

# Population development and breeding success of Dark-bellied Brent Geese *Branta b. bernicla* from 1991–2011

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## Abstract

The Dark-bellied Brent Goose *Branta bernicla bernicla* is the largest of the six Brent Goose populations, which collectively number around 600,000 birds globally. After a major decline to 16,500 geese in 1958, numbers recovered during the 1970s and 1980s to a peak of *c.* 330,000 individuals between 1992 and 1994. From 1994 onwards the population declined again to 200,000–250,000. This decline has been attributed to poor breeding, associated with faltering cycles of Siberian Brown Lemming *Lemmus sibiricus* (predominantly) and Palearctic Collared Lemming *Dicrostonyx torquatus* abundance on the breeding grounds on the Taimyr Peninsula, where lemmings are a main food resource for potential predators of goslings. Dark-bellied Brent Geese only breed well in peak lemming years (Summers & Underhill 1991), and this usually occurs every three years, but the frequent failure since 1994 of lemming numbers to peak (except in 2005) has resulted in the absence of very good breeding years for the geese (Nolet *et al.* 2013). The mid-winter distribution has shown a marked shift towards France over the last decade. France currently supports 50% of the population in January, Great Britain 35–40%, the Netherlands 15–20%,

and Germany and Denmark 2%. In spring, almost the entire population gathers in the Wadden Sea, leaving only 4% of the population in Great Britain, and virtually none in France, with the Dutch part of the Wadden Sea supporting 40–45%, the German section 45–50% and Denmark 6%.

**Key words:** breeding success, Dark-bellied Brent Goose, population development.

Salomonsen (1958) first attempted to estimate the size of the Dark-bellied Goose *Branta bernicla bernicla* and Light-bellied Brent Goose *Branta bernicla brota* populations in Europe, following a dramatic decline of both sub-species during the 1930s. Salomonsen's review revealed that no more than 16,500 Dark-bellied Brent were left of this once common coastal goose in 1958, estimated at < 8% of the population that wintered in Europe in the early decades of the 20th century. He concluded "we cannot ever expect to see such large flocks again in Europe, but we can endeavour to check the decline and let the population grow to a reasonable height".

However, the "unexpected" (Salomonsen 1958) recovery of this subspecies in the 1970s (Ogilvie & St. Joseph 1976; Prokosch 1984; Ebbing 1985, 1991; Ebbing *et al.* 1999; Ward 2004) resulted in well over 300,000 Dark-bellied Brent Geese being recorded during the mid-winter census in January 1992. In this paper we describe and assess subsequent population trends over the period 1991–2011.

## Methods

Each January, Dark-bellied Brent Geese are counted by experienced volunteer bird counters at all important coastal sites in western Europe, within the framework of the International Waterbird Censuses

(IWCs) coordinated by Wetlands International. Each country has a national coordinator who communicates with members of the national count network and collates the count data. The area covered includes the Atlantic coast of France, the south and east coast of Great Britain, the southwest Delta area in the Netherlands and the Wadden Sea from the northern part of the Netherlands, through Lower Saxony (Germany), Schleswig-Holstein (Germany) to Denmark. As Brent Geese also forage inland on grassland and winter wheat near the sea shore, such areas are also included in the survey.

In addition to this mid-winter census, a spring census in late April or early May is carried out in most years covering the same area, except for France, which holds hardly any Dark-bellied Brent Geese (20–50 sick or injured birds) at this time (R. Maheo & S. Le Dréan-Quénech'hdu, *in litt.*). In the Wadden Sea, this census forms part of the Trilateral Assessment and Monitoring Programme which is carried out simultaneously in the Netherlands, Germany and Denmark (Laursen *et al.* 2010). Results from the spring censuses presented in this paper are for 1995 onwards, as before 1995 not all sites were necessarily covered in Great Britain.

Both mid-winter and spring counts are made from the ground, except for Denmark where some sites in the Baltic archipelago

and in the Wadden Sea are surveyed by aircraft. To a minor extent the national coordinators have used data imputing techniques to allow for the few sites where actual counts were missing (Soldaat *et al.* 2007). Population estimates were calculated by summing the country totals resulting from these counts, and rounding these to the nearest thousand. Both mid-winter and spring counts are carried out in the same week, and there is very little movement of Brent Geese at the time of these counts. Mass migration from France and Britain to the Wadden Sea takes place in March (Ebbinge *et al.* 1999), so the risk of missing birds or counting the same birds twice is minimal in mid-winter and spring.

Breeding success for the preceding summer is estimated annually by assessing the proportion of first-winter birds in wintering flocks, which can be distinguished from adults by plumage characteristics. These age ratio assessments are carried out from October–February in the Netherlands, Great Britain and France. In spring, moult of the wing coverts makes it more difficult to distinguish first-winter birds from adults. Family groups, as opposed to failed or non-breeding birds, usually arrive somewhat later in Britain and France, because they linger in the Wadden Sea in autumn, whereas many adults without young fly straight to the wintering areas in Britain and France during October (Lambeck 1990). Thus the proportion of first-winter birds tends to increase in Britain and France from October to January, and to decrease over the same period in the northernmost part of the wintering range – *i.e.* at the Wadden Sea in the Netherlands (Lambeck 1990), Germany

