Supporting Materials

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

Annex S1. General information about lemmings on the Taimyr peninsula

The dynamics of several species living in the Arctic are determined largely by the cyclic presence of high densities of lemmings – rodents weighing 70–90 gm when adult, which look like large voles. Worldwide there are 12 different species in the *Lemmus* and *Dicrostonyx* genera (Supporting Materials Fig. S1), which do not hibernate but instead are very active under the protective layer of snow. To find lemmings one must go to northern latitudes, to areas covered by snow for nine months each year where, under a thick, dry layer of snow, lemmings are capable of producing large numbers of offspring. Of the Eurasian species, the Siberian Lemming *Lemmus sibiricus* lives exclusively under the snow in winter and keeps its browny pelage, whereas the Collared Lemming *Dicrostonyx torquatus* (which fluctuates in numbers in a less extreme way) has white winter pelage, and is also equipped with special claws to get though a crust of snow, so can also be found above the snow layer in winter. They are the preferred prey items for many predators (*e.g.* Arctic Foxes *Vulpes lagopus*, raptors, Snowy Owls *Nyctea scandiaca*, Long-tailed Skuas *Stercorarius longicaudus*, Pomarine Skuas *Stercorarius pomarinus* and the larger gulls *Larus* sp.), so that lemming density largely determines the breeding success of these predatory species, but at the same time has a great impact on the nesting success of waders and geese. Snowy Owls, which feed predominantly on lemmings, can only breed successfully in peak lemming years.

Lemming numbers can build-up very quickly under a safe cover of dry snow. A young female can become pregnant at the age of one month, the gestation period is only three weeks and average litters are of seven young for Siberian Lemmings with five young for Collared Lemmings (Popov in Ebbinge & Mazurov 2006). Numbers thus increase very fast. To illustrate: a single lemming female giving birth in October to seven offspring (of which half are female) can by the end of the winter period be pregnant simultaneously with her daughters, granddaughters and great-granddaughters. Such a breeding capacity can give rise to 1,000 females and a similar number of males in one winter (Ebbinge 2014, calculated from data of Popov without taking into account predation during the winter months). This leads to densities of 300–400 lemmings/ha in peak lemming years (Rykhlikova & Popov 2000).

Along Lidia Bay in the northern part of the Pyasina Delta we did not see any lemmings at the start of 1990 field season (a build-up year), after the snow had melted in June. It was not until the end of July that the first lemmings suddenly appeared, in an old unoccupied fox den.

One of these lemmings was caught and marked and was a few days later retrapped 1 km away, which illustrates the distances that lemmings can cover in a short time and indicates that they can occupy a large area during the rising phase of the lemming cycle. The following winter (1990–1991) must have been very favourable for lemmings because, upon returning in June 1991 everywhere under the helicopter landing area, lemmings were running away. In the extremely late spring of 1992 (a non-lemming year), we only saw a few lemmings after the snow had melted, a small fraction of the numbers in 1991. The peak was over. In most peak lemming years, high densities of lemmings are observed across the entire Taimyr Peninsula, but spatial differences in lemming densities may also occur in some years.

On the Taimyr Peninsula, lemmings were not always able to peak every third year. During our field seasons there were two years (2002 and 2008) when a build-up towards a peak year in the Pyasina Delta totally collapsed, though in 2002 in Uboynaya and Medusa Bay the abundance of lemmings was still sufficient to allow at least some Snowy Owls to breed (Table 2). In 2008 we detected narrow ice layers in the huge layer of snow, indicating short spells of snowmelt (maybe even with some rain) during the winter, followed by refreezing. When all the snow had melted, we found totally iced-up lemming nests, and lemming tunnels filled with cores of ice. The total density of old lemming nests was equal to that of 2005, which had resulted in a peak lemming year (De Raad *et al.* 2011; Feige *et al.* 2012). As an indication of initial high lemming abundance in 2008 the icefloes in the bay were covered with "lemming hay", so apparently the last and critical set of births that would have caused a lemming peak was frustrated by the melting and refreezing water running into the nests and through the lemming tunnels under the snow. "Lemming hay" is a remarkable feature of lemming peaks. Under the snow the lemmings graze vegetation, both for food and to line their nests, and all this grazed material is flushed with the melting snow to the still ice-covered

