Trends in abundance and wintering phenology of the Dark-bellied Brent Goose *Branta b. bernicla* in France between 1982 and 2012

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Abstract

Trends in abundance, the timing of arrival and departure, and the number of goosedays at internationally important sites, are presented for Dark-bellied Brent Geese Branta bernicla bernicla wintering in France during 1982-2012 inclusive. Numbers wintering in France increased more rapidly than the increase in the population as a whole: c. 30% of the world population occurred in France in 1982 and just over half in 2012. Throughout the past 30 years, c. 75% of Brent Geese wintering in France have concentrated at just six sites. Two of them (Bassin d'Arcachon and Golfe du Morbihan) have shown a sharp rise in numbers in mid-January, most notably a fivefold increase in 30 years at the Bassin d'Arcachon, which now accounts for c. 43% of the total in France (compared with c. 21% in 1982) and c. 22% of the world population (c. 5% in 1982). Wintering phenology at the six main sites, determined from the dates on which 50% of the annual peak count had arrived and departed, has varied over time. At five of the sites, this proportion of Brent Geese now arrives 3-4 weeks earlier than 30 years ago. The total number of goose-days has increased almost fivefold at Bassin d'Arcachon and doubled in Baie de Bourgneuf, although the reasons for these changes remain unclear. In particular, the increase at Bassin d'Arcachon merits investigation, given a long-term decline in eelgrass Zostera sp. abundance at this site.

Key words: arrival dates, censuses, departure dates, France, trend analyses, wintering sites.

The Dark-bellied Brent Goose *Branta* bernicla bernicla migrates each year between breeding grounds on the coastal tundra of

arctic Russia (mainly on the Taimyr Peninsula), and wintering sites in western Europe. Throughout its staging and wintering areas, the population relies mainly on a network of natural habitats, composed of mudflats and salt marshes, along the northwest European coastline (Scott & Rose 1996; Ebbinge et al. 1999). Confinement to these particular habitats is due to the dietary requirements of this strict herbivore, which feeds preferentially on beds of eelgrass Zostera sp. (Ganter 2000) and, when these are depleted or are naturally absent from a site, switches to algae (Ulva sp. and Enteromorpha sp.; Inger et al. 2006), or to salt marshes where the birds forage on swards dominated by Common Salt-marsh Grass Puccinellia maritima (Charman & Macey 1978; Vickery et al. 1995; Clausen 1998; Rowcliffe et al. 2001). This strong dietary specificity concentrates the species geographically, making it particularly vulnerable to changes in environmental conditions, and thus to human activities that are often the cause of such changes.

In view of its vulnerability to habitat change, the world population size of Darkbellied Brent Geese has been monitored every year since the 1950s, based on counts carried out in January across all wintering areas (Ebbinge et al. 1999). These counts, which help to monitor the conservation status of the species, indicate that after a period of steady growth from the 1950s to a peak of c. 329,000 individuals in 1992, numbers have declined since then and are now tending to be stable or showing a slight decline. The latest assessment of the world population size, of c. 211,000 birds in 2011 (Ebbinge et al. 2013), is close to that of 1983 (when c. 206,000 individuals were counted).

Whereas the world population is the subject of regular assessments (e.g. Ebbinge

et al. 1999; Delany & Scott 2006; Fox et al. 2010), publication of national syntheses outlining major trends at internationally important wintering sites is rare or, as in the case of France, virtually non-existent. Yet changes in human activities over the last 30 years have probably modified conditions at the wintering grounds, which may in turn have affected goose numbers at the different sites. In France, this species has been protected by ministerial decree from hunting since 1962, but two other threats have become evident since then, namely: 1) the reduction in size and/or quality of feeding areas, mainly caused by shell farming/harvesting (Desmonts et al. 2009), changes in water quality (Plus et al. 2010), and the invasion of salt marshes by Sea Couch Grass Elymus athericus (Valéry et al. 2008; Schricke 2010); and 2) increased disturbance due to the development of economic and recreational activities on the coast (Schricke 2004). This paper therefore aims to provide a summary description of the major trends in abundance, wintering phenology, and intensity of use (number of goose-days) of Dark-bellied Brent Geese at their most important wintering sites in France over the last three decades, with a view to supporting future assessments of the reasons for the observed changes.