and Denmark. This pattern is most obvious in years when the proportion of young birds is high, which has been linked to an abundance of lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus* on the breeding grounds, where lemmings are a main food resource for potential predators of goslings (Summers & Underhill 1991; Ebbinge *et al.* 1999; Nolet *et al.* 2013). Ideally, one should only use age ratio assessments made simultaneously across the wintering range in January each winter, but as it was difficult to coordinate such age counts, in this analysis data from only the three main wintering countries that were gathered between October and January were used. To calculate an overall estimate of the proportion of young for the entire population we have therefore used the figures for France, Britain and the Netherlands and calculated weighted means. The weighted mean was calculated using a ratio of 2:2:1 for France, Britain and the Netherlands, respectively, roughly in proportion to the total number of Dark-bellied Brent present in January in each of these countries (see Nolet *et al.* 2013). To detect a trend pair-wise comparison of Dark-bellied Brent Goose breeding success recorded in each decade from the 1970s to the 2000s was made using logistic regression analysis.

## Results

### Population estimates

Following two decades of spectacular recovery, from the early 1970s through to 1992, the number of Dark-bellied Brent Geese peaked at 329,000 birds in January 1992 (Figs. 1 and 2, Appendix 1).

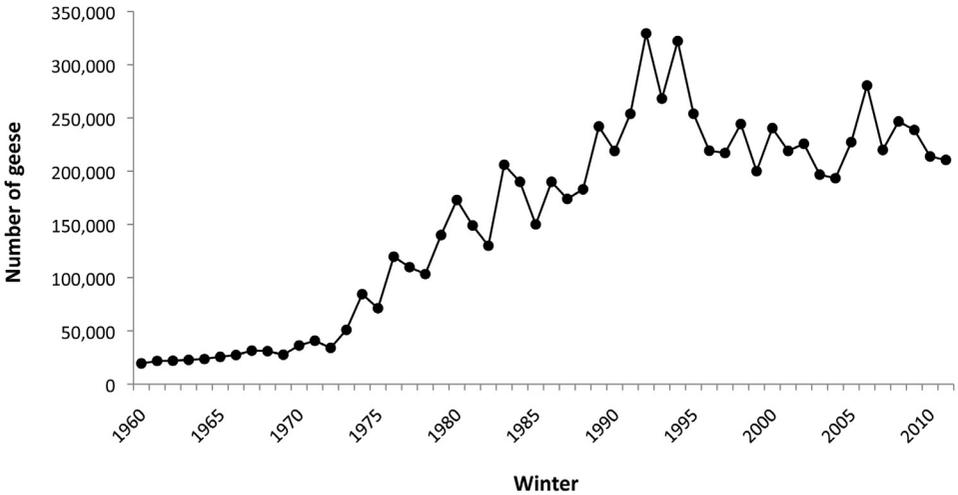


Figure 1. Population counts for Dark-bellied Brent Geese from 1960–2011.

Subsequently the population declined, with numbers fluctuating between 200,000–250,000 birds from 1996 onwards. The only exception was in January 2006 when the population increased again to number 280,000 birds following a very good

breeding season in the peak lemming year of 2005 (Figs. 1 and 2).

**Breeding success**

Breeding success over the last two decades varied from year to year in a less extreme

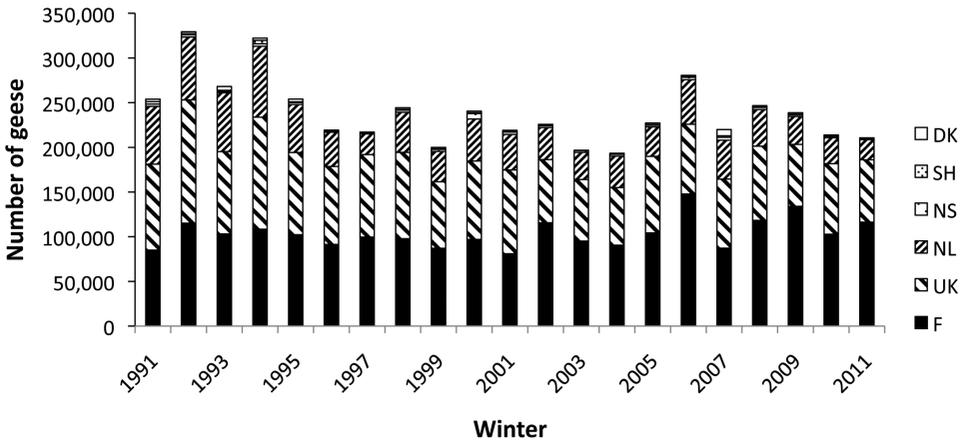
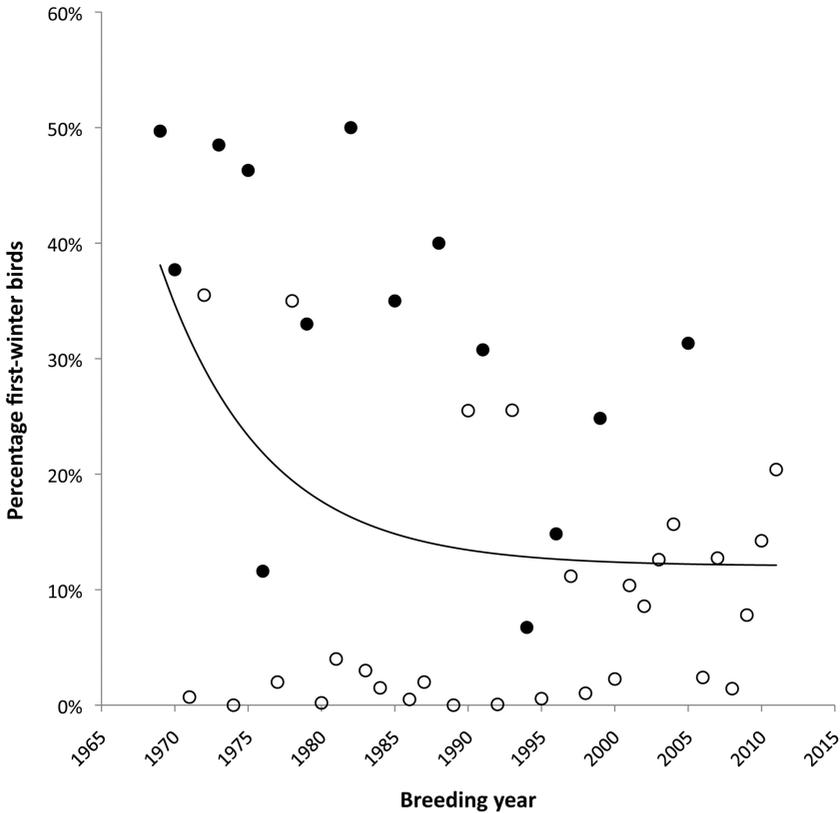


