the other 12 Bird Islands and the three Beacon Islands in 1990–1995 inclusive. While initially we mapped only Brent nests on Big Bird Island, from 2002 onwards we registered the exact nest locations of both gulls and Brent on all islands using GPS devices. On Big Bird Island electronic balances were also deployed under Brent nests, to study weight changes during incubation and the frequency of nest recesses (Spaans *et al.* 2007). Geese nesting on mainland tundra at Pyasina were monitored in the same years, where tens of Brent were caught on nests and ringed with engraved plastic rings for subsequent individual identification. West of Big Bird Island, where the Bird Islands extend as a chain of 12 more rocky islands, the position and clutch size of all Brent and gull nests were recorded just once, in early July, to minimise human disturbance. The large, flat outermost Beacon Islands were checked in the same way as the other 12 islands, with Brent, Taimyr Gull and Red-throated Diver *Gavia stellata* nests recorded. These Beacon Islands (marked by two derelict wooden beacons formerly used to guide ships into the mouth of the Pyasina River) supported up to 6,000 moulting non- or failed breeder Brent in late July. In 1995, 2006 and 2008 a total 3,491 of moulting Brent were caught and measured here, with the adult females checked for broodpatches and ringed. Other

catches of moulting Brent (including goslings) were made on two of the Bird Islands and on the mainland along Lidia Bay and Pyasina Bay coastlines, where most of the family flocks from the Bird Islands and Beacon Islands congregated to moult and raise their goslings.

Data regarding geese nesting in Snowy Owl territories were collected at Medusa Bay (near Dikson) from 1994–2006 inclusive (13 seasons), with additional information collected at six other sites in some years to investigate whether numbers of Brent varied from year to year. Clutch sizes were measured mid-term during the nesting season, at *c.* 1 July. Clutch size records therefore are affected by partial nest predation, and may also include clutches for Brent that initially nested elsewhere before moving to a different location following the loss of a first clutch (see Results). Overall breeding success of the Brent was first assessed on catching and marking moulting flocks after the breeding season in late July, both on the islands and along the shores of Lidia and Pyasina Bays. The proportion of juveniles in the population was subsequently measured by age-ratio counts made of flocks wintering in western Europe (Ebbinge *et al.* 2013).

Predation of Brent eggs, young and adult birds, by Arctic Foxes, Snowy Owls and other predators is hard to observe in the field, because it happens so quickly. Moreover, many prey species have evolved various protective adaptations such as camouflage, nest site selection and anti-predator behaviour. The best information on predation therefore came from recording the remains of predated prey and eggs, pellets, or prey items stored in and around the nests of predators. In the later years of these expeditions, digital cameras (new at that time) were used to record data on interactions between Pomarine Skuas, Snowy Owls and Arctic Foxes.

Lemmings and the build-up of peak numbers

To cover all stages of the lemming cycle, lemming abundance was monitored using both live- and snap-trapping on the Pyasina Delta's mainland tundra, visited in 12 years of the study (Fig. 1c; Table 1). This allowed us to compare directly the breeding success of Brent in years when lemmings were abundant (and Snowy Owls would nest) with years with hardly any lemmings. On this tundra site, Rykhlikova and Popov achieved 2,000–3,000 trapnights per season using snap- and live-traps in three peak lemming years (1991, 1994 and 2005; Rykhlikova & Popov 2000; de Raad *et al.* 2011), and similar trapping effort was maintained in the other years. Lemming abundance is presented as the number of lemmings caught in 100 "trapnights". Because the sun never sets in the Arctic summer a "trapnight" is a 24 h period. More general details about lemmings can be found in the Supporting Materials (Annex S1).

Arctic Foxes and Snowy Owls

All 14 fox dens in a wide area around Lidia Bay (16 km^2; de Raad *et al.* 2011) were checked every year for Arctic Foxes. Around Medusa Bay numbers of fox dens were regularly counted by Sergey Kharitonov (Kharitonov *et al.* 2008, 2013, 2017). The presence of Arctic Foxes, and of all avian

predators of lemmings (*e.g.* Snowy Owls, Pomarine Skuas, Long-tailed Skuas *Stercorarius longicaudus* and Rough-legged Buzzards *Buteo lagopus*), was determined by counting the number of nests and the number of occupied fox dens. In the summer of 1990 (a lemming build-up year), we did not see any Arctic Foxes in our permanent study plot along Lidia Bay, but we did find 14 unoccupied fox dens. The dens were easy to recognise as small hills with lush vegetation with many Arctic flowers, and the extensive burrows were well fertilised with the remains of prey and excrement of foxes that had previously occupied the den. It was in one of these fox dens that we discovered our first lemmings in 1990.

In the peak lemming years (1991, 1994 and 2005), and even in years when lemmings failed to reach peak numbers (2002 and 2008), many of these fox dens were suddenly reoccupied by Arctic Foxes, apparently attracted by the sound of increasing numbers of lemmings from under the snow. In winter 1994/95, a local trapper (Yu. Ostrovski) caught 128 Arctic Foxes on the Pyasina Delta, but during summer fox trapping is not allowed. Hence, in summer, denning and the presence of roaming foxes were not affected by human activity, and we could study the impact they had on nesting birds.

Results

Lemmings

In the three peak lemming years along Lidia Bay, in typical tundra vegetation, lemmings were particularly abundant in 2005, but there were also many lemmings in 1991 and 1994 (Fig. 2). On the adjacent Bird Islands, lemmings were evidently present (from the

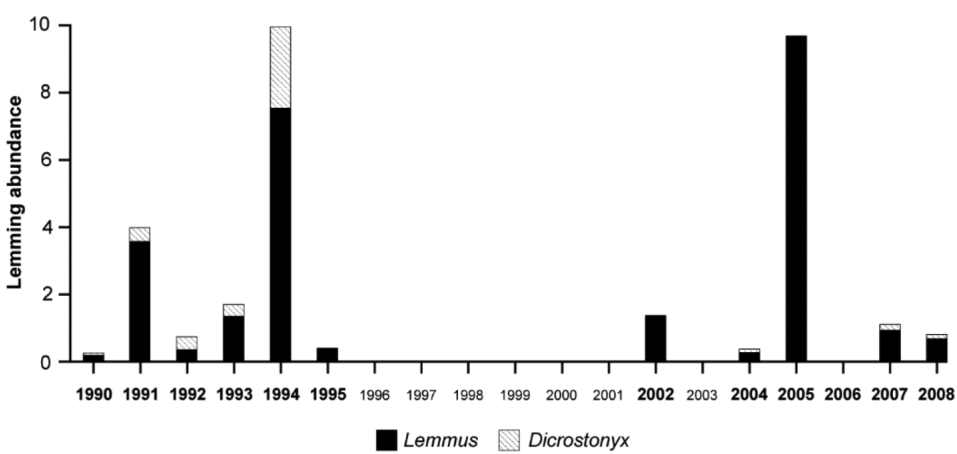

Figure 2. Lemming (Siberian Lemming *Lemmus sibiricus* and Collared Lemming *Dicrostonyx torquatus*) abundance along Lidia Bay, Pyasina Delta, expressed as number caught per 100 snap-traps in 24 hours. No lemmings were caught despite ongoing trapping effort in 2006 (following a peak lemming year in 2005), and from 1996–2001 and in 2003 the site was not visited. Years when data on lemmings were collected are indicated in bold.

heavily grazed vegetation and lemming droppings) but the gulls quickly caught all lemmings on these islands, and gulls (particularly in 1991 and 1994) were also regularly observed flying to the mainland tundra, returning with lemmings to the islands. Dead lemmings were commonly found next to gull nests in these years. In 2006, the year after the lemming peak of 2005, with the same trapping effort (2,652 "trapnights") as in 2005, not a single lemming was caught. The high peak in 2005 consisted only of Siberian Lemmings; no Collared Lemmings were caught that year.