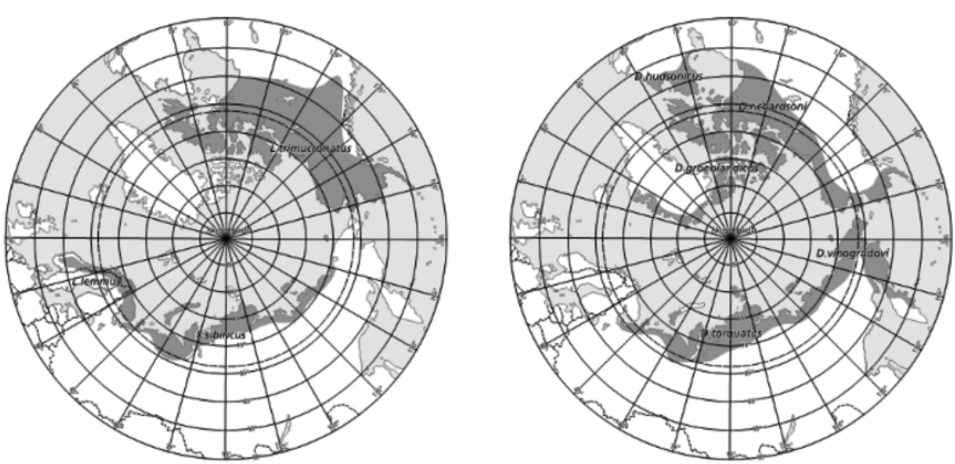

Figure S1. Circumpolar distribution of various lemming species. Left = *Lemmus* sp.; right = *Dicrostonyx* sp., from Ebbinge *et al.* (2021).

bay. After a winter in which lemming numbers had increased strongly, we always found such packages of "lemming hay". This phenomenon was only witnessed in peak lemming years.

Overall, some potential peak lemming years anticipated by the three-year cycle did not lead to high numbers (in 2002 and 2008), in 2008 despite a good start because of weather conditions. Apart from 1996, however, the three-year pattern of lemming peaks generally remained, in 1991, 1994, 1996, 1999, 2002, 2005 and 2008. In 1994 the next peak occurred two years later, but from 1996 onwards the three-year rhythm persisted.

The only mammalian predator that is capable of a similar rate of reproduction as lemmings, and can also use lemming tunnels and nests under the snow, is the Least Weasel *Mustela nivalis nivalis*. Between 1990 and 2004 we never observed any Least Weasels in the Pyasina Delta, but in 2005 these small predators suddenly appered in large numbers. Subsequently, in 2006 and 2008 many Least Weasels were also present (Feige *et al.* 2012).

Annex S2. Testing the difference in clutch size of Brent in different conditions.

On the more exposed outer flat islands (named "Beacon Islands"), we always found somewhat smaller clutches than on the Bird Islands, which lie to the northeast of the Beacon Islands. This may be attributable to it being easier for the gulls to predate on eggs on the Beacon Islands, because there is a lower density of gulls than on the Bird Islands which also provide more sheltered rocky outcrops which make it easier for Brent to defend their clutches. Clutch size always varied between one and six eggs. Empty (fully predated) nests were not taken into account, but partially predated nests were included on determining mean clutch sizes. Only mean clutch size values were available for 1990 (3.0 eggs/nest for all islands combined), and for 1991 (3.5 eggs/nest for the Beacon Islands; 4.0 eggs/nest for the Bird Islands; Fig. 3), but the frequency distributions (*n* values) for each clutch size in Fig. 3 were available for all other years.

The year 2004, in which many Brent were nesting, is the only year in which similar mean clutch sizes (2.9 eggs) were recorded for both island groups. In 2005 (a peak lemming year) the number of gulls on the Bird Islands was also much higher than in 2004, increasing from 2,515 to 3,000 pairs for these two years. The number of gulls on the Beacon Islands rose by 26%, while the number of Brent declined by 63%. The number of gulls on the rocky islands likewise increased, by 10%, while the Brent declined by 46% (Ebbinge & Mazurov 2006). Clutch sizes for both island groups within the Bird Islands increased in 2005.