Figure 2. Distribution of Dark-bellied Brent Geese over western Europe in January: France (F), Great Britain (UK), the Netherlands (NL), Niedersachsen, Lower Saxony (NS), Schleswig-Holstein (SH) and Denmark (DK). Count data for each country are provided in Appendix 1.



**Figure 3.** Proportion of first-winter Dark-bellied Brent Geese in January. Annual values and fitted logistic regression curve (Table 1). Lemming peak years (filled circles); years with no or few lemmings (open circles).

way than it had done in the previous two decades (Fig. 3, Appendix 2). Before 1990, between 40–50% of the winter flocks consisted of first-winter birds following successful breeding years, coinciding with lemming peak years on the Taimyr Peninsula (Fig. 3). At that time, a regular three-year pattern was present, with many young every third year when lemming numbers peaked, *e.g.* in winters following the summers of 1982, 1985 and 1988 (Summers & Underhill 1991). The last peak followed the summer of

1991 (peak population count in January 1992), but thereafter the three-year pattern has been less clear. During the last two decades, even in the very best years (1991 and 2005), the population comprised only 30% of first-winter birds. Extremely poor years with almost no young, which occurred in the years after a lemming peak, have also become less frequent since 2000 (Fig. 3).

A series of expeditions to Taimyr by Alterra (a research institute of Wageningen University) from 2002–2008 revealed just

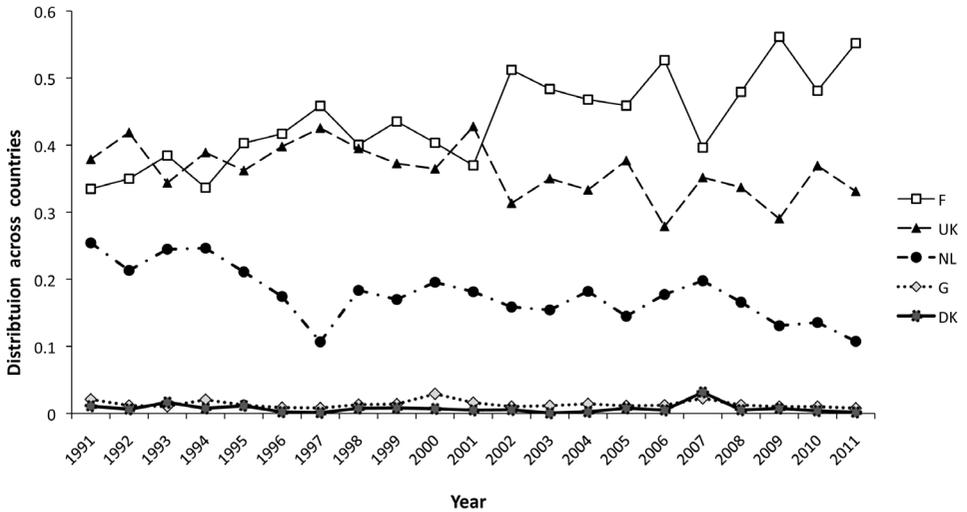
**Table 1.** Pair-wise comparison of Dark-bellied Brent Goose breeding success recorded in each decade from the 1970s to the 2000s. Results show pair-wise  $P$  values from logistic regression analyses, comparing the percentage of juveniles recorded each winter across the decades. Breeding success in the 1970s differed significantly (was higher) than in the 2000s (bold font); all other comparisons were not significant.

