Flexibility in faithfulness of Dark-bellied Brent Geese *Branta b. bernicla* to moulting sites

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Abstract

The distribution of Dark-bellied Brent Geese *Branta b. bernicla* moulting on the Taimyr Peninsula, in the Russian arctic, varies between years depending on whether the birds had a successful breeding season. Counts made of moulting flocks show that major shifts in numbers occur, particularly in non-breeding years, when in line with Salomonsen's (1968) hypothesis a higher proportion of the population moults further north. For instance, the delta of the Lower Taimyr River in the northern part of the Taimyr Peninsula held 10-times more moulting Dark-bellied Brent Geese in 1989, a non-breeding year, than it did in the good 1990 breeding season. At a more local scale, in good breeding years family groups with small goslings tend to move away from breeding islands in the Pyasina Delta, western Taimyr, to avoid gosling predation by Taimyr Gulls *Larus taimyrensis* which nest in colonies on the same islands, whereas in poor breeding years adult geese concentrate on these same islands to moult and avoid the mainland sites used for moulting in good breeding years. Failed breeders have greater freedom than parent birds to choose where to moult as successful breeders remain with their goslings to protect and guide them to the safest nursery and moult areas. Re-captures of ringed Dark-bellied Brent Geese at a moulting site in the Pyasina Delta found that, in poor breeding years, up to one-fifth the birds had moulted at the site previously, but that the majority of ringed birds known to be still alive were not site-faithful to their moulting grounds.

Key words: Dark-bellied Brent Geese, site tenacity, wing moult.

Many arctic goose species migrate to sites north of their nesting areas to renew flight feathers (a "moult migration"; Salomonsen 1968), which are all shed simultaneously making the birds flightless for about 3–4 weeks each year. Whereas successful breeding birds have to stay with their goslings and moult on or near their breeding territories, unsuccessful and non-breeding birds generally migrate to special moulting areas where they are relatively safe from predation and have a secure food supply. Moult migration is an important part of the birds' annual cycle, being an established movement at a time when the birds are vulnerable due to their inability to fly. Yet compared to studies made on the breeding and wintering grounds, the use of moulting sites by the geese has received very little attention (Derksen *et al.* 1982).

Dark-bellied Brent Geese *Branta b. bernicla* breed along the arctic coasts of Russia, including the Taimyr Peninsula where they nest on small islands among Taimyr Gull *Larus taimyrensis* nests (Spaans *et al.* 1993; Ebbinge & Spaans 2002), and within the "safe havens" from Arctic Foxes *Alopex lagopus* created around Snowy Owl *Nyctea scandiaca* nests in years with peak lemming *Lemmus sibiricus* and *Dicrostonyx torquatus* abundance when the Snowy Owls also breed (Summers *et al.* 1994; Ebbinge & Mazurov 2006; van Kleef *et al.* 2007). There is considerable annual variation in their breeding success; in some years, particularly in peak lemming years, breeding success is high because lemmings provide a main food resource for potential predators of goslings, whereas in years with low lemming numbers predation pressure increases and almost all adults fail to raise any young (Ebbinge *et al.* 2013). Given the marked annual differences in Dark-bellied Brent Goose breeding success, one would therefore expect many more birds to undertake a moult migration in non-breeding years than in good breeding years, in line with Salomonsen's (1968) conclusions.

In this paper we investigate the use of moult sites by Dark-bellied Brent Geese on the Taimyr Peninsula. We consider whether the tenfold difference between the numbers of Dark-bellied Brent Geese that moulted in the northernmost part of the Taimyr Peninsula in 1989 and 1990 can be explained in terms of differences in the degree of moult migration that takes place in breeding *versus* non-breeding years by analysing data collected between 1990 and 2008 in the Pyasina Delta in western Taimyr. Data recorded for marked individuals are also used to examine the return rates of Dark-bellied Brent Geese and to determine their fidelity to moult locations in non-breeding years.

Study areas

Dark-bellied Brent Geese were studied in two main areas on the Taimyr Peninsula: in the delta of the Nizhnyaya Taimyra (*i.e.* the Lower Taimyr River; 76.10°N, 99.50°E) and in the Pyasina Delta (74.07°N, 86.31°E) (Fig. 1). The Lower Taimyr Delta is a vast area with a network of polygon pools, small and larger lakes, and meandering river channels (Fig. 2). Wet plains on either side of the main river delta, formed by fine sediments of smaller tributaries to the Lower Taimyr River, are used by the geese to