Brent clutch sizes on the gull islands were similar for all three peak lemming years (Fig. 3), but 10 days of strong winds just after hatching in 1994 resulted in many goslings being taken by gulls as the broods left the Bird Islands for the mainland tundra, with the wind making it easier for the gulls to avoid counter-attacks by Brent trying to protect their young. Catches of moulting Brent flocks in 1994 included only 19% goslings (n = 74), compared to 30% in 2005 (n = 273). The three peak lemming years were also evident in measures of Brent breeding success made the following winter (Table 1; Fig. 4), excepting 1994 when only 8% young birds were recorded in winter, compared with 38% in 1991 and 33% in 2005. We infer that these strong winds occurred over a wider area, causing great loss of goslings subsequently reflected in the winter age-ratio counts at the population level (Fig. 4).

Further information on lemmings is provided in the Supporting Materials (Annex S1)

Brent nesting on gull islands

Most Brent in the Pyasina Delta nest between large gull colonies on small islands (the Bird and Beacon Islands; Table 1); rarely on mainland tundra. The first birds usually arrive after 10 June (in some years a week later), and the first eggs laid within a few days (Spaans *et al.* 2007). Unlike

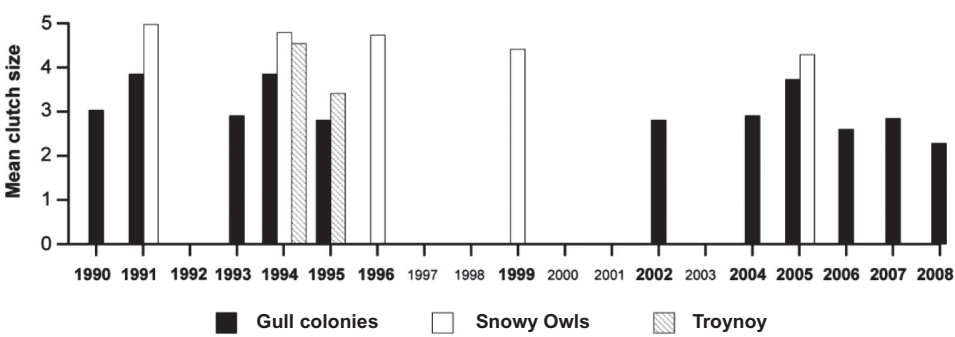

Figure 3. Clutch sizes recorded for Brent Goose nesting in gull colonies (black), near Snowy Owls (white), and on a remote offshore island Troynoy (hatched). Based on data from Summers *et al.* 1994; Kharitonov *et al.* 2008; de Fouw *et al.* 2016; Bangjord *et al.* 1994; Spaans & Cottaar 1996. Years indicated in bold figures are when data were collected. Peak lemming years were in 1991, 1994, 1996, 1999 and 2005. In 1992 hardly any Brent laid eggs.

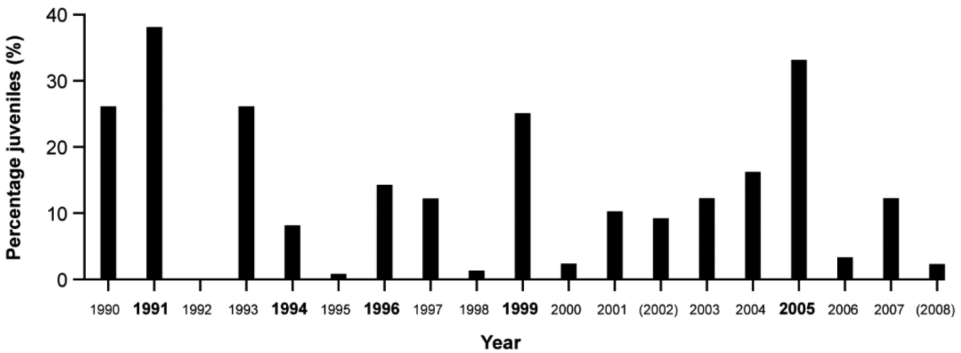

Figure 4. Brent Goose breeding success in 1990–2008, based on the percentage of juveniles recorded in wintering flocks in western Europe (data also provided in Table 1). The percentage of juveniles has been calculated excluding second-year birds, which were estimated from the percentage of juveniles one year earlier (Ebbinge 1989). Peak lemming years are indicated in bold. Two failed lemming years (2002 and 2008) are given in brackets. In 2002 in parts of Taimyr (Uboynaya and Medusa Bay) some Snowy Owls did nest, indicating local lemming abundance (Table 2). Both are exactly three years after the previous lemming peak (see Annex S1).

Barnacle Geese *Branta leucopsis*, Brent nests are spaced out, because females lack the body stores needed to complete incubation without supplementary feeding around the nest within their territory, which is heavily defended by their mates against conspecifics (Spaans *et al.* 2007).

On the Bird Islands and Beacon Islands, 200–300 Brent pairs nested between 2,000–3,000 pairs of Taimyr Gulls and several tens of pairs of Glaucous Gulls each year. On Oleni Islands (a similar archipelago near Medusa Bay), up to 51 Brent nests were recorded in gull colonies, and one lucky encounter was of a Brent caught and ringed at a nest on the Oleni Islands in 2004, found nesting on the Bird Islands study area (250 km further northeast) in 2005; rare direct proof of nomadic behaviour within the breeding range. The Taimyr Gulls, which winter along the coasts of China, return to their colonies from 1 June onwards (van Dijk *et al.* 2011), and in most years these islands are very difficult for Arctic Foxes to reach following the June ice melt. This is important for the gulls because they are incapable of defending their eggs against Arctic Foxes (as witnessed in the extremely late spring of 1992 when foxes reached the islands over the ice; Spaans *et al.* 1998), so they also nest on the islands rather than on mainland tundra. Gulls can and will prey on Brent eggs and goslings, but the geese are remarkably good in keeping gulls at bay before their eggs hatch, and rarely is an entire clutch taken (de Fouw 2005).

In addition to an absence of Arctic Foxes, Brent breeding on gull islands derive the advantage of higher quality vegetation (fertilised by gull guano) for pairs to feed on during the incubation period. King Eider *Somateria spectabilis* and Red-breasted Geese *Branta ruficollis* also nested between the gulls on Big Bird Island, as did the larger Greater

White-fronted Geese (which can complete incubation through to hatching without additional feeding; Spaans *et al.* 1999), but Snowy Owls never nested there or on the other gull islands. Visiting Snowy Owls were heavily attacked and driven off by gulls. Post-hatching, most Brent families leave the islands to raise their offspring along the many small tundra streams and rivers on the mainland, away from the large gulls.

Annual numbers of Brent nests recorded at the different study locations, and the overall annual breeding success of the population (determined as the percentage of young in wintering flocks; Ebbinge *et al.* 2013) are presented in Table 1 and Fig. 4. Data from the Bird Islands and Beacon Islands cover three peak lemming years (1991, 1994 and 2005), three predation years (1992, 1995 and 2006), four in-between-years (1990, 1993, 2004 and 2007), and two years in which the lemming peak failed (2002 and 2008). Numbers of Brent nesting within gull colonies on the islands were highest in 1995 (390 nests) and 2004 (736 nests), presumably because Snowy Owls did not nest to provide additional safe areas elsewhere in these non-lemming years. In two years (1992 and 2008) Arctic Foxes visited the islands, and we found 15 and 129 Brent nests, respectively. In all other years, the mean number of Brent nests was 260 (range = 151–325; Table 1).