Decade	1970s	1980s	1990s	2000s
1970s	*			
1980s	0.091	*		
1990s	0.943	0.943	*	
2000s	<b>0.041</b>	0.753	0.698	*

one real lemming peak year, in 2005, at which time the whole tundra was teeming with life (Nolet *et al.* 2013). Snowy Owls *Nyctea scandiaca* were nesting surrounded by nesting Brent Geese. Waders were nesting in much higher densities. Extremely high densities of Pomarine Skuas *Stercorarius pomarinus* made it difficult for Arctic Foxes *Vulpes lagopus* to roam freely over the tundra. Also Snowy Owls that tried to take goslings just as Brent families were leaving the nesting sites were so heavily attacked by Pomarine Skuas that most goslings safely reached the nursery grounds. To the benefit of waders and geese, all predators more or less restricted one another in capturing non-lemming prey. Even Brent Geese nesting in gull (notably Taimyr Gull *Larus taimyrensis*) colonies were more successful, because lemmings were also available as alternative food for the gulls, which reduced the rate of goose egg predation by gulls.

A weighted average of productivity recorded for the three main wintering countries – France, Great Britain and the

Netherlands – was calculated to represent overall breeding success for the entire population (Appendix 2). Because the difference between countries is much smaller than the difference between years, taking a straightforward average would have yielded virtually the same values. Mean values for breeding success for the four decades (1969–1979, 1980–1989, 1990–1999, and 2000–2011) were 27.3% juveniles in the population for the 1970s, 13.6% for the 1980s, 14.1% for the 1990s and 11.7% for the first decade of the 21st century. Pair-wise comparison by logistic regression shows that only the values for the 1970s and the first decade of the 21st century differed significantly ( $P = 0.041$ ) (Table 1). The boom- and bust-years, characteristic of Dark-bellied Brent Goose breeding success (Fig. 3) makes it hard to demonstrate a significant change in breeding success over time. The difference found between the 1970s and the first decade of the 21st century is mainly attributable to lemming peak years (black dots) becoming rarer in recent years (Nolet *et al.* 2013).



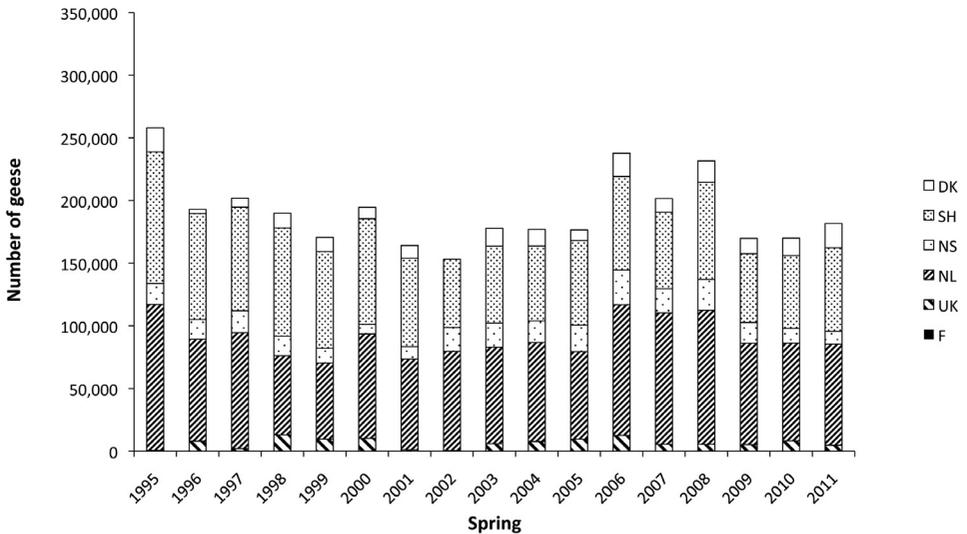
**Figure 4.** Proportional distribution over the five countries of Dark-bellied Brent Geese in January: France (F), Great Britain (UK), the Netherlands (NL), Niedersachsen, Lower Saxony (NS), Schleswig-Holstein (SH) and Denmark (DK).

### Mid-winter distribution

In mid-winter, 80% of the population winters in France and Great Britain, both countries where peak numbers occur in mid-winter, and from which many Dark-bellied Brent Geese depart in March. Some 18% of the population winters in the Netherlands where, particularly in the Wadden Sea, numbers peak in spring. The southwest part of the Netherlands, known as the Delta area, is similar to France and Great Britain in having peak numbers in mid-winter.

Only a small proportion of the population, about 2%, winters in northern Germany (Lower Saxony and Schleswig-Holstein) and in Denmark, mainly in the Wadden Sea region. These two countries support much higher numbers in autumn and particularly in spring.

When the mid-winter distribution over the five countries is expressed as a percentage of the entire population, it is evident that there has been a shift in distribution from Great Britain towards France during the last decade, with France receiving more than half of the Dark-bellied Brent Goose population in recent years (Fig. 5). Of particular note is the decline of 9% in the number of Brent Geese wintering in Great Britain from January 2005 to January 2006 (Table 2); following the very good breeding season in 2005, total numbers might have been expected to increase as they did in France, the Netherlands and Lower Saxony where numbers rose by 40–50%. Only in the northernmost parts of the Brent Goose's wintering area was there also no increase (in Schleswig-Holstein) or a similarly marked decrease (Denmark) in mid-winter



**Figure 5.** Distribution over the five countries of Dark-bellied Brent Geese in spring (late April/early May): France (F), Great Britain (UK), the Netherlands (NL), Niedersachsen, Lower Saxony (NS), Schleswig-Holstein (SH) and Denmark (DK).

in a year with a high proportion of juveniles in the wintering flocks. The first major shift to France (+43%) occurred in January 2002, coinciding with a decline in numbers in both Great Britain (–25%) and the Netherlands (–11%). In that winter there were about 10% young, and given an annual mortality of 15% (Ebbinge *et al.* 2002), no major change in overall population size would have been expected.