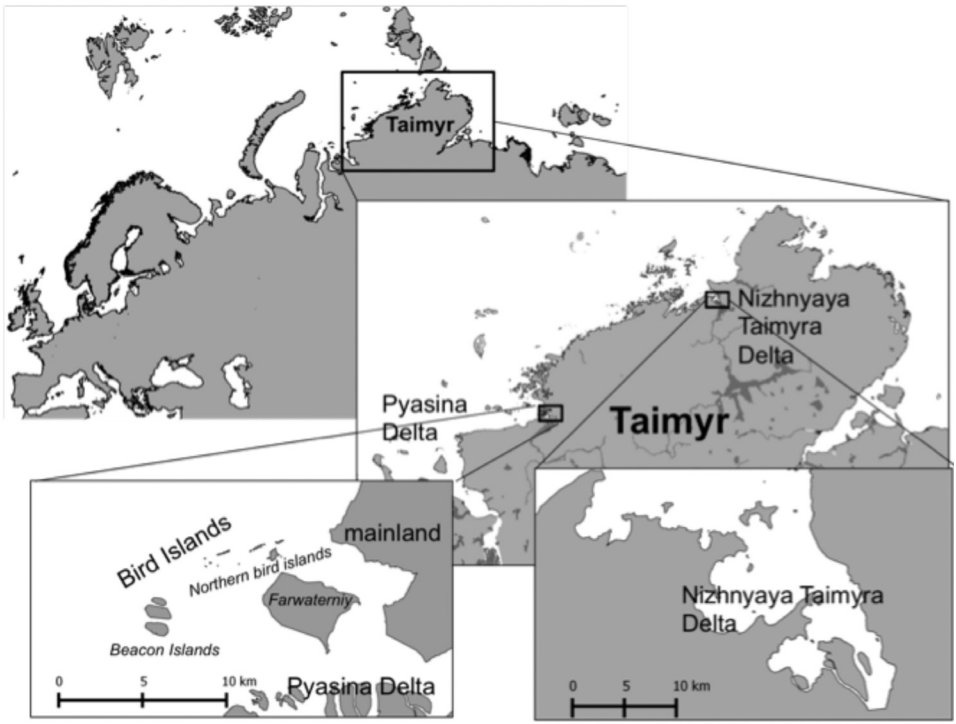

Figure 1. Location of the delta of the Lower Taimyr (Nizhnyaya Taimyra) River and the Pyasina Delta on the Taimyr Peninsula in northern Siberia, Russia.

moult. Vegetation on the plains is dominated by grasses and sedges and, although a freshwater wetland, the landscape is reminiscent of the short-grazed saltmarshes and adjacent mudflats of the Wadden Sea in spring. In addition to being an important moulting area, the delta of the Lower Taimyr River was also used by Brent Geese for nesting in 1990.

Bird Islands in the northern part of the Pyasina Delta comprise two archipelagos, one consists of 16 small islands ("northern Bird Islands") with rocky outcrops covering a total area of 24 ha, of which the Big Bird Island (16 ha) is the largest. On average, 150 pairs of Dark-bellied Brent Geese and 1,000–1,200 pairs of Taimyr Gulls nest here (Spaans *et al.* 1993). Up to 200 Brent Geese moult on the northern Bird Islands. A second group of very flat sandy islands (total area *c.* 175 ha), the "Beacon Islands", is situated further offshore on the outer western fringe of the Pyasina River delta to the north of the mouth of the Pyasina River (Fig. 3). These are a preferred moulting site for 1,100–7,000 Dark-bellied Brent Geese, all non- or failed breeders (Ebbinge & Mazurov 2006). An area of very shallow waters, 10–20 cm deep, extends to *c.* 1 km around the islands. Beyond these shallow waters, deeper channels prevent Arctic Foxes from reaching the Beacon Islands. In

Figure 2. Aerial view of the Dark-bellied Brent Goose moulting area on the Lower Taimyr River delta. (Photograph by Peter Prokosch.)

this paper the two groups of islands are treated as a single site, referred to as "Bird Islands". Dark-bellied Brent Geese nest or attempt to nest on these islands in most years; only occasionally (*e.g.* in 1992) do they fail to build nests and forego breeding in this area (Spaans *et al.* 1998).

Methods

Moulting flocks of Dark-bellied Brent Geese were located and caught between 16 July and 11 August, in the delta of the Lower Taimyr River from 1989–1990 inclusive (Prokosch 1995) and in the northern part of the Pyasina Delta, including its smaller tributaries the Lidia River and Spakoina River (Fig. 3) in 1991, 1993–1995, 2005–2006 and 2008 (Ebbinge & Mazurov 2005, 2006, 2007 and unpubl. reports). In the Lower Taimyr River delta the geese were also counted by aerial (helicopter) surveys in 1989 and 1990 (Fig. 2).

During the seven summers in which moulting Dark-bellied Brent Geese were observed in the northern part of the Pyasina Delta (Fig. 3), their distribution was determined by checking and mapping all potential moulting sites by boat, covering both the Bird Islands and also the shores of Lidia Bay and Pyasina Bay. All adult birds and goslings encountered during the boat surveys were counted, and a 2 × 2 chi-squared test was used to determine whether the age structure (*i.e.* the ratio of adults to