In comparison with the peak lemming years of 1991 and 2005, when there were 38% and 33% juveniles in the wintering flocks, the in-between-years (still without lemmings but with greatly reduced numbers of predators) resulted in 26%, 26%, 16% and 27% juveniles recorded in western Europe. The three "predation" years were followed by just 0.1%, 0.5% and 3.9% juveniles in western Europe, and the two failed lemming years also resulted in poor breeding (9% and 2% juveniles; Fig. 4), albeit for different reasons. The many foxes visiting the islands over the late ice in 1992 prevented Brent from laying eggs at the outset. In 1994 there were hardly any foxes and the Brent bred well, but the strong winds after hatching caused heavy predation on goslings by gulls (see above). In 2006, predation by gulls was much stronger during the nesting phase and many Brent left the islands without completing a clutch, despite there being no foxes on the islands.

Because Brent defend large territories (minimum nearest neighbour distance = 33 m), gull colonies can become overcrowded with Brent. For instance, in 2004 (the year preceding a lemming peak), instead of the usual 250–300 pairs of Brent nesting on the Bird and Beacon Islands we found 736 nests, double those of other years. The large inter-nest distances reduce the likelihood of egg-dumping by Brent in nests of conspecifics, but those that have lost their clutches may still try to egg-dump when predation pressure is high, and even lay eggs in gull nests. On checking 3,000 Taimyr Gull nests in 2004, we found 10 gull nests containing single Brent eggs (Ebbinge & Mazurov 2005), indicating that egg-dumping by Brent in other birds' nests does occur, but we have no evidence of successful egg-dumping in the nests of conspecifics.

Final average clutch sizes recorded for Brent (determined after clutches were completed, at around 1 July) are illustrated in Fig. 3, with frequency distributions for

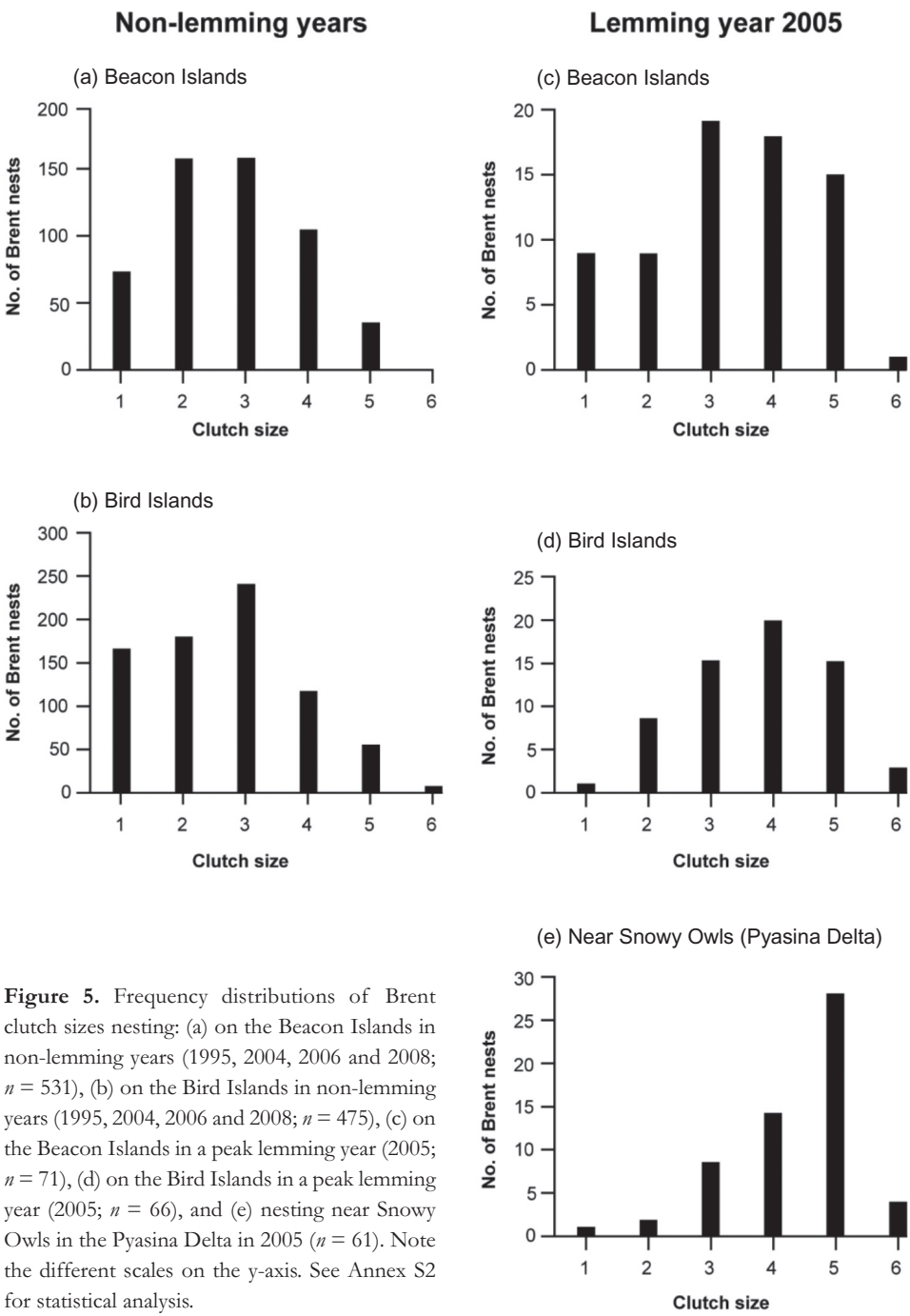

Figure 5. Frequency distributions of Brent clutch sizes nesting: (a) on the Beacon Islands in non-lemming years (1995, 2004, 2006 and 2008; $n = 531$), (b) on the Bird Islands in non-lemming years (1995, 2004, 2006 and 2008; $n = 475$), (c) on the Beacon Islands in a peak lemming year (2005; $n = 71$), (d) on the Bird Islands in a peak lemming year (2005; $n = 66$), and (e) nesting near Snowy Owls in the Pyasina Delta in 2005 ($n = 61$). Note the different scales on the y-axis. See Annex S2 for statistical analysis.

years 1995, 2004, 2005, 2006 and 2008 (for which original nest data are available) given in Fig. 5. These are grouped into: (1) non-lemming years (for both the Bird Islands and Beacon Islands; Fig. 5a,b), (2) the 2005 peak lemming year (also for both island groups; Fig. 5c,d), and (3) for Brent nesting in Snowy Owl territories elsewhere (Fig. 5e). Though clutch sizes on the Beacon Islands in years with very few lemmings were somewhat smaller than on the Bird Islands, this difference was not significant (Kruskal-Wallis test: $H = 2.59$, d.f. = 1, $P = 0.11$; Fig. 5a,b). In the peak lemming year of 2005 however (Fig. 5c,d,e), there were significant differences between clutch size and nest location (Kruskal-Wallis test: $H = 28.64$, d.f. = 2, $P < 0.001$). *Post-hoc* tests showed that there was no significance between the clutch sizes recorded on Bird and Beacon Isands (Dunn's test: $Z = –165$, $P = 0.29$, n.s.) but clutch sizes for Brent nesting near Snowy Owls (away from gulls) elsewhere in the Pyasina Delta (Fig. 8) were significantly larger in comparison with both island groups (Dunn's tests: $Z = –3.65$, $P < 0.001$ for Bird Islands and $Z = –5.28$, $P < 0.001$ for Beacon Islands; see Supporting Materials Annex S2). Mean clutch sizes for Brent breeding on the gull islands were of nearly four eggs in peak lemming years (1991, 1994 and 2005; Fig. 3), but ≤ three eggs in other years, which we consider due to more intensive gull predation on eggs in years without lemmings. This difference was also statistically significant (Kruskal-Wallis tests: $H = 13.62$, d.f. = 1, $P < 0.001$, Fig. 5a,c and $H = 43.05$, d.f. = 1, $P < 0.001$, Fig. 5b,d, for Beacon Islands and Bird Islands, respectively).