### Spring distribution

In late February and particularly in March Dark-bellied Brent Geese shift from their southern winter quarters to stage in the Wadden Sea, where they remain until the end of May (Ebbinge *et al.* 1999; Fig. 5).

The spring counts (Appendix 3) yielded on average 85% of the total number counted in mid-winter. Since annual

mortality is 15% (Ebbinge 1992; Ebbinge *et al.* 2002), and it is very unlikely that all mortality takes place only in the short time span between January and early May, the difference between January and May cannot be explained solely by mortality. A survival analysis for Light-bellied Brent Geese *Branta bernicla brota* staging in spring in Denmark also shows that mortality is very low in that period (Clausen *et al.* 2001). The difference is more likely the result of some birds that are missed during the spring counts. In some years, flocks of Dark-bellied Brent Geese remain at sea in the western part of the Dutch Wadden Sea even during high tide and are then missed (C. Swennen, pers. comm.). Additionally, birds staging in the Baltic (Germany and Denmark) are not always well covered, but in years when the Baltic islands of Denmark were monitored

**Table 2.** Number of Dark-bellied Brent Geese recorded during the January censuses (*i.e.* total population size estimates), before and after the peak lemming year of 2005.

Country	No. geese counted in 2005	No. geese counted in 2006	% change in total numbers	% young birds
France	104,301	147,708	+42%	24%
Great Britain	85,664	78,194	−9%	28%
Netherlands	32,946	49,753	+51%	42%
Lower Saxony, Germany	1,870	2,713	+45%	?
Schleswig-Holstein, Germany	703	720	+2%	?
Denmark	1,774	1,387	−22%	?

more effectively by aerial surveys, usually *c.* 5,000 and never > 10,000 Dark-bellied Brent Geese were counted there during the period when the total population exceeded 300,000 individuals. Moreover there could also be some birds staging then in France, though these numbers are very small.

In late April–early May, 6% of the population were recorded in Denmark, 39% in Schleswig-Holstein, 8% in Niedersachsen, 43% in the Netherlands (mainly in the Wadden Sea, but also in the Delta area), and 4% in Great Britain, with almost all of the Dark-bellied Brent Geese wintering in France having departed by then (Fig. 5).

## Discussion

### Density dependence or climate change

It is tempting to explain the overall decrease in numbers since 1992 as an effect of density-dependence on Brent Goose

survival and breeding success, but Summers and Underhill (1991) failed to detect any significant density-dependent effect in breeding success in their analysis. A more recent analysis by Nolet *et al.* (2013), covering a longer time series, indicates that faltering lemming cycles resulting in a marked reduction in overall breeding success is the most likely explanation for the observed decline. The reason why lemmings have failed to reach the previous high peak levels during the last two decades (except in 2005) is thought to be related to changes in winter climate, which have resulted in short periods of snow-melt or even rain in late spring followed by re-freezing. Such conditions can cause lemming tunnels to collapse or to fill with water under the protective snow cover, which then becomes solid with ice, all highly detrimental to lemming overwinter survival (Kausrud *et al.* 2008; Nolet *et al.* 2013).

Nolet *et al.* (2013) also found a significant,

albeit weak, effect of density-dependence. If lemmings had continued to the cyclical abundance patterns evident in the 1970s and 1980s, the models developed by Nolet *et al.* (2013) indicated that there would have been a further increase in population size to 450,000 geese.

### Shift in mid-winter distribution

A southward shift in the mid-winter distribution of Dark-bellied Brent Geese in the early 21st century, mainly from Great Britain to France, differs from observations made for many other migratory waterbird species which found that the birds tend to winter further north, closer to the breeding grounds, due to the milder weather associated with climate change (*e.g.* Lehtikoinen *et al.* 2013). The changes recorded for the geese could be caused by Brent Geese preferring to feed on eelgrass *Zostera* sp. in autumn and winter, a plant species that is more abundant along the French coast. Even as far south as Morocco, small numbers of up to 30 Dark-bellied Brent Geese have been reported feeding on Dwarf Eelgrass *Zostera noltii* in Kniffiss Lagoon (Radi *et al.* 2009; Imad Cherkaoui, pers. comm.)

Another striking aspect is the effect of cold winters on the proportion staging in the Netherlands. The cold spells in January in 1997, and in 2009–2011 inclusive, are reflected in a reduced proportion of Dark-bellied Brent Geese wintering in the Netherlands, resulting in a higher proportion of birds either in Great Britain or in France. In 1997 an increase was noticeable in both Great Britain and France, whereas in 2009 and 2011 there was an

increase in France, but not in Great Britain, and in 2010 the reverse happened and numbers increased in Great Britain but not in France.

The marked decline between January 2005 and January 2006 in the proportion of the Brent Geese population recorded in Great Britain in mid-winter (Table 2) is of note, as it follows the very good breeding season in 2005. The similar lack of an increase in the more northern parts of the Brent Goose's wintering area (in Schleswig-Holstein and in Denmark) in a year with many young is in line with Lambeck's (1990) conclusion that families winter further south than non- or failed breeders. It is unlikely that large numbers would have been overlooked in Great Britain during the January 2006 census, and later in the same winter, numbers in Great Britain did increase from 78,200 in January to reach a peak of 84,700 in February, but even that peak number was 1% lower than the peak number in January 2005. If the low mid-winter numbers in Great Britain in 2006 was due to birds remaining longer in the Netherlands, then one would also have expected to see lower numbers in France. The overall population increase was reflected in the spring counts for Great Britain, however, which increased by 30% between 2005 and 2006.