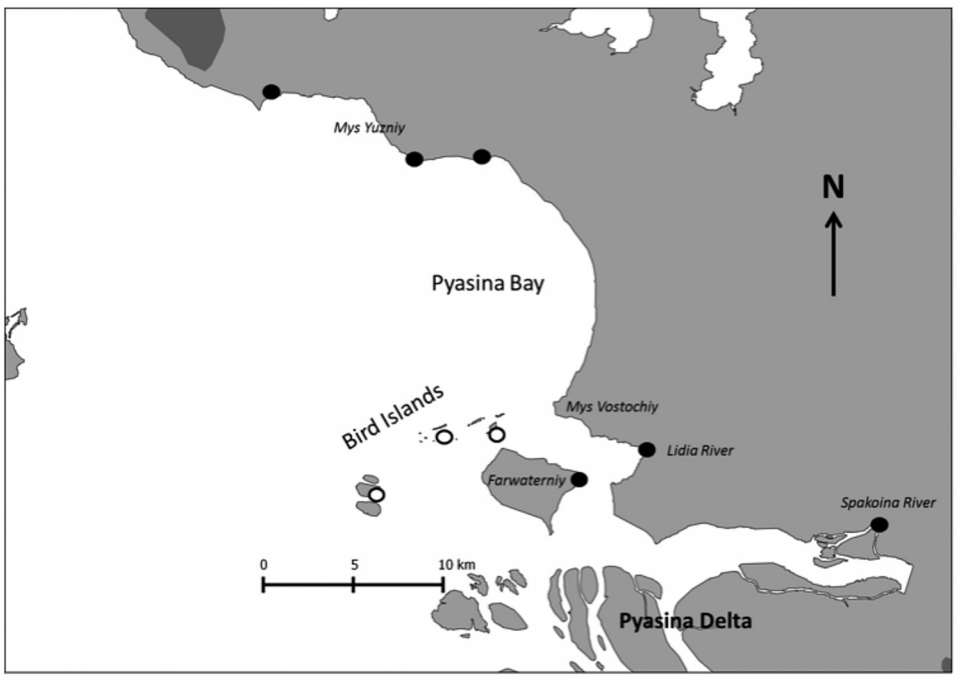

Figure 3. Map of the Pyasina Delta located in western Taimyr, Russia. Black (filled) circles indicate where Dark-bellied Brent Goose families moult along the mainland coast in successful breeding years; open circles indicate where many non-breeders and some family groups moult in all years.

young) differed between the mainland shore and the islands. In the later years of the study – in 2005, 2006 and 2008 – other areas in the central part of the Pyasina Delta were also checked for moulting Dark-bellied Brent Geese.

Once the moult sites had been located, flightless birds were caught by corralling them into nets (as described by Owen 1980), shepherded by a helicopter in the delta of the Lower Taimyr River in 1989 and 1990 (Prokosch 1995), and by small boats and on foot in other years in the Pyasina Delta. The geese were then marked either with coloured leg-rings (marking programme: Alterra, the Netherlands) or with metal rings provided by the Ringing Centre in Helgoland (Germany) in 1989 and 1990 or by the Bird Ringing Centre in Moscow, Russia in all other years. In catches of > 1,000 birds, part of the catch was counted and the birds immediately released without being ringed or measured, though for all re-trapped birds their ringing details were noted. Eighteen Dark-bellied Brent Geese out of *c.* 8,000 marked at wintering sites in Europe were recaptured during the summer, but only birds previously marked as moulting birds on the Taimyr Peninsula were considered in this study.

Following the initial catching and marking of moulting Dark-bellied Brent Geese in

1989–1994, the degree of moult site fidelity was determined from the recapture of ringed birds during three large catches on the Bird Islands in the Pyasina Delta in 1995, 2006 and 2008.

The total number of marked birds present on the Bird Islands was estimated by extrapolation from the total number actually caught to the total number moulting at that site, by multiplying the number of re-trapped birds by *N*t/*N*c, in which *N*t = the total number of moulting birds, and *N*c = the total number caught. In this case, both colour-ringed birds and those marked only with metal rings were combined, because on being caught they have the same probability of 1, of being detected. *N*t was estimated visually by telescope and also verified using the formula *N*t = (*N*mo * *N*c)/*N*mc, in which *N*mo = number of marked individuals observed before the catch in the entire moulting flock, *N*c = total number caught and *N*mc = number of earlier observed marked birds that were re-trapped. Only colour-ringed birds were used on estimating total flock size (*N*t) from this formula, however, as metal-ringed birds are almost impossible to identify by telescope.

It was assumed that previously marked birds were evenly distributed among the caught and non-caught birds, albeit that such extrapolation was not needed for the much smaller number of birds moulting on the northern Bird Islands, because all birds present were caught. Numbers recaptured on the northern Bird islands were added to those estimated to be on the Beacon Islands.

The number of previously marked birds still alive was estimated by using an annual survival rate of 85%, calculated both from both ring re-sightings (Ebbinge 1991, 1992) and from annual survival estimates derived from annual population censuses and age ratio estimates recorded on the Dark-bellied Brent Goose wintering grounds in western Europe (Ebbinge *et al.* 2002). These estimates were used to describe the total number of marked birds present at the moulting sites as a percentage of the total number of previously marked birds still alive when the catch was made.

Results

A total of 5,703 different individuals (including 182 goslings) were caught and ringed during 25 separate catches made of moulting flocks on the Taimyr Peninsula between 1989 and 2008, of which 18 birds had previously been marked at wintering sites in western Europe. A further 2,000 geese (including 10 goslings) caught on the Taimyr were released unringed (Table 1). In 1995 all Dark-bellied Brent Geese moulting on the islands in the Pyasina Delta region (*c.* 7,000 birds) were initially driven into the nets but two-thirds of the birds escaped prior to processing. This still left a total of 2,785 birds caught, of which 1,200 were released without ringing because of the large numbers involved.