Brent are skilled in defending their nests against gulls, so gulls must trade potential injuries arising from stealing Brent eggs against the benefit of gaining the eggs, and when lemmings provide an abundant food resource it may not be worth the risk. A comparison of mean clutch sizes recorded for each of the 16 different Bird Islands and Beacon Islands showed that Brent had larger clutches on islands with higher nesting gull densities (Linear regression: $F_{1,13} = 6.81$, $R^2 = 0.29$, $P = 0.022$; Fig. 6), which may reflect gulls helping to defend Brent nests against egg predation by other gulls through defence of their own clutch from predation by conspecifics. On the larger, more open Beacon Islands the number of gulls is greater but their density is lower. On the more sheltered and rocky Bird Islands it is easier for Brent to defend their nests against gulls, yielding larger

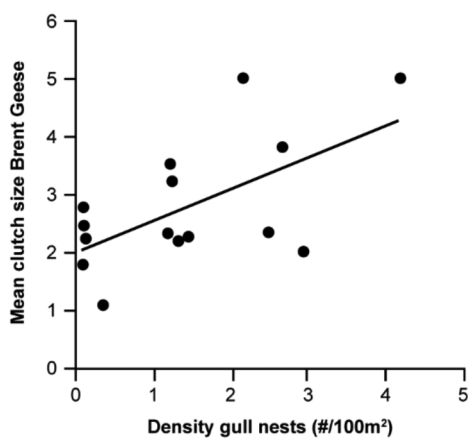

Figure 6. Mean clutch size Brent breeding in gull colonies on 15 different islands (Bird Islands and Beacon Islands combined) in the Pyasina Delta, in relation to the density of nests of gulls on the islands. Linear regression: $F_{1,13} = 6.81$, $R^2 = 0.29$, $P = 0.022$.

clutches. Brent clutch sizes never exceeded six eggs (Ebbinge 2014).

Only in 1992 did very few Brent nest on the Bird Islands. Spring was extremely late across the entire Arctic in that year, with deep snow covering the tundra following the eruption of the Pinatubo Volcano in the Phillipines (Ganter & Boyd 2000). Many Arctic Foxes had been born and survived from the previous year, and the late ice made it easy for foxes to reach the islands. We regularly watched up to four different Arctic Foxes visit the islands, and initially the regular number of geese defended territories. On the appearance of foxes, however, the geese regrouped into flocks and no eggs were laid. In contrast, the gulls did start to lay eggs, all of which were systematically collected and buried by visiting Arctic Foxes (Spaans *et al.* 1998). In 2008, late sea ice similarly enabled access by one Arctic Fox which predated many nests, including Brent nests, causing most geese to leave (Nolet & de Fouw in de Raad *et al.* 2011).

Brent nesting near Snowy Owls

A second option for Brent to nest safely is to do so within Snowy Owl territories, which is only possible in peak lemming years. In some areas, Brent only nest in peak lemming years, when nesting Snowy Owls are present (Table 1). Brent nesting association with Snowy Owls was first noticed near Maria Pronchishcheva Lake on eastern Taimyr in 1991 (Fig. 7). Two out of 10 Snowy Owl territories in the study area

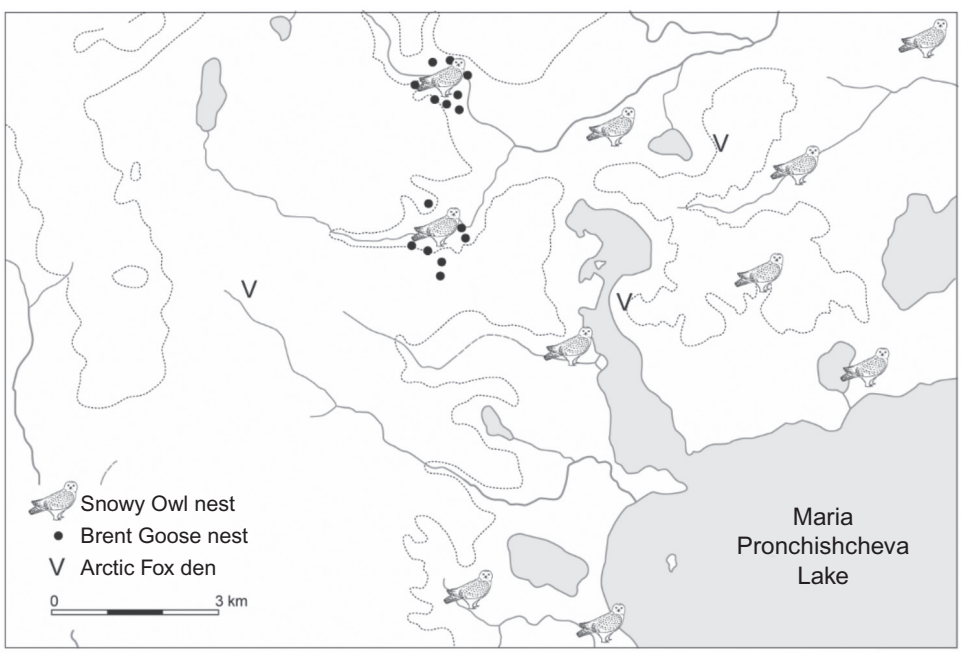

Figure 7. Brent (black dots) nesting around nesting Snowy Owls (owls) near Maria Pronchishcheva Lake, eastern Taimyr, in 1991 (after Underhill *et al.* 1993).

contained nesting Brent (Underhill *et al.* 1993), with a mean clutch size of 5.0 eggs (n = 12; Summers *et al.* 1994). When the site was revisited in 1992 (a non-lemming year), Snowy Owls were absent near the lake and only one Brent nest was located containing one egg, which was soon predated.

Snowy Owls defend large territories at densities of 0.06–0.13 nests/km^2 (Kharitonov *et al.* 2013). Their egg laying commences in late May, when the entire Taimyr Peninsula remains snow-covered, but with abundant lemmings under the snow. Owls nest on small hillocks, blown snow-free by the wind, and clutch size varies from 5–10 (maximum 15 eggs), depending on lemming density, incubated for *c.* 33 days. In May, Snowy Owls, Arctic Foxes and Least Weasels *Mustela nivalis nivalis* are the only lemming predators, but in June, as the snow starts to melt and lemmings become easier to catch, Taimyr Gulls, Glaucous Gulls, Pomarine Skuas, Long-tailed Skuas and Rough-legged Buzzards arrive. When lemming numbers are low, the Pomarine Skuas are first to leave, but most large gulls begin nesting because they can also feed on fish, bird eggs and chicks. In June, the waders and geese also return to their Arctic nesting grounds on the Taimyr Peninsula.

Most data on Brent nesting associations with Snowy Owls were gathered on the tundra along Medusa Bay, 25 km south of Dikson (Fig. 1). Here Brent were found nesting within Snowy Owl territories only in peak lemming years (in 1994, 1996, 1999, 2002 (though not in the Pyasina Delta) and 2005; Kharitonov *et al.* 2008, 2013; van Kleef *et al.* 2007; Table 1). The advantage for Brent is that Snowy Owls actively defend their territories against Arctic Foxes, allowing foxes to come no closer than 500 m from their nest (Litvin *et al.* 1985). Mean clutches in nests near Snowy Owls contain an extra egg compared to those on the gull islands in peak lemming years (Fig. 3). In 1999, an exceptional 125 Brent pairs nested around six Snowy Owls close to the Willem Barents Station. Brent clutches in nests closest to the nesting owls were larger than those further away (van Kleef *et al.* 2007), and the mean distance (± s.d.) between Brent and Snowy Owl nests was 235 m ± 14.6 m (Kharitonov *et al.* 2008). The same year, there were three Arctic Fox dens active in the area, and the lower clutch sizes further from the owls were probably caused by higher fox predation. In 2005 (another peak lemming year), 22 Arctic Fox dens were located and only 38 pairs of Brent nested. These Brent nested much closer (79 m ± 12.6 m) to the Snowy Owls' nests than in 1999 (Kharitonov *et al.* 2008).