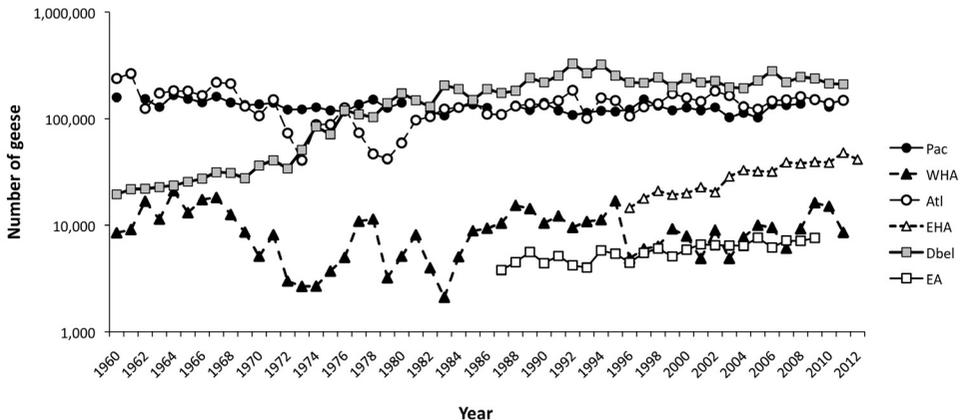
The unexpectedly low number in Great Britain in January 2006 could perhaps be a result of scaring, which may have driven Brent Geese from Great Britain to both the Netherlands and France. In the autumn of 2005, 86 licences to shoot Brent Geese in order to prevent crop damage were issued in Great Britain, and 833 Brent Geese were

reported shot under these licences. In the previous year the number of licences issued was similar (88), but then 527 birds were reported shot (D. Stroud, pers. comm.). Great Britain is the only country issuing such licences in western Europe in order to protect crops of winter wheat from serious damage. It is known that particularly in years with many young, Dark-bellied Brent Geese move much earlier in the season inland from their coastal habitat to feed on farmland (Ebbing *et al.* 1999). Because scaring takes place only on farmland, the impact of scaring activities on the geese may be much greater in a year with many young. A thorough analysis of the effects of British scaring activities is required, however, to

determine whether this hypothesis is correct.

### Comparison with other Brent Goose populations

It is interesting to compare the change in abundance of the Dark-bellied Brent Goose population with those of the other five Brent Goose populations in the world. During the 15th Conference of the Wetlands International/IUCN-Species Survival Commission Goose Specialist Group, held in Arcachon, France, in January 2013 latest information on all Brent Goose populations was compiled (Fig. 6), and it became evident that following its remarkable recovery during the 1970s, the



**Figure 6.** Trends in population size on a log scale from 1960–2012 of all six Brent/Brant populations world-wide, Pac = population of Pacific Black Brant *Branta b. nigricans* including small numbers that winter in East Asia that winters on the West Coast of North America, WHA = population of Western High Arctic Brant, also known as Gray-bellied Brant an admixture population resulting of interbreeding of *Branta b. brota* and *Branta b. nigricans* that winters on the West Coast of North America, Atl = population of Atlantic Brant *Branta b. brota*, that winters on the East Coast of North America, EHA = population of Eastern High Arctic Brant *Branta b. brota*, that winters mainly in Ireland, Dbel = population of Dark-bellied Brent Geese *Branta b. bernicla*, that winters in western Europe, and EA = population of East Atlantic Light-bellied Brent *Branta b. brota*, that breeds on Svalbard and NE-Greenland and winters in Denmark and NE-Britain.

Dark-bellied Brent Goose population is now the most numerous population of all.

Altogether there are currently about 600,000 Brent Geese globally, divided between six different populations. The second and third largest are two of North America's populations, namely the Pacific Black Brant (including the small numbers wintering in East Asia), and the Atlantic Light-bellied Brant (Fig. 6). The two large North American populations are still hunted and have been quite stable in numbers over the last fifty years. Only the Atlantic Light-bellied Brant has shown two major crashes in numbers, but quickly recovered following a temporary hunting ban. The numbers in Fig. 6 are plotted on a log scale, so the rate of increase is directly comparable for each population. The exceptional high rate of increase of the Dark-bellied Brent Goose in the 1970s is matched only by that of the Atlantic Light-bellied Brant, when hunting was banned to allow this population to recover after major crashes due to hard winters and over-hunting. The Dark-bellied Brent Goose has been fully protected over almost its entire range since Schleswig-Holstein finally introduced legislation to protect this sub-species in 1976. Prior to this, the population had been protected from hunting in the Netherlands since 1950, in Great Britain since 1954, in France since 1966, and in Denmark since 1972. Only in Russia is there still some hunting of these birds both in autumn and in spring.