Recoveries of Dark-bellied Brent Geese ringed as moulting birds on the Taimyr Peninsula

Recoveries (*n* = 267) of 4,721 birds caught and fitted with metal rings that were found dead, reported as shot, re-trapped or (for a few individuals) re-sighted illustrate the migration route for Dark-bellied Brent Geese ringed on the Taimyr Peninsula (Fig. 4).

Table 1. Total number of moulting Dark-bellied Brent Geese caught on the Taimyr Peninsula, Russia from 1989–2008 inclusive. [1] = 1,200 released without ringing; [2] = 24 released without ringing; [3] = 553 released without ringing; [4] total ringed = total caught minus re-trapped birds that were released unringed.

Date	Adult	Young	% young	Total	Taimyr-ringed-re-traps	Europe-ringed re-traps	Catching area
1989	909	0	0.0	909		2	Lower Taimyr River
1990	632	0	0.0	632		1	Lower Taimyr River
1991	197	36	15.5	233			Pyasina Delta
1993	179	8	4.3	187	1	1	Pyasina Delta
1994	104	14	11.9	118	44		Pyasina Delta
1995	2,774[1]	11	0.4	2,785	39	6	Pyasina Delta
2005	292	116	28.4	408	1		Pyasina Delta
2006	1,060[2]	7	0.7	1,067	54	5	Pyasina Delta
2008	1,364[3]	0	0.0	1,364	57	3	Pyasina Delta
Total caught	**7,511**	**192**	**2.5**	**7,703**			
Total ringed	**5,521[4]**	**182**		**5,703**	**196**	**18**	

Re-sightings of the 1,442 birds that were (only) marked with colour-rings are not shown, as this would cause a serious bias towards western Europe where many observers are active. The recoveries of metal-ringed birds show that the population generally follows the coastline of arctic Russia to the White Sea, and then crosses Karelia to the Baltic Coast, though a small number of three individuals were recovered further inland. Once in the wintering range the geese are clearly distributed at sites along the coasts of western Europe, particularly in Denmark, Germany, the Netherlands, southern and southeast England, and northern and western France (Fig. 4).

Moulting flocks in the delta of the Lower Taimyr River

Large concentrations of *c.* 45,000 moulting Dark-bellied Brent Geese were found in the delta of the Lower Taimyr River in 1989, along both the east bank (76.10° N, 100.00° E) and the west bank (76.10° N, 99.50° E)

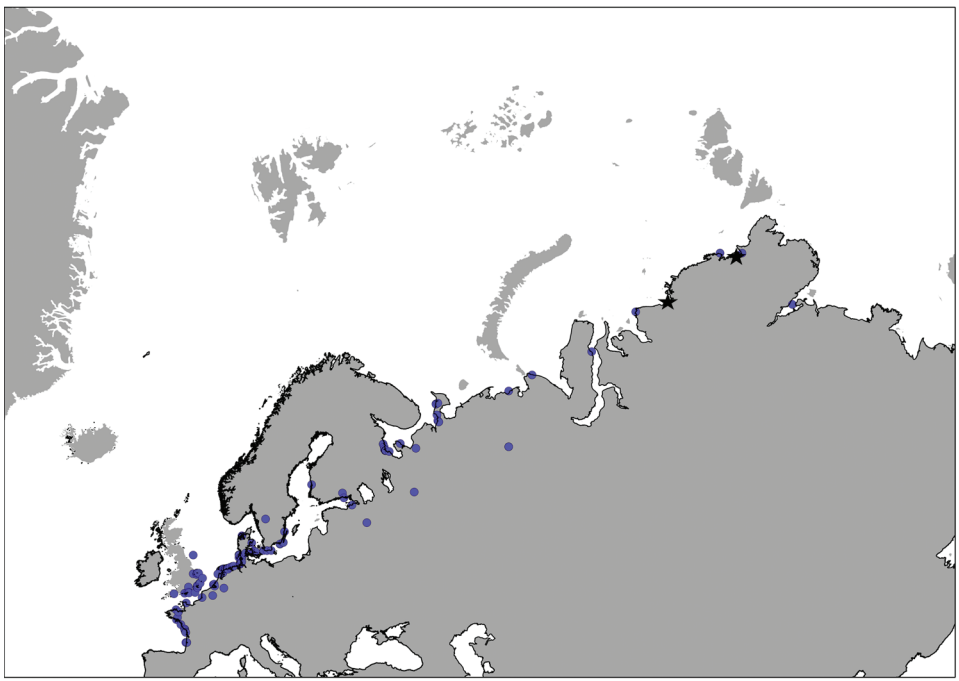

Figure 4. Recovery sites for Dark-bellied Brent Geese marked with metal rings as moulting birds on the Taimyr Peninsula. Stars indicate the two ringing sites.

of the estuary, but a much smaller number of *c.* 4,000 geese were counted there in 1990 (Prokosch 1995). No surveys were made in this area in other years, but a total of 1,541 geese were caught for ringing in 1989–1990. All were adult birds, including three re-trapped birds originally ringed on the wintering grounds in western Europe (Table 1).