Observations made on Taimyr from 1990–2008 (at sites indicated by the boxes in Fig. 1b) show that, when lemmings were abundant, Snowy Owls nested in variable numbers (Table 2). Wherever Snowy Owls nested, Pomarine Skuas were also nesting. Hundreds of Pomarine Skuas arrived at the Pyasina Delta in June each year, but they only nested there in the lemming peaks of 1991, 1994 and 2005. In the same 5 km^2 tundra plot, which was searched carefully for all nests each year, 10–20 Pomarine Skua pairs nested in 1991, 17 pairs in 1994 and in 31 pairs 2005 (de Raad *et al.* 2011).

From 1994–1996 there was a shorter (2-year) interval between two successive lemming peaks, while in 2004 (two years

after the locally failed lemming peak in 2002), six Snowy Owls started to nest near Medusa Bay, but in the end only one bred successfully.

Snowy Owls as predators of adult Brent and goslings

In the years immediately after a peak lemming year, we always observed Snowy Owls wandering in the Pyasina Delta (Fig. 1b,c), but these birds did not nest and we presume that they were mainly hatched the previous year. In 1992 and 1995 (both non-lemming years following a peak lemming year) we observed 30 owls and six owls, respectively, around our base camp at Lidia Bay on the delta (Ebbinge *et al.* 2000), and in 2006 we also regularly observed Snowy Owls in the area, but hardly any in 2007. Snowy Owls are true nomads, to an even greater extent than Arctic Foxes (Jacobsen *et al.* 2009; Warren & Cox 2002), as described in further detail in the Supporting Materials (Annex S3).

Snowy Owls not only protect nesting Brent from other predators but can also prey on goslings and even adult Brent (Kharitonov *et al.* 2008; this paper). In 2006 (*i.e.* the year following the 2005 lemming peak) we witnessed Snowy Owls attacking flocks of Brent and King Eider arriving in spring. One Snowy Owl sat on the same spot on the ice for three consecutive days, sometimes surrounded by several Taimyr Gulls. When it finally disappeared, we walked over the ice and found the remains of a female King Eider (Ebbinge *et al.* 2021), indicating that a Snowy Owl can kill and eat prey as large as this species. They apparently have difficulty in carrying it elsewhere, however, so the prey was defended and consumed *in situ*.

In 2004 (a year prior to a lemming peak) we found one of our colour-ringed Brent next to her nest on one of the Bird Islands. The breastbone was broken, the flight muscles completely eaten, and it was considered highly likely that a Snowy Owl was responsible (J.-F. Therrien, pers. comm. in Ebbinge *et al.* 2022), although we cannot exclude the possibility that a Peregrine Falcon *Falco peregrinus* (occasionally observed in this area) was responsible. In 2006, a Snowy Owl caught a King Eider on its nest on Big Bird Island, remaining several days on the same spot to eat it. When we approached this owl, it tried to fly off with its prey but could fly no more than a few metres and we left this owl with its prey (Ebbinge & Mazurov 2007).

Apart from lemmings, goslings and wader chicks are also attractive food for Snowy Owls. On Farwaternie Island in the Pyasina Delta, we saw a Snowy Owl trying to capture small Brent goslings in 1994 and 1995. In both these cases, goose families just managed to reach the safety of water and escaped, but in 2005, we found leg remains of a Brent gosling in a Snowy Owl nest (Ebbinge *et al.* 2022). In 1995 (a year after a lemming peak) on Troynoy Island, a wandering Snowy Owl predated an adult Brent, among the 400 nesting there that year (Table 1).

Snowy Owls creating safe havens for Brent

We observed how important the presence of Snowy Owls is for Brent at Medusa Bay in greater detail during the fairly late spring of 2004 (the year before a real lemming peak),

when lemming numbers were building up, but not very high. Six Snowy Owl pairs initially occupied territories, but four failed to lay eggs and left their territories in June. By 26 June, no owl eggs had been laid, although one pair eventually bred successfully (Table 2). On 24 June, we found 17 Brent nests on the tundra; three along small streams, and two clusters (of six and eight nests) within a Snowy Owl territory. Average clutch size was four eggs, but the Brent were probably still laying so their clutch sizes could increase. Three of the Brent nesting in the cluster of six Brent Goose nests were caught and colour-ringed, including one with four eggs which we marked G-YN. The Snowy Owl had a nest, but still no eggs. Three days later (on 27 June) we discovered G-YN again, this time on a nest containing only two eggs but 1 km away from her previous nest. This unique observation of repeat-clutching by a Brent Goose involved her laying at least six eggs, equal to the maximum clutch size we have observed for the species. On checking the colony where she was ringed, both the owl and all Brent had gone, suggesting that members of an active colony of six Brent pairs defending their territories had dispersed when the owl abandoned its nesting attempt.

Brent nesting near Snowy Owls in the Pyasina Delta during the 2005 peak lemming year

In three of the peak lemming years (1991, 1994 and 2005) we also worked along Lidia Bay in the Pyasina Delta, where most Brent nest on gull islands. In 1991 and 1994, although some Snowy Owls were nesting on the mainland tundra (two and six pairs, respectively; Table 2), there were no Brent nests close to them (Table 1), but in 2005 eight pairs of Snowy Owls nested in the same area with no fewer than 25 pairs of Brent nesting in association with four of these owls. Thus, in the eight years we visited Lidia Bay between 1990 and 2004, not a single Brent was seen to nest in association with Snowy Owls, but in 2005 they did so (Fig. 8). Further east in the delta in 2005, we found 43 more pairs of Brent nesting within another four Snowy Owl territories (Kharitonov *et al.* 2013). Clutch sizes for Brent nesting near Snowy Owls in the Pyasina Delta are given in Fig. 5.

The 2005 breeding season was also notable for the abundance of Pomarine Skuas at our mainland study site, nesting at a density of 6.0 pairs/km^2. Pomarine Skuas are a hazard for human tundra visitors in peak lemming years as they fiercely defend their nests against any intruder (be it a researcher, Arctic Fox or Snowy Owl; Fig. 9a), and their high density in 2005 made the impact of their presence very evident. Frequent attacks by Pomarine Skuas on nesting owls and roaming Arctic Foxes, made life difficult for these other predators, to the extent that the owls could hardly fly and made only short flights to deliver lemmings to their owlets (Fig. 9b). One nesting Snowy Owl had a Brent Goose nest nearby, and we were lucky to be in the vicinity when the goslings had just hatched, to see the goose family trying to depart with their offspring. Through our telescopes we could see five small goslings leaving the Snowy Owl territory. A hatched gosling is the same size as a lemming, easy prey for a Snowy Owl. The owl flew from her nest and tried to snatch a gosling, which immediately