We compared the frequency distribution of clutch sizes for the lemming-year (2005) and the other for years combined for both the Beacon Islands and the Bird Islands. For statistical testing, we constructed a contingency table of clutch size by year group (lemming-year *vs.* non-lemming years). Due to small and unequal sample sizes, we used Fisher's exact test with a simulated *P* value based on 100,000 replicates, which provides a reliable measure of association between year group and clutch size. Analyses were performed in Program R. To visualise differences, we created bar charts showing the distribution of clutch sizes for 2005 and for the combined years, as proportions to account for unequal sample sizes (Figs. S2 & S3). *P* values

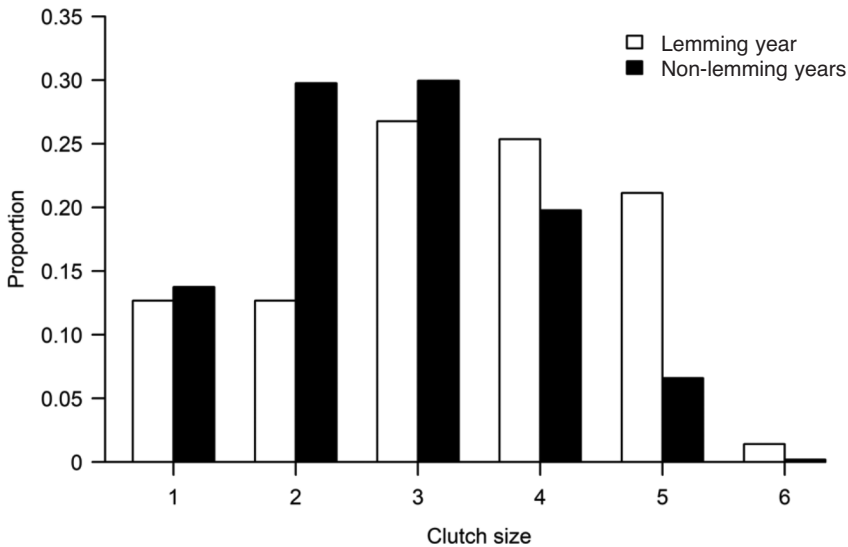

Figure S2. Frequency distribution (given as a proportion of the clutches recorded) for Brent clutch sizes on Beacon Islands in a peak lemming year (2005) compared with non-lemming years (1995, 2004, 2006 and 2008).

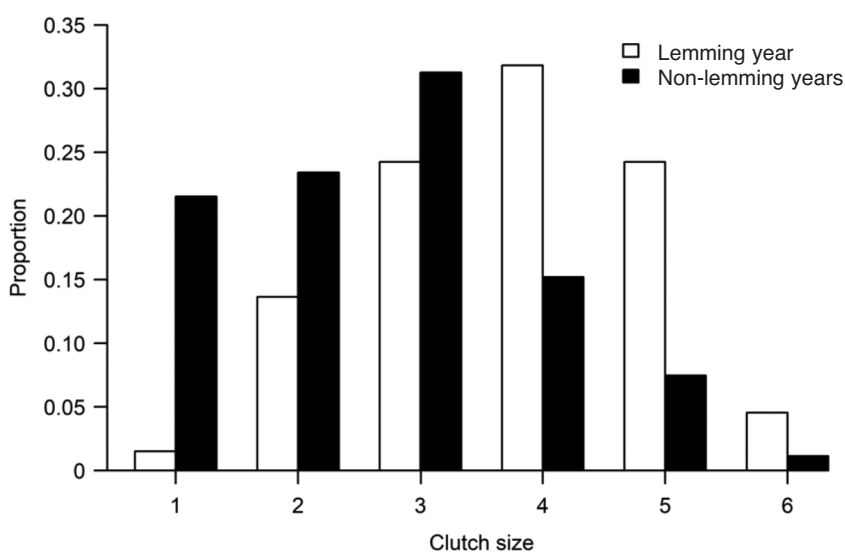

Figure S3. Frequency distribution (given as a proportion of the clutches recorded) for Brent clutch sizes on Bird Islands in a peak lemming year (2005) compared with the non-lemming years (1995, 2004, 2006 and 2008).