Moulting flocks in the Pyasina Delta

Dark-bellied Brent Geese both nest and moult on the Bird Islands in the outer fringe of the Pyasina Delta. If breeding is successful, some pairs that nested on the northern Bird Islands may remain there to moult, but most disperse with their goslings to moulting areas along the mainland coast (Ebbinge & Spaans 2002; Ebbinge & Mazurov 2005, 2006, 2007). On the Beacon Islands (i.e. the southern three Bird Islands), however, a much larger number of mainly non- or failed breeders moult every year (Table 2). Moulting along the mainland coast (*i.e.* at sites from Mys Yuzny, to the Lidia River estuary, and the large Farwaterny Island and the Spakoina River; Fig. 3) generally occurs only in fairly good breeding seasons, such as in 1991, 1993, 1994 and 2005 (Fig. 5, Table 3; Spearman Rank correlation: $r_s = 0.991$, $n = 7$, $P < 0.0001$). The proportion of goslings was significantly higher at the mainland sites than on the northern Bird Islands in 1993 and 2005, but

Table 2. Number of Dark-bellied Brent Geese recorded moulting at sites in the northern part of the Pyasina Delta, and the overall breeding success of the population each year. Counts were recorded during surveys made along the coasts of the Lidia Bay, the Northern Bird and Beacon Islands, and the coast of the Pyasina Bay to the north of the Bird Islands (Fig. 3). Breeding success was measured as the percentage of first-winter birds recorded in flocks at sites across western Europe the following winter (Ebbinge *et al.* 2013).

Year	Mainland shore	Northern Bird Islands	Beacon Islands	Breeding success
1991	488	51	≥ 1,000	30.9%
1993	134	53	1,125	25.5%
1994	48	70	no data	6.4%
1995	0	270	7,000	0.5%
2005	214	194	≥ 2,000	29.2%
2006	33	301	6,900	2.3%
2008	0	54	5,700	1.3%

not in 1991 and 1994 when the proportions did not differ significantly (Table 3). In 1991, however, the total number of goslings on the mainland was much higher than on the islands, and 1994 was a relatively poor breeding season with few goslings in either area. Overall, as successful families move away from the breeding islands in good breeding years, the flocks moulting on the Bird Islands usually hold fewer goslings. Nesting within the gull colony on the islands may be a safe option for the adult geese themselves, but raising goslings there is not (Ebbinge & Spaans 2002).

In years with almost complete breeding failure (*e.g.* 1995, 2006 and 2008) most Dark-bellied Brent Geese stayed away from mainland sites and used the Bird Islands to moult (Table 2). Gulls are not a threat for adult geese without goslings, although non-nesting Snowy Owls (which, because of the many defending gulls, have much more limited feeding options on the gull-inhabited islands than on the mainland) may pose some risk to the birds.

A total of 4,162 geese were caught for ringing in the Pyasina Delta in the years 1991–2008. A further 15 geese originally ringed on the wintering grounds were recaptured at Pyasina moulting sites (Table 1).

Site tenacity to moulting sites

Of the 5,703 different individuals (including 182 goslings) caught and ringed at the moulting sites between 1989 and 2008, 196 (3.4%) recaptured geese had been marked as moulting or nesting birds earlier in the study, and 18 (0.3%) had been ringed at wintering sites in Europe. Of the 196 recaptured individuals, 133 had originally been ringed as