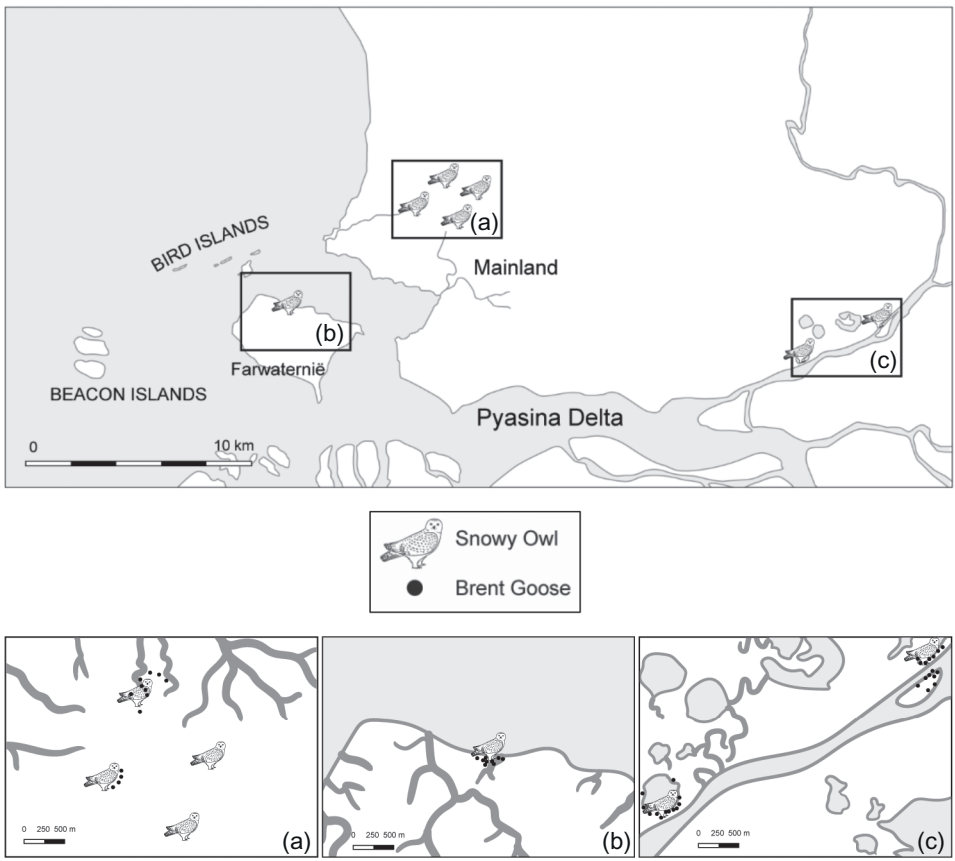

Figure 8. Snowy Owl nests (owls) and associated Brent Goose nests (black dots) in the Pyasina Delta in 2005. Maps (a), (b) and (c) give finer detail.

sought shelter under its mother's wings. At that moment, a Pomarine Skua nesting nearby attacked the owl, which was forced back to her nest. Later, the goose family continued to move out of the Snowy Owl territory, and again the owl attacked, this time managing to grasp a gosling despite another attack by the skua. Eventually the goose family managed to leave with four goslings.

Effects of fierce attacks by Pomarine Skuas have regularly been reported by researchers elsewhere (Portenko 1995); for instance, at Bely Island on the Yamal Peninsula (just west of the Taimyr Peninsula) a pair of Snowy Owls was forced to abandon their nest because of the many Pomarine Skua attacks in 2005 (A. and N. Sokholov, pers. comm.). Several photographs of Pomarine Skuas attacking Snowy Owls illustrate the impact of Pomarine Skuas (Fig. 9 and Supporting Materials Fig. S5). After 2005 we were convinced that such attacks seriously hinder the activities of

Figure 9. Snowy Owl on her nest (a) being attacked by a Pomarine Skua, and (b) returning to her owlets with damaged left wing because of Pomarine Skua attacks, by Doortje Dallmeijer.

both Snowy Owls and Arctic Foxes, to the extent that even waders benefit from the limits placed by Pomarine Skuas on the activity of other predators. Rough-legged Buzzards also failed to raise any offspring in our study area in 2005, despite there being many lemmings, it seems because skuas inhibited effective hunting activity.

Raising the goslings

Most Brent pairs will leave the nest with their one to two day-old goslings, both from gull islands and from Snowy Owl territories, to raise them elsewhere. Among the moulting flocks with goslings caught in late July, the proportion of young was much higher on the mainland than on the gull islands. In the Snowy Owl territories there were no moulting families at all; on the gull islands only 10% of geese in the flocks caught were young birds (n = 193); but at the mainland sites the proportion of young was 44% (n = 220; Ebbinge & Mazurov 2006). In one flock, caught near Lidia Lake on 7 August 2005, we retrapped seven ringed adult females, previously caught during incubation. The entire flock consisted of 33 adults and 46 juveniles of about three weeks old. Sixteen of the adults were females, so we had caught 16 pairs with on average three young per pair. Of these ringed females, one came from the Bird Islands and the other six had nested near Snowy Owls. This flock therefore was a mix, originating from various breeding sites but now moulting together. Later 20 of the 33 adults were seen again on the wintering grounds, but all in different flocks at different sites along the coasts of western Europe. Only the families remained together in winter (Ebbinge 2014).

Brent nesting without any protection

A third option for the Brent is to nest solitarily on the mainland tundra. This occurs in years when Arctic Foxes are rare or absent, when some of these nests hatch successfully. We were able to study this strategy on the mainland part of our Pyasina Delta study area (see Table 1), a 16 km^2 mainland area north of Lidia Bay, and we also included the large Farwaternie Island (just south of Lidia Bay) as "mainland" because this island had a fox den with Arctic Foxes breeding there in 1991 and 1994.

In 1990, a year in which we did not see a single Arctic Fox, all 12 of the Brent nests on Pyasina Delta's mainland tundra hatched successfully. In 1993 there were 15 nests in the northeastern part of Farwaternie, where there was one Taimyr Gull nest. These also all hatched successfully, and the group even remained at the site to moult. In the peak lemming years, however, in 1991 (nine Brent nests) and 1994 (six Brent nests), almost all were taken by Arctic Foxes, despite the abundance of lemmings (Ebbinge & Spaans 2002). In 1990, 34 Brent nested near Cape Sterlegova without any protection, but in the next two peak lemming years (1991 and 1994) only four Brent nested there. Following this strategy, Brent really have to be lucky not to be visited by an Arctic Fox.

Brent also nest on remote islands such as Troynoy, which is situated > 100 km offshore in the Kara Sea. It is so far out at sea that lemmings can never reach it, but Arctic Foxes are still able to get there over the sea ice in winter, and non-breeding Snowy Owls also occur. From the three years of data available, no Brent nested in

the extremely cold and late summer of 1992, but in 1994 a Norwegian-Russian team visited this island and estimated 700–1,200 pairs of Brent nesting there. At least 623 nests were checked, with an average clutch size of 4.5 eggs, but not a single Snowy Owl or Arctic Fox was observed (Bangjord *et al.* 1994). The crew of the weather station on that island trapped foxes for their pelts and told that the foxes would come over the ice in winter. Because of the lemming peak on the mainland in 1994, the Snowy Owls may have gathered on the mainland tundra, but Taimyr Gulls and Glaucous Gulls were also nesting on the island. In the absence of foxes, predation on Brent eggs appeared to have been low (mean clutch size = 4.5 eggs). During 8–15 July 1994, *c.* 600 Pomarine Skuas also visited the island, with *c.* 130 constantly present. These consisted mainly of immature birds that chased locally nesting Ivory Gulls *Pagophila eburnea*, Arctic Terns *Sterna paradisaea* and eiders, but did not themselves nest on the island, perhaps originating from the many skuas that had nested successfully on the mainland in 1994.

We visited Troynoy in 1995 and observed three Snowy Owls but, as in 1994, no foxes. Because lemmings were completely absent, the owls had to live on other prey, and the total number of Brent nests was reduced to 400 (less than half the number recorded in 1994; Table 1), with a mean clutch size of 3.4 eggs (n = 103; Fig. 3).

Four female Brent were found killed on nests, with Snowy Owl feathers next to two of these nests suggesting this species was responsible (Spaans & Cottaar 1996). Presumably because of Snowy Owl activity, a third of all 400 Brent nests were without eggs in 1995, compared to 12% in 1994, with eggs in these nests also potentially taken by Glaucous Gulls or Arctic Skuas *Stercorarius parasiticus* after the incubating goose was taken or scared off by a Snowy Owl. Pomarine Skuas were also observed daily in 1995, but not in the numbers as seen in 1994. It therefore seems that these wandering Snowy Owls can cause not only major reductions in nesting Brent, but also in the proportion of successful nests, at a site where lemmings are absent.