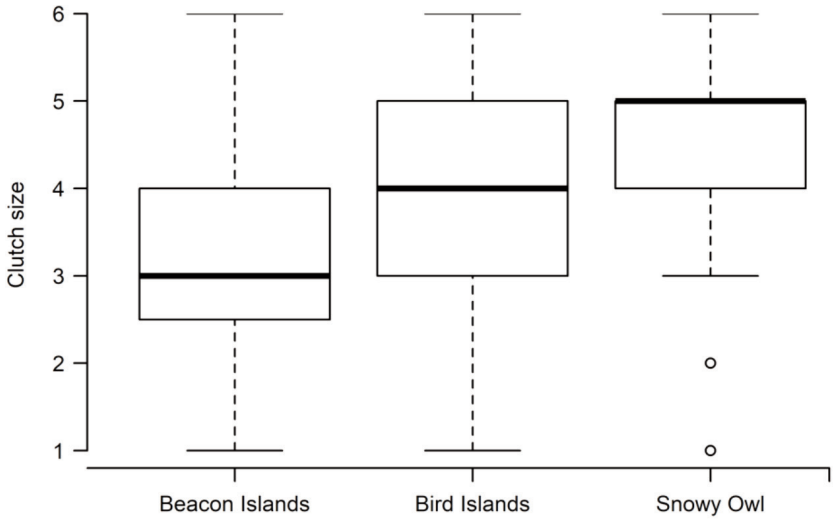

Figure S4. Clutch sizes recorded for Brent nesting on Beacon Islands, Bird Islands and in Snowy Owl territories in a peak lemming year (2005). Thick horizontal lines show median values, top and bottom lines of the box show the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points that fall within 1.5 times the interquartile range from the lower and upper quartiles. Data points beyond this range are displayed individually as dots and considered potential outliers.

on comparing clutch sizes for the peak lemming year (2005) with those in non-lemming years were 0.0002 and < 0.0001 for the Beacon Islands and the Bird Islands, respectively.

Clutch size distributions in 2005 were compared across locations. Because the data were not normally distributed, we used a Kruskal-Wallis test to test for overall differences among locations. Significant results were followed up with *post-hoc* pairwise comparisons using Dunn's test with Bonferroni correction. There was a significant difference in clutch size distributions among locations (Kruskal-Wallis test: $H = 28.64$, d.f. = 2, $P < 0.001$; Fig. S4). The *post-hoc* Dunn's tests revealed that clutch sizes at Snowy Owls differed significantly from Bird Islands ($Z = 3.65$, $P < 0.001$) and Beacon Islands ($Z = –5.28$, $P < 0.001$), whereas there was no difference between Bird Islands and Beacon Islands ($Z = –1.65$, $P = 0.29$, n.s.).

Annex S3. Supplementary text on territory defence and nest site selection by individual Brent, identified by their ring codes.

The inter-nest distance of Brent breeding in the Pyasina Delta is at least 33 m (Spaans *et al.* 2007), and male Brent heavily defended such territories against conspecifics, allowing their mates to feed within the territory during the incubation period. The importance of territory defence is illustrated by R-GA (a female marked with colour rings: a red ring with a single bar on the left leg and a green ring inscribed with letter A on the right). She was caught on her nest, which contained a clutch of six eggs, on Big Bird Island on 10 July 1991, and left this

island with five goslings. Later, on 7 August 1991 she was recaptured in a moulting flock on the mainland tundra *c.* 10 km away from the island. Then her mate and young were also ringed. In the winter she was seen on the Dutch island of Terschelling with her mate R7GH and two goslings (O9B6 and O9B2). On 16 June 1992 she again arrived on the Big Bird Island with R7GH but without offspring but failed to nest in that "fox-year".

In 1993 she returned with an unringed mate, but the pair was continuously chased away by other Brent. Apparently, her former mate had died, and the new mate was not able to defend a territory. In 1994 she again returned with an unringed partner (probably the same as in 1993), this time the pair did establish a territory, and R-GA laid five eggs. She did so again in 1995, and again laid five eggs. This shows that Brent can be site-faithful, but also that is is not easy to maintain a territory on these gull islands without a strong mate.

R7GH was last seen on 25 April 1993 on Terschelling still in the company of R-GA. R-GA was last seen on 6 July 1995 on the Big Bird Island. In total she was observed 175 times.

O9B2, the daughter of R7GH and R-GA returned to the Big Bird Island in June 1993 (when two years old), and again a year later, on 22 June 1994, with an unringed mate. Then she was making a scrape, giving the impression that she was going to nest on the island, but on 3 July 1995 we found her nesting 10 km away on the mainland tundra, in the area where she was caught as a gosling with her mother in 1991. This shows that Brent do search and test various places before choosing an adequate nest site.

Annex S4. An overview of nomadism in the Snowy Owl, and their predation of bird species.

Snowy Owls are true nomads, to a greater extent even than Arctic Foxes, and they only nest when and where lemmings are abundant (Krebs *et al.* 2002). This nomadism was revealed by research in Alaska, when nesting Snowy Owls were equipped with satellite transmitters by Denver Holt, who founded the Owl Research Institute in Montana USA. A Snowy Owl which nested in Alaska in 1999, and the following year nested 1,000 km further west, in eastern Siberia, features as a major article in the National Geographic (Warren & Cox 2002).