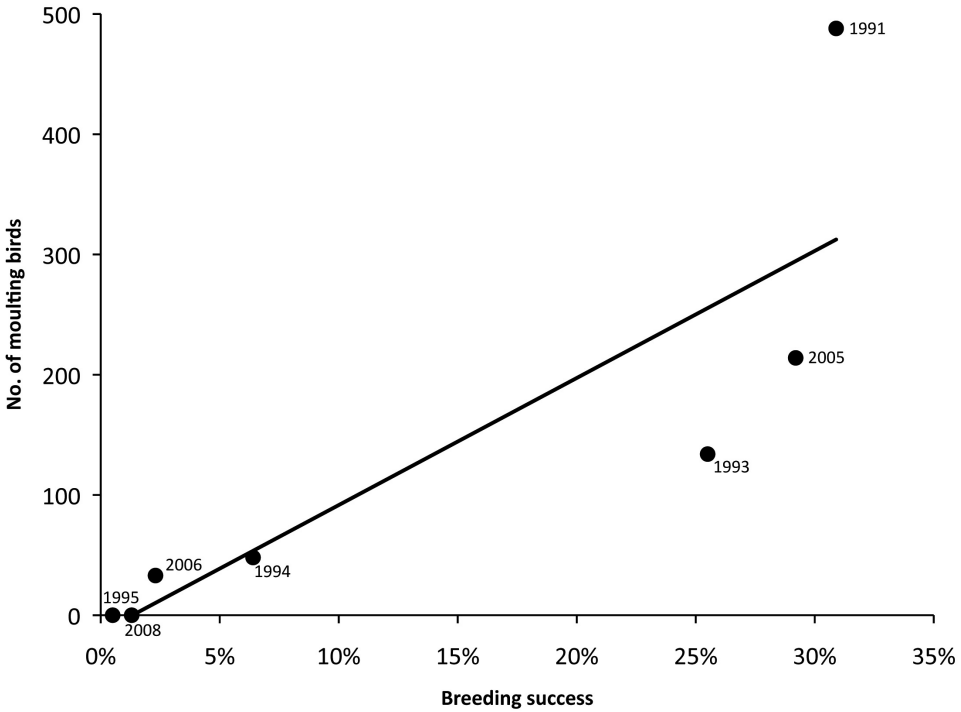

Figure 5. Number of Dark-bellied Brent Geese moulting at sites along the mainland shore on the northern part of the Pyasina Delta, in relation to the overall breeding success of the population in that year. Breeding success of the population is measured as the proportion of first-winter birds recorded in western Europe the following winter. The same moulting sites were visited in all years, as indicated on the map in Fig. 3. Years are given next to each data point.

moulting birds and were re-trapped during the large catches in 1995, 2006 and 2008 (*i.e.* included in Appendix 1); all other re-traps were birds ringed in earlier years on the nest, or re-trapped in other years.

Site fidelity was estimated for birds originally ringed in the Pyasina Delta from 1991 onwards that were recaptured in the non-breeding summers of 1995, 2006 and 2008, when large numbers of geese were observed and caught at the site. The 1,585 geese caught and ringed in 1995 (including 229 birds moulting on northern Bird Islands), and a further 1,200 checked but released unringed, included 13 re-trapped birds on Beacon Islands and 16 re-traps on the northern Bird Islands. Adjustment of the Beacon Islands total in relation to the number of birds counted but not caught at the site gave an estimated 39 ringed geese caught and ringed there in previous years, and the total number of re-traps for the Pyasina Delta (*i.e.* also including those on the northern Bird Islands) was put at 55 birds (Appendix 1a).

Prior to the goose catching in 2006,

Table 3. Percentage of goslings recorded in flocks moulting on the northern Bird Islands, compared to those in flocks along the mainland shore of Pyasina Bay in those years when goslings were present. *P* values are for chi-squared tests, comparing the proportion of young recorded in the two moulting areas each year; n.s. = not statistically significant.

Year	Mainland		Northern Bird Islands		*P* value
	% goslings	(*n*)	% goslings	(*n*)	
1991	18%	(488)	24%	(51)	0.35 (n.s.)
1993	7%	(118)	0%	(69)	0.027
1994	19%	(48)	7%	(70)	0.081 (n.s.)
2005	45%	(214)	10%	(194)	0.0001

21 colour-ringed individuals were identified on Beacon Islands out of an estimated total of 7,000 birds by reading their rings through a telescope. Amongst the 753 Dark-bellied Brent Geese caught were two of the 21 birds identified earlier. This provided an

Figure 6. Moulting non-breeding Dark-bellied Brent Geese on the Beacon Islands, Pyasina Delta, Russia. (Photograph by Harry Horn, taken from a hide.)

independent estimate of (21*753)/2 = *c.* 7,900 for the total number of Dark-bellied Brent Geese moulting on the Beacon Islands. On the northern Bird Islands 281 birds were caught including 46 re-trapped birds, and the total number of re-trapped birds present in the Pyasina Delta area was estimated at 86 geese for 2006 (Appendix 1b).

In 2008, a total of 39 colour-ringed birds were identified during the surveys made before the goose catches, of which nine were subsequently re-trapped during a catch of 1,310 geese at Beacon Islands on 31 July 2008 (Fig. 7). The total number moulting on the Beacon Islands therefore was estimated at 5,676 (= (39/9)* 1,310) geese. In addition to these nine, 42 other ringed individuals were re-trapped on Beacon Islands (total = 51), with a further five re-trapped in a catch of 54 birds on the northern Bird Islands. The estimated number of previously ringed birds moulting at Beacon Islands was 221 birds (*i.e.* 51 * 5,676/1,310), and the total number returning to the Pyasina Delta area in 2006 therefore was put at 226 geese (Appendix 1c).

Given an annual survival rate of 85% (Ebbinge *et al.* 2002) it was estimated that the numbers of birds originally ringed in the Pyasina Delta from 1991 onwards that were still alive in 1995, 2006 and 2008 were 319,

Figure 7. The 2008 catch of moulting Dark-bellied Brent Geese on Beacon Islands in the Pyasina Delta. (Photograph by G. Müskens.)

658 and 1,187 respectively. The number of ringed birds returning to the same Pyasina Delta moulting area therefore was 17% (based on 55 geese returning) in 1995, 13% (86 geese returning) in 2006 and 19% (1,187 geese returning) in 2008 (Appendix 1a,b,c).