Discussion

The role of lemmings

Lemming population eruptions provide an abundant prey base for a variety of predators (Pielou 1994) and as keystone herbivores showing pulsed abundance dynamics, they drive strong multi-trophic spatially heterogeneous effects on the entire Arctic ecosystem. The best measure of such peaks on the Taimyr Peninsula is the number of nesting Snowy Owls, which breed only in peak lemming years, with Arctic Foxes (the key predator of nesting Brent) also concentrating (and reproducing) in areas where lemmings are abundant. Pomarine Skuas additionally were reported in high numbers on all occasions when Snowy Owls were found to be nesting on the Taimyr Peninsula, and thus when lemmings were abundant. Because lemming peaks are not synchronous across the entire Russian Arctic, it is most profitable for Snowy Owls and Arctic Foxes to redistribute over large areas to find suitable breeding sites. Despite high densities of

predators, however, Brent and waders usually breed very successfully in the peak lemming years.

Nomadism *versus* site-faithfulness

This review of long-term data illustrates major differences between years in the numbers of breeding Brent pairs (Table 1), depending on the lemming cycle. It also shows that individual Brent may select for a safe nesting place each year, rather than returning to the same nesting site. In some areas, nesting Snowy Owls offer unpredictable opportunities for safe nesting by Brent. Other, more predictable sites offering annual protection exist on small islands within gull colonies, although geese nesting there suffer from losing some eggs (and under certain conditions small goslings) to gulls. While many Brent return every year to such sites, in years without lemmings many more Brent settle and may become overcrowded on gull islands.

In 2005 (another Snowy Owl and peak lemming year), Brent suddenly nested along Lidia Bay (an area for 11 years completely without nesting Brent), indicating that these geese prospect over large geographical areas to find favourable nesting conditions. We have at least one case of a Brent nesting at sites 250 km apart in 2004 and 2005. Such cases must occur much more frequently, to explain local variation in nesting numbers, such as on Troynoy where 700–1,200 Brent nested in 1994, compared with only 400 the following year.

Thus, the nomadic behaviour of Snowy Owls and Arctic Foxes, governed by lemming cycles, forces Brent to be nomadic as well. Arctic Foxes and Snowy Owls may travel over thousands of kilometres, and Brent over hundreds of kilometres within their breeding range. To explain this nomadic behaviour, E.E. Syroechkovskiy Jr. launched the hypothesis that all smaller goose species, such as Brent, explore to survey conditions at different potential breeding areas for several days each year before deciding where to nest (Syroechkovskiy Jr. 1999).

In only one out of every three years can Brent choose between nesting either with gulls or with Snowy Owls. In the two other years, nesting within gull colonies or on the tundra are the only options. Thus, in the peak lemming years, the Snowy Owl option provides additional opportunities, which results in the entire Brent population returning to western Europe with greater numbers of offspring the following winter. Our data show that this three-year pattern still largely continues, and that following anomalies between 1994 and 1996 the three-year pattern was resumed, although the very high proportions of juveniles recorded in the 1980s (Summers *et al.* 1998; see below) have not occurred again.

Clutch size

Brent are determinate layers (Klomp 1970), never laying more than six eggs (Fig. 5 and Supporting Materials Annex S2). When we started to study Brent on the breeding grounds, we strongly believed that individual body condition determined their breeding success (Ebbinge 1989), because the heavier females leaving Wadden Sea spring staging sites in May were more likely to return with offspring (Ebbinge & Spaans 1995). While body condition evidently continues to play a role, more factors are involved in

determining reproductive outcomes, such as head winds during spring migration and breeding season predation pressure.

Nesting strategies of Brent affect clutch sizes, mainly influenced by partial predation on eggs. Within Snowy Owl territories, the absence of egg predation results in average clutches of about five eggs. Within gull colonies Brent clutches vary from an average of four eggs in peak lemming years to three eggs in other years. Nesting centrally in a gull colony also results in larger clutch sizes for Brent, where the intensity of protection resulting from gulls defending their own nests against conspecifics helps reduce Brent egg predation. Brent clutches within gull colonies are more prone to partial predation in years when the gulls do not have access to lemmings as an extra food source, with gulls preferring to avoid the counter-attacks by Brent on stealing their eggs under normal conditions.

The variation in mean clutch sizes according to nesting circumstances (*e.g.* whether nesting between gull nests in non-lemming years, or between gulls or near Snowy Owls nests in peak lemming years) makes it likely that avoiding predation plays a key role in reducing clutch size. Our lucky encounter with the same bird starting a repeat clutch of two eggs, having lost her earlier nest with four eggs to fox predation, shows how this works. Smallest clutches are potentially the result of birds renesting immediately after losing an incomplete clutch. Thus, Brent found nesting near Snowy Owls with a relatively small clutch might well be birds starting a repeat clutch after having lost their first nesting attempt elsewhere.

The role of Arctic Foxes

According to the Russian goose biologist E.V. Syroechkovskiy, who studied geese across the Russian Arctic (Lesser Snow Geese *Anser caerulescens carulescens* on Wrangel Island; Barnacle Geese, Greater White-fronted Geese and Bean Geese *Anser fabalis* on Vaygach Island and Novaya Zemlya), the Arctic Fox is by far the most important nest-predator for geese across the entire Arctic ecosystem. The key factor allowing Brent to reproduce successfully therefore is to avoid Arctic Foxes (Syroechkovskiy 2016). He describes how Arctic Foxes were isolated on a small island (Pukhovoy Island, 1 km from Novaya Zemlya) by the sea ice melting in spring. This completely inhibited breeding by Barnacle Geese on Pukhovoy in that year, when researchers found only six pairs of geese and not a single nest, whereas the following year (without foxes and without lemmings) 700 pairs of Barnacle Geese nested there.

The suggestion of prey-switching behaviour by Arctic Foxes, from taking bird eggs to lemmings when the latter are abundant, is questioned by a photograph taken by Jan van de Kam in the 1991 peak lemming year. Although just a single incident, it shows a predated Brent nest on the mainland tundra at Lidia Bay, with two dead lemmings next to it and all four eggs had gone. It seems that an Arctic Fox must have had swapped two lemmings for the Brent Goose eggs so, even when lemmings are available, birds' eggs remain very attractive to foxes. The long-distance movements of Arctic Foxes throughout the entire Arctic region is however a much more likely explanation for the boom-and-bust levels

in annual breeding success among Brent. In some summers there are large areas with hardly any foxes, whereas as soon as lemmings are peaking foxes reappear and have large litters, increasing their local numbers enormously. Although our study did not commence until the 1990s, a fox-trapper/fisherman who lived for years in the Pyasina Delta confirmed that the three-year pattern extended over a longer period. He told us that 1982, 1985 and 1988 were extremely good lemming years, after which he trapped many Arctic Foxes. In those years Brent returned to Europe with 51%, 35% and 41% young, respectively (Summers *et al.* 1998). The so-called prey-switching hypothesis implicitly assumes that Arctic Foxes are always around, and simply ignore eggs when lemmings are plentiful. However, a much more important factor is that the numbers and distribution of Arctic Foxes varies greatly from year to year, with the information presented here illustrating these huge differences. Both Snowy Owls and Arctic Foxes can travel large distances across the Arctic region in winter, and when lemmings are peaking somewhere these two predators concentrate on such areas, attracted by the sound of lemmings under the snow.

Interactions with other lemming predators, in particular Pomarine Skuas, restrict the hunting possibilities of both Snowy Owls and Arctic Foxes to a great extent, and therefore Brent can nest relatively safely within fox-free zones around nesting Snowy Owls. The use of digital cameras allowed us to document the impact of Pomarine Skuas (*e.g.* Fig. 9a,b) and showed how hard they can attack and restrict the activities of Snowy Owls, constraining them to fly as little as possible. Under such circumstances, Arctic Foxes were also greatly hindered by the skuas in their search for bird nests.