The other three populations are much less numerous. The western High Arctic Light-bellied Brant (also known as Grey-bellied Brant, considered to be the result of interbreeding by *Branta b. nigricans* and *Branta b.*

*brota*) winters along the west coast of North America, where it is hunted to a moderate extent. The remaining two populations, both of the race *Branta b. brota*, are the Eastern High Arctic Light-bellied Brent, which winters in Ireland, and the East Atlantic Light-bellied Brent Goose population which winters in Denmark and Great Britain. Both are protected from hunting. Of these three Grey- and Light-bellied Brent Goose populations, the Eastern High Arctic Light-bellied Brent in particular has increased rapidly in numbers over the last decade.

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### References

- Clausen, P., Frederiksen, M., Percival, S.M., Anderson, G.Q.A. & Denny, M.J.H. 2001. Seasonal and annual survival of East Atlantic Pale-bellied Brent Geese *Branta bernicla brota* assessed by capture-recapture analysis. *Ardea* 89: 101–111.
- Ebbinge, B.S. 1985. Factors determining the population size of arctic-breeding geese, wintering in western Europe. *Ardea* 73: 121–128.
- Ebbinge, B.S. 1991. The impact of hunting on mortality rates and spatial distribution of

- geese wintering in the Western Palearctic. *Ardea* 79: 197–209.
- Ebbinge, B.S. 1992. Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla bernicla* on spring staging sites. *Ardea* 80: 203–228.
- Ebbinge, B.S., Berrevoets, C., Clausen, P., Ganter, B., Günther, K., Koffijberg, K., Mahéo, R., Rowcliffe, M., St Joseph, A.K.M., Südbeck, P. & Syroechkovsky, E.E.J. 1999. Dark-bellied Brent Goose *Branta bernicla bernicla*. In J. Madsen, G. Cracknell & A. D. Fox (eds.), *Goose Populations of the Western Palearctic. A Review of Status and Distribution*, pp. 284–297. Wetlands International, Wageningen, the Netherlands and National Environmental Research Institute, Rønde, Denmark.
- Ebbinge, B.S., Heesterbeek, J.A.P., Ens, B.J. & Goedhart, P.W. 2002. Density dependent population limitation in dark-bellied brent geese *Branta b. bernicla*. *Avian Science* 2: 63–75.
- Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T. & Stenseth, N.C. 2008. Linking climate change to lemming cycles. *Nature* 456: 93–98.
- Lambeck, R.H.D. 1990. The applicability of age ratio and brood size counts in population dynamic studies of the Brent Goose *Branta b. bernicla*. *Ardea* 78: 414–425.
- Laursen, K., Blew, J., Eskildsen, K., Günther, K., Hälterlein, B., Kleefstra, R., Lüerßen, G., Potel, P. & Schrader, S. 2010. *Migratory waterbirds in the Wadden Sea 1987–2008*. In Joint Monitoring Group of Migratory Birds in the Wadden Sea (eds.), *Wadden Sea Ecosystem, Volume 30*, pp. 1–170. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.
- Lehikoinen, A., Jaatinen, K., Vähätalo, A., Clausen, P., Crowe, C., Deceuninck, B., Hearn, R., Holt, C.A., Hornman, M., Keller, V., Nilsson, L., Langendoen, T., Tománková, I., Wahl, J. & Fox, A.D. 2013. Rapid climate driven shifts in winter distributions of three common waterbird species. *Global Change Biology* 19: 2071–2081.
- Nolet, B.A. Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Yu. & Ebbinge, B.S. 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. *Journal of Animal Ecology* 82: 804–813.
- Ogilvie, M.A. & St Joseph, A.K.M. 1976. Dark-bellied Brent Geese in Britain and Europe 1955–76. *British Birds* 90: 422–439.
- Prokosch, P. 1984. Population, Jahresrhythmus und traditionelle Nahrungsplatzbindungen der Dunkelbäuchigen Ringelgans (*Branta b. bernicla*, L. 1758) in Nordfriesischen Wattenmeer. *Ökologie der Vögel* 6: 1–99.
- Radi, M., Patrick Bergier, P., El Idrissi, A., Qninba, A., Zadane, Y. & Dakki, M. 2009. Hivernage de la Bernache cravant *Branta bernicla* à Khnifiss. *Go-South Bulletin* 6: 72–75.
- Salomonsen, F. 1958. *The present status of the Brent Goose (Branta bernicla (L.)) in western Europe*. International Waterfowl Reserch Bureau Publ. No. 4. IWRB, Slimbridge, UK.
- Soldaat, L., Visser, H., van Roomen, M. & van Strien, A. 2007. Smoothing and trend detection in waterbird monitoring data using structural time-series analysis and the Kalman filter. *Journal of Ornithology* 148 (Supplement No. 2): 351–357.
- Summers, R.W. & Underhill, L.G. 1991. The growth of the population of dark-bellied brent geese *Branta b. bernicla* between 1955 and 1988. *Journal of Applied Ecology* 28: 574–585.
- Ward, R.M. 2004. Dark-bellied Brent Goose *Branta bernicla bernicla* in Britain 1960/61–1999/2000. Waterbird Review Series, The Wildfowl and Wetlands Trust/Joint Nature Conservation Committee, WWT, Slimbridge, UK.

**Appendix 1.** Mid-winter counts of Dark-bellied Brent Geese from 1991–2011 inclusive. F = France, UK = Great Britain, NL = the Netherlands, NS = Niedersachsen, Lower Saxony, Germany, SH = Schleswig-Holstein, Germany, and DK = Denmark.