Discussion

The study of Dark-bellied Brent Geese on the Pyasina Delta has shown substantial variation in their moulting distribution between good breeding seasons and years with poor breeding success. Most family flocks with goslings swim to the mainland shore shortly after hatching to raise their broods. In years with poor breeding, however, very few Brent Geese are found along these shores, with the majority moulting on the islands within the gull colonies. Gulls are not a threat to adult Brent Geese, and their guano fertilises the vegetation which provides a good food for the geese during moulting.

On Beacon Islands, in the outer reaches of the Pyasina Delta, some 1,000–7,000 moulting non- or failed breeders can be found each year, although the total number of Brent Geese moulting in the Pyasina Delta is lower in non-breeding years. This may be caused by even better feeding conditions further north during the moulting period, though data on food quality are lacking. This fits with counts made of large numbers (*c.* 45,000) of Dark-bellied Brent Geese seen moulting in the delta of the Lower Taimyr River in 1989, also a year of complete breeding failure, contrasting with only 4,000 moulters in the same area in 1990 when many Dark-bellied Brent Geese bred successfully (Prokosch 1995). Thus, even in a high-arctic nesting species as the Dark-bellied Brent Goose, moult migration to sites still further north (in this case the delta of the Lower Taimyr River) does occur in some years. Moult migration to more northerly areas is also known for Pacific Black Brant *Branta b. nigricans* on Wrangel Island, (Salomonsen 1968), where small numbers nest in peak lemming years, but much larger numbers arrive to moult (Ward *et al.* 1993). Similarly, Pacific Black Brant stay to moult in lower numbers in the main nesting area for this subspecies (in the Yukon-Kuskokwim Delta, southern Alaska) in poor breeding years, when they migrate further north to moult (Sedinger pers. comm.) and the reverse pattern has been reported for the geese at Teshekpuk Lake in northern Alaska in these years, when more moulting birds are recorded following an influx of failed breeders from further south, mainly from the Yukon-Kuskokwim Delta (Bollinger & Derksen 1996). That Brent Geese do not always moult at the same site is also supported by the recaptures in the Pyasina Delta in 1995 of two birds that were known to have moulted elsewhere (in the Lower Taimyr River Delta) in 1989 and 1990. These birds represent 0.2–0.4% of 683 birds from those catches thought to be still alive in 1995. None of the birds ringed on the Lower Taimyr River were caught in the later catches in the Pyasina Delta, in 2006 and 2008, but this is not surprising because few birds from the 1989–1990 catches would have been still alive > 17 years later when (having been ringed as adults) they would be at least 19 years old.

Other studies have similarly found that

geese may change their moulting sites. For instance, Cotter & Hines (2006) found that a significant proportion (5%) of moulting Brant caught on Bank's Island in arctic Canada (73.02° N, 124.35° W) in 1992–1994 had previously been marked as moulting birds elsewhere, in areas ranging from the Yukon-Kuskokwim Delta and North Slope in Alaska to Wrangel Island in east Siberia and the Anderson River in the west Canadian arctic. In 1993 and 1994, they also recaptured 10% (248 individuals from 2,423 local moulters marked in 1992 and 1993) on catching 60–70% of all Brant moulting at the site. Correcting for marked birds not included in the catch provides a crude estimate of at least 15% (*i.e.* 10%/0.65) of ringed Brant returning to the same moulting site in these years. This estimate would be even a little higher if annual survival is taken into account. Our own study found that in three years when breeding was poor (1995, 2006 and 2008) the proportion of non- or failed breeders still alive which returned to the same site to moult was no more than *c.* one-fifth (17% in 1995, 13% in 2006 and 19% in 2008), a figure comparable to the site fidelity estimates made for the geese moulting at Banks Island. At Teshekpuk Lake in North Alaska the recapture rate, corrected for survival was also fairly similar: 15.6% for locally-ringed Pacific Brant. At Teshekpuk Lake up to 5.6% of Brant ringed in breeding colonies elsewhere were also caught, demonstrating the exchange between different moulting sites. Birds that did return to the Teshekpuk Lake area showed a very high rate of 94.5% local site fidelity to smaller sub-sites within the larger area (Bollinger & Derksen 1996). This phenomenon of very local site fidelity, with birds returning to a moulting site being faithful to particular areas within the site, was also found by Cotter & Hines (2006), as their recaptured birds were all re-trapped ≤ 5 km of the place where they were caught in previous years.

If random mixing of marked birds would occur across the entire population during the moulting period, the number expected to moult at the Bird Islands in the absence of site fidelity can be estimated (Table 4). The higher number present, in comparison with the numbers expected with random mixing, indicates that some site-fidelity does occur, but nevertheless *c.* 80% of the birds are more nomadic in their choice of moult site. Thus although random mixing does not occur, a large proportion of the Dark-bellied Brent Geese selects different places to moult from year to year.

Comparably low site fidelity has also been found for nesting Brent Geese: only 28% of marked females returned to the same breeding islands in the Pyasina Delta (Ebbinge 2004). This nomadic behaviour in the selection of breeding and moulting areas contrasts sharply with high levels of site fidelity to spring staging areas in western Europe, where Spaans & Postma (2001) found that 94% of the surviving geese returned to the same feeding area in spring each year.