The role of Snowy Owls

Snowy Owls start to lay eggs in late May before Brent arrive and keep Arctic Foxes at bay. Nevertheless, as documented by Kharitonov (2008) extremely high numbers of Arctic Foxes near Medusa Bay in 2005 resulted in fewer Brent nesting near Snowy Owls, and those that did so nested more closely to an owl. Nesting near Snowy Owls – if constrained by Pomarine Skuas – generally seems a better choice for Brent, leaving them with an average of almost five eggs per clutch (Figs. 3 & 7), but this option is available only when lemmings are abundant, once every three years. Variation in numbers elsewhere (particularly at sites like Medusa Bay, where Brent use Snowy Owls as protectors against foxes) likewise shows that the Brent are nomadic. Apart from Brent, the Greater Snow Geese *Anser caerulescens atlanticus* are also known to nest in association with Snowy Owls on Bylot Island, Canada (Bêty *et al.* 2001) and Red-breasted Geese nest in association with Peregrine Falcons on Taimyr (Prop & Quinn 2003; Quinn & Ueta 2008).

The advantage of nesting on gull islands

A second possibility is to protect a clutch against predation by foxes, for instance by nesting on small islands in colonies of large gulls (de Fouw *et al.* 2016). This offers a chance of successful breeding in two out of three years. These gull colonies are occupied annually, offering a highly predictable option

for nesting Brent, and have the additional advantage of gull guano fertilising the vegetation upon which geese feed during nest recesses. Gull colonies are restricted to small islands, difficult for foxes to access as soon as ice has melted, leaving only gulls as potential predators. In peak lemming years egg predation by gulls is reduced, resulting in mean clutches of four eggs for the Brent, but in the absence of lemmings clutch size falls to three eggs, because of higher gull partial clutch predation (Figs. 4 & 5). Colour-marked Brent returning to gull colonies on Bird Islands showed site-fidelity, but the huge increase in numbers breeding in 2004 also demonstrates that in some years many other Brent additionally try to nest among the gulls. The difficulty of maintaining a territory was illustrated by goose R-GA, which after losing her mate could not maintain her old territory with a new mate, although one year later she was able to nest successfully again (Supporting Materials Annex S4).

The year after a lemming peak

Almost always in the year following a lemming peak, predation pressure is so high that it is nearly impossible for the geese to raise any offspring. Foxes are then not territorial but wander freely, because they are not being attacked by Pomarine Skuas. Moreover, adult geese can then be taken by non-nesting Snowy Owls (as on Troynoy in 1995), as the owls can kill adult geese and King Eiders on the nest and during migration (Therrien *et al.* 2014), as well as preying on goslings. The owls would not have evolved such long talons if lemmings were to be their only source of prey (G. Gauthier, pers. comm.). The only reason why Snowy Owls do not use this capacity to kill geese when nesting is, in our opinion, the presence of Pomarine Skuas in peak lemming years. The frequent attacks by these skuas, both on Snowy Owls and Arctic Foxes, make a huge impact by restricting owl and fox activity. In the year following a lemming peak, however, Pomarine Skuas only briefly visit the tundra, as if sampling the food supply, before disappearing from the scene.

Why do Brent not simply nest near Pomarine Skuas?

The fact that Brent do not seek protection by Pomarine Skuas in peak lemming years may be because both Brent and Pomarine Skuas arrive at the same time. Brent have to choose where to nest before Pomarine Skuas have established their own nesting territories, whereas Snowy Owls and gulls are already present and nesting before the first Brent arrive.

Clues that Brent can use in selecting a safe nesting place

A visual clue that Brent might use to select a suitable nesting site is looking for obvious big white birds: either gulls or Snowy Owls. Gull presence indicates islands difficult for Arctic Foxes to reach during the Arctic summer. Snowy Owls chase foxes away from their territories, creating fox-free zones of *c.* 500 m around their nests where the geese can also nest. Another possibility is that the Brent monitor a potential site for fox activity and, if no or hardly any foxes are present, decide to nest there.

Whether they nest on gull islands or within a Snowy Owl territory, soon after

hatching Brent leave to raise their offspring elsewhere on the tundra, away from the gulls and owls, and close to water so that they can avoid gosling predation by foxes and gulls.

Conclusions

The three-year lemming cycle continues to have a great impact on Dark-bellied Brent Goose productivity. In peak lemming years, Brent are most productive (with 30–50% juveniles in the winter flocks) and nest either within Snowy Owl territories or within gull colonies on small islands. Additionally, some Brent may nest "unprotected", on the open tundra. In the summer following a lemming peak, predators such as Arctic Foxes and Snowy Owls have increased strongly in number, and safe nesting is virtually impossible for Brent, which often return to Europe with < 1% juveniles in the population the following winter. Moreover, Snowy Owls may prey on nesting adult Brent in non-lemming years. In the unpredictable third year of the cycle (preceding the next lemming peak) there are still hardly any lemmings, but predator numbers are also greatly reduced, and breeding success for Brent can be moderate, with 10–25% juveniles in the winter flocks. Although Snowy Owls can kill large prey like Brent, they eat these on the spot and have great difficulty flying with such prey; lemmings therefore provide better food for feeding to their owlets in a year when they are abundant. In peak lemming years, many Pomarine Skuas nest and in defending their own territories they harass both Snowy Owls (Fig. 9a,b and Supporting Materials Fig. S5) and Arctic Foxes to such an extent that their predation of adult Brent and goslings is greatly hindered. In this way the skuas help to protect Brent by limiting owl and fox activity. Nevertheless, the abundance of lemmings is so high that both Snowy Owls and Arctic Foxes manage to reproduce very well. Most Brent leave their safe nesting areas (Snowy Owl territories and gull islands) soon after hatching to raise their goslings on the mainland tundra along the many streams that offer safety from Arctic Foxes. This also keeps the Snowy Owls and gulls from preying on goslings. In comparison with the maximum clutch size of six eggs recorded for Brent, average clutch sizes were of five eggs when nesting near Snowy Owls, four eggs on nesting within gull colonies in peak lemming years, and three eggs on nesting within gull colonies in years with very few lemmings.

Acknowledgements

This paper is based on many hours of field observations made by tens of biologists working on the Taimyr Peninsula in northern Siberia between 1990 and 2008. Initially the international expeditions to Taimyr were made possible by the late Prof. E.E. Syroechkovskiy Sr., Peter Prokosch and Gerard Boere, supported financially by the Dutch government, and the Alterra research institute of Wageningen University (Boere 2007). Apart from this, a number of Snowy Owl researchers in North America, Norway and Yamal have supplied us with important additional information. We are grateful to all of them for collecting and making available this information. In particular, we would like to thank Thomas Alerstam, Doortje Dallmeijer, Nick Davies, Laurent Demongin, Dorothée Ehrich,

Nicole Feige, Jim de Fouw, Petr Glazov, Vasily Grabovski, Denver Holt, Sergei Kharitonov, Raymond Klaassen, Hein van Kleef, Jaap Mulder, Bart Nolet, Damian Novak Agnieszka Novak, Laura Kooistra, Ingar Øien, Bas Pedroli, Norman Smith, Roar Solheim, Bernard Spaans, Jacques de Raad, Pertti Saurola, Hans Schekkerman, Aleksandr Sokolov, Natalya Sokolova, Jean-François Therrien, Johan Thissen, Ingrid Tulp and Les Underhill for comments on the work and assistance in the field. We are grateful to Maaike Ebbinge for carefully preparing the figures and maps. We also thank the directors of the Great Arctic Reserve, Vladimir Badukin and Valery Chuprov, for permission to undertake fieldwork in their reserve, and finally Aleksandr Abolits, Maxim Sinitsin, Nikita Vronski, Aleksandr Yunak and Yuri Mazurov for all the practical help provided in organising these expeditions. We would like to thank Ron Summers, an anonymous referee, Eileen Rees and Tony Fox for their constructive comments on earlier drafts of the paper.

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Photograph: Brent Geese with downy goslings on one of the Bird Islands in 2005, by Doortje Dallmeijer.