<b>Year</b>	<b>F</b>	<b>UK</b>	<b>NL</b>	<b>NS</b>	<b>SH</b>	<b>DK</b>	<b>Total</b>
1991	85,000	96,201	64,564	2,651	2,684	2,789	<b>254,000</b>
1992	115,229	137,943	70,224	2,341	1,562	2,047	<b>329,000</b>
1993	103,121	92,146	65,644	1,446	1,373	4,402	<b>268,000</b>
1994	108,416	125,304	79,379	2,747	3,864	2,470	<b>322,000</b>
1995	102,336	91,946	53,609	2,064	1,086	2,914	<b>254,000</b>
1996	91,422	87,252	38,227	1,431	475	476	<b>219,000</b>
1997	99,563	92,368	23,173	1,446	316	235	<b>217,000</b>
1998	97,870	96,482	44,862	2,415	813	1,876	<b>244,000</b>
1999	87,019	74,510	33,987	2,229	555	1,639	<b>200,000</b>
2000	97,000	87,668	47,044	5,989	1,050	1,662	<b>240,000</b>
2001	81,000	93,713	39,739	2,543	978	1,083	<b>219,000</b>
2002	115,621	70,745	35,820	1,928	383	1,239	<b>226,000</b>
2003	95,146	68,874	30,352	1,990	288	84	<b>198,000</b>
2004	90,485	64,453	35,197	2,088	682	479	<b>193,000</b>
2005	104,301	85,664	32,946	1,870	703	1,774	<b>227,000</b>
2006	147,708	78,194	49,753	2,713	720	1,387	<b>280,000</b>
2007	87,156	77,379	43,515	3,210	1,734	6,951	<b>220,000</b>
2008	118,223	83,135	40,921	2,377	716	1,275	<b>247,000</b>
2009	134,016	69,294	31,230	1,823	593	1,780	<b>239,000</b>
2010	102,840	78,944	28,982	998	1,179	828	<b>214,000</b>
2011	116,275	69,747	22,637	1,272	359	370	<b>211,000</b>

**Appendix 2.** Age ratio assessments of Dark-bellied Brent Geese in France (F), Great Britain (UK) and the Netherlands (NL), expressed as the percentage of first-winter birds recorded in the wintering flocks.

Winter	F	UK	NL	Weighted mean
1990/91	34.0	21.4	21.1	26.4
1991/92	31.2	31.1	30.0	30.9
1992/93	0.1	0.0	0.1	0.1
1993/94	33.0	18.0	25.6	25.5
1994/95	5.8	5.8	8.6	6.4
1995/96	0.5	0.3	0.9	0.5
1996/97	15.4	8.3	20.8	13.6
1997/98	11.8	9.0	12.7	10.9
1998/99	1.3	0.9	0.9	1.1
1999/00	27.7	23.6	23.2	25.2
2000/01	0.5	0.6	5.7	1.6
2001/02	10.4	6.2	14.5	9.5
2002/03	9.3	6.8	9.6	8.4
2003/04	9.7	10.0	18.1	11.5
2004/05	13.8	11.9	21.3	14.5
2005/06	23.6	28.4	42.0	29.2
2006/07	2.2	2.0	3.0	2.3
2007/08	10.7	11.0	16.5	12.0
2008/09	0.9	1.1	2.3	1.3
2009/10	6.2	5.3	11.9	7.0
2010/11	12.2	12.7	17.8	13.5
2011/12	21.4	16.2	23.6	19.8

**Appendix 3.** Spring counts of Dark-bellied Brent Geese in France (F), Great Britain (UK), the Netherlands (NL), Niedersachsen, Lower Saxony (NS), Germany, Schleswig-Holstein (SH), Germany and Denmark (DK)

<b>Year</b>	<b>F</b>	<b>UK</b>	<b>NL</b>	<b>NS</b>	<b>SH</b>	<b>DK</b>	<b>Total</b>
1995	–	588	116,443	16,701	105,048	19,190	<b>258,000</b>
1996	–	7,993	81,310	15,731	84,487	3,291	<b>193,000</b>
1997	–	2,016	92,435	17,550	82,720	6,985	<b>202,000</b>
1998	–	13,045	63,055	15,615	86,416	11,686	<b>190,000</b>
1999	–	9,563	60,730	11,628	77,237	11,339	<b>170,000</b>
2000	–	10,234	83,301	7,641	84,287	9,030	<b>194,000</b>
2001	–	1,100	72,336	10,000	70,639	10,000	<b>164,000</b>
2002	–	486	79,108	19,072	54,471	No data	<b>&gt;153,000</b>
2003	–	5,903	76,988	19,260	61,406	14,251	<b>178,000</b>
2004	–	7,636	79,110	17,219	59,642	13,244	<b>177,000</b>
2005	–	9,532	69,854	21,061	67,599	8,454	<b>177,000</b>
2006	–	12,495	104,373	27,689	74,568	18,595	<b>238,000</b>
2007	–	5,335	105,000	19,330	61,098	10,657	<b>201,000</b>
2008	–	5,330	106,973	24,673	77,494	17,163	<b>232,000</b>
2009	–	5,136	81,000	16,460	54,883	12,295	<b>170,000</b>
2010	–	8,185	78,000	11,729	58,048	13,909	<b>170,000</b>
2011	–	4,688	80,713	10,251	66,577	19,445	<b>182,000</b>