Another example of this nomadic behaviour comes from Norway. Because of lack of lemmings for many years, Snowy Owls had not nested in Scandinavia for a long time.

In 2007, however, a real lemming peak occurred in Scandinavia, and immediately Snowy Owls were nesting there again. Three Snowy Owls were caught on the nest and fitted with transmitters, and two of these were detected the next year on Novaya Zemlya and Taimyr, 2,500 km further east (Jacobsen *et al.* 2009).

In 2014 on Bylot Island (Canada), Jean-François Therrien studied the nest of an extremely aggressive female Snowy Owl. Within a month, no fewer than seven carcasses of Greater Snow Geese *Anser caerulescens* were found, all within 20 m of her nest, and all looking like the remains of our Brent Goose female with the broken breastbone which we recovered on one of the Bird Islands. Denver Holt, who studied Snowy Owls near Barrow (Alaska) for 30 years, during which time he collected 46,500 prey from owl pellets and 3,300 prey remains brought

Figure S5. Pomarine Skua attacking a male Snowy Owl, by Sim Broekhuizen.

to the owl's nest, wrote that he found the remains of 31 different bird species in this collection. The bird species varied from Snow Bunting *Plectrophenax nivalis* to Greater White-fronted Goose *Anser albifrons* but also included King Eider *Somateria spectabilis* and Brent. Though some Snowy Owls are capable of also bringing larger prey to their nest, by far the most common prey were Brown Lemming (also *Lemmus sibiricus*) and Collared Lemmings. Arctic Foxes and Least Weasels were also present in Denver Holt's collection (Holt *et al.* 2024; see also Ebbinge *et al.* 2021).

References

de Raad, J.A., Mazurov, Y.L. & Ebbinge, B.S. 2011. *Pristine Wilderness of the Taimyr Peninsula: 2008 Expedition to the Pyasina Delta, Taimyr Peninsula, Russian Federation*. Alterra Rapport No. 2190. Alterra, Wageningen, the Netherlands.

Ebbinge, B. 2014. *De Rotgans.* [*The Brent Goose.*] Atlas Contact, Amsterdam, the Netherlands. [In Dutch.]

Ebbinge, B.S. & Mazurov, Yu.L. 2006. *Pristine Wilderness of the Taimyr Peninsula 2005 Report*. Heritage Institute, Moscow, Russia.

Ebbinge, B., Bom, R.A., Broekhuizen, S., Cottaar, F. & Müskens, G. 2021. Why are nesting Brent Geese seeking protection within the territories of Snowy owls? Observations on the Taimyr-peninsula, *Uilen* 11: 134–160. [In Dutch.]

Feige, N., Ehrich, D., Popov, I.Y. & Broekhuizen, S. 2012. Monitoring least weasels after a winter peak of lemmings in Taimyr: body condition, diet and habitat use. *Arctic* 65: 273–282.

Holt, D.W., Larson, M.D., Seidensticker, M.T. & Hiro, S.P. 2024. A worldwide review of Snowy Owl feeding ecology: the importance of lemmings and voles in a changing climate. *Birds* 5: 341–351.

Jacobsen, K.-O., Solheim, R., Oien, I.J. & Aarvak, T. 2009. Snøuglenes vandringer fortsetter. *Vår Fuglefauna* 32: 172–176.

Krebs, C.J., Kenney, A.J., Gilbert, S., Danell, K., Angerbjörn, A., Erlinge, S., Bromley, R.G., Shank, C. & Carrière, S. 2002. Synchrony in lemming and vole populations in the Canadian arctic. *Canadian Journal of Zoology* 80: 1323–1333.

Rykhlikova, M.E. & Popov, I.Yu. 2000 Population dynamics and habitat selection of lemmings in arctic tundra of northwestern Taimyr. *In* Ebbinge *et al.* 2000 (eds.), *Heritage of the Russian Arctic: Research, Conservation and International Cooperation*, pp. 544–553. Ecopros Publishers, Moscow, Russia.

Spaans, B., van't Hoff, C.A., van der Veer, W. & Ebbinge, B.S. 2007. The significance of female body stores for egg laying and incubation in Dark-bellied Brent Geese *Branta b. bernicla*. *Ardea* 95: 3–15.

Warren, L. & Cox, D. 2002. The magic of owls. *National Geographic* (December 2002): 104–112.

Photograph: Incubating Brent Goose female on her nest on one of the Beacon Islands, Pyasina Delta, Russia in 2005, by Bart Ebbinge.