A larger part of the central Pyasina Delta was surveyed by boat in 2005, 2006 and 2008, but only in the good 2005 breeding season were many dispersed moulting flocks of Dark-bellied Brent Geese found there, including 63 families (mean brood size = 4.1 goslings; Ebbinge & Mazurov 2006). In the

Table 4. Population size of Dark-bellied Brent Geese (to the nearest 100 birds; Ebbinge *et al.* 2013), and the number of marked birds expected to be recorded on the Bird Islands (density of marked birds * number of moulting birds) under random mixing, compared to the number actually present (Appendix 1a,b,c). The density of marked birds is calculated as the proportion of live birds in relation to the total population size.

Year	Population size	Marked Pyasina-birds alive	No. Pyasina moulters	Density marked birds	Expected	Actually Present
1995	251,500	319	7,000	0.1%	9	55
2006	280,500	658	6,900	0.2%	16	86
2008	246,600	1,187	5,700	0.5%	27	226

same year in the central part of the delta, where numbers of gulls are low, 258 adult Dark-bellied Brent Geese and 202 goslings (44% of birds counted) were observed on Vjerchny Island, in the centre of the Pyasina Delta. The next year, in 2006 when predation levels were high, despite at least 200 pairs of Dark-bellied Brent Goose pairs having nested on this same island, all the geese had disappeared in late July, which then held three non-breeding Snowy Owls and one immature White-tailed Eagle *Haliaeetus albicilla* , which were absent on that island in 2005 (Ebbinge & Mazurov 2007).

The choice of a moulting site therefore is a trade-off between successfully raising goslings against the parent birds selecting the best place for themselves to moult. The mainland shore has many small patches of food for raising goslings in good breeding years, and remaining on the Bird Islands is hazardous for goslings because of the risk of predation by gulls. That relatively few adults go to the mainland in non-breeding years could reflect predation risk for adults, which is probably higher on the mainland in years when lemming numbers are low (which coincides with non-breeding years) because when lemmings are abundant Pomarine Skuas *Stercorarius pomarinus* also nest, and their frequent attacks on other predators such as Snowy Owls and Arctic Foxes make it more difficult for the owls and foxes to predate adult geese (Ebbinge 2009). That so many non- or failed breeders move further north could also be another example of birds following the green wave of emerging vegetation (Van der Graaf *et al.* 2006), because plant growth in the far north will undoubtedly be later in the Lower Taimyr River Delta than in the Pyasina Delta, resulting in better food quality with a higher protein content during the moult period.

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Appendix 1. Number of Dark-bellied Brent Geese caught on the Taimyr Peninsula, Russia, that were subsequently recaptured on Bird Islands in the Pyasina Delta during the non-breeding years of (a) 1995 (total number caught and ringed = 1,585 geese, with a further 1,200 checked but released unringed), (b) 2006 (total number caught = 1,067) and (c) 2008 (total number caught = 1,364). NT89 and NT90 = birds originally ringed at Nizhnyaya Taimyra (Lower Taimyr River) in 1989 and 1990 respectively; P91, P93, P94, P95, P05 and P06 = birds marked in the Pyasina Delta. Estimates of number of birds ringed on the Taimyr still alive in 1995, 2006 and 2008 were based on annual survival rates of 85% (from Ebbinge *et al.* 2002; see text); [1] = originally caught in the Pyasina Delta (*i.e.* from 1991 onwards), so omits NT89 and NT90 birds.

Year	Where ringed	No. ringed	Years passed	Estimated no. still alive in recap. Year	Beacon Islands	Adjusted Beacon Islands	Northern Bird Islands	Total Bird Islands	% of birds estimated to be still alive re-trapped in the Pyasina Delta
1995	NT89	907	6	342	1	3		3	1%
	NT90	631	5	280	1	3		3	1%
	P91	233	4	122	5	15	6	21	17%
	P93	185	2	134	4	12	5	17	13%
	P94	74	1	63	4	12	5	17	27%
	Total Pyasina[1] in 1995			319	13	39	16	55	17%

Appendix 1 (continued).

Year	Where ringed	No. ringed	Years passed	Estimated no. still alive in recap. Year	Beacon Islands	Adjusted Beacon Islands	Northern Bird Islands	Total Bird Islands	% of birds estimated to be still alive re-trapped in the Pyasina Delta
2006	NT89	907	17	57				0	0%
	NT90	631	16	47				0	0%
	P91	233	15	20	0	–	1	1	5%
	P93	185	13	22	0	–		0	0%
	P94	74	12	11	0	–		0	0%
	P95	1,540	11	258	3	32	3	35	13%
	P05	408	1	347	1	11	40	51	15%
	Total Pyasina[1] in 2006			658	4	42	44	86	13%
2008	NT89	907	19	41				0	0%
	NT90	631	18	34				0	0%
	P91	233	17	15	1	4		4	29%
	P93	185	15	16	0	–		0	0%
	P94	74	14	8	0	–		0	0%
	P95	1,540	13	186	4	17		17	9%
	P05	408	3	251	5	22	4	26	10%
	P06	984	2	711	41	178	1	179	25%
	Total Pyasina[1] in 2008			1,187	51	221	5	226	19%