Methods

Criterion for identifying main wintering sites in France

Numbers of Dark-bellied Brent Geese have been counted in mid-January each year since the 1960s, as part of the International Waterbirds Censuses (IWCs) coordinated by Wetlands International. Sites selected for the current analyses were those sites which ranked in the top ten in France every year of the 30-year study (i.e. 1982-2012). Six internationally important sites met this criterion (the main food items are indicated in brackets): 1) Bassin d'Arcachon (mainly Zostera sp.); 2) Réserve Naturelle de Moëze-Oléron (hereafter, R.N. Moëze-Oléron) (Zostera sp. and green algae); 3) Ile de Ré (Zostera sp. and green algae); 4) Baie de Bourgneuf (mainly Zostera sp.); 5) Golfe du Morbihan (mainly Zostera sp.); and 6) Baie du Mont-Saint-Michel (mainly Puccinellia maritima) (Fig. 1). Each year, these six sites alone accounted for an average of 75.1 \pm

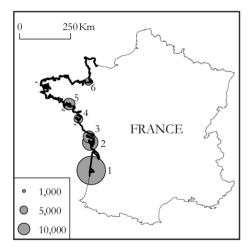


Figure 1. The six main sites for Dark-bellied Brent Geese wintering in France over the period 1982–2012: 1) Bassin d'Arcachon; 2) R.N. Moëze-Oléron; 3) Ile de Ré; 4) Baie de Bourgneuf; 5) Golfe du Morbihan; and 6) Baie du Mont-Saint-Michel. For each site, circle sizes represent (proportionately) the number of geese counted in January 2012; the emboldened coastline indicates the wintering range within France.

0.6% s.e. (range = 64.1-80.9%) of the total number of wintering geese in France.

Goose numbers

Trends in the numbers of Dark-bellied Brent Geese recorded over the past three decades, for the world population size, numbers wintering in France and the numbers wintering at each of the six main sites, were determined using linear regression analysis based on mid-January count data, to facilitate comparisons between sites and to identify the main trends. As there were a number of uncontrolled biases in the raw data (e.g. change of the observer during the 30 years, change of the counting date in the month, weather conditions), using a more advanced mathematical approach (e.g. non-linear regression models) would not have provided more accurate results. It is also important to note that the mid-January count does not always correspond to the peak in goose numbers, which may occur between November and February, depending on the sites and years.

Goose phenology

For each of the six main wintering sites in each year, Dark-bellied Brent Goose arrival and departure dates were determined from monthly counts made throughout the winter, from September to April inclusive. As the actual dates of these counts were not known precisely, we considered for the sake of simplification that they occurred on the 15th of each month in all cases. These counting dates were then coded as follows: 15 September = 0.5, 15 October = 1.5, 15 November = 2.5, up to 15 April = 7.5. Arrival patterns were described directly from the monthly counts (which represent the cumulative net influx) up to the peak count date, with departure patterns measured as the difference between the peak count and each of the monthly counts thereafter (*i.e.* the cumulative net departures). The median arrival and departure dates of the geese were defined, for this study, as the dates on which goose number counted accounted for 50% of its annual maximum number at the site each winter.

Logistic regressions were performed to model the arrivals and departures of Brent Geese. These regressions were of the form $y = 1 / (1 + \exp (a * x + b))$ with y =cumulative number of departures or arrivals and x = coded dates. Each logistic regression showed a good fit, *i.e.* the areas under the Receiver Operating Characteristic (ROC) curves were always > 0.75 (most often >0.85). The dates of departure and arrival (*i.e.* value on the abscissa) were calculated for y = 0.5 (*i.e.* 50 % of the maximum number) from the parameters a and b of each regression with the formula x = -b/a, with x representing the coded date. For each site, the trends in arrival and departure dates over the last three decades were analysed using linear regression models with year as the independent variable in each case.

Site use by the geese (cumulative goose-days)

To account for variation in the numbers of goose-days at each of the six main wintering sites (*i.e.* the intensity of site use by geese), the number of goose-days recorded over the whole winter was calculated for each site in each year. This was estimated as the number

of birds counted per month multiplied by the number of days (28, 30 or 31, depending on the month) and then summed for the winter season. Changes in the intensity of site use by the geese over the 30-year period could reflect the potential carrying capacity of those sites. For example, if the number of goose-days is: 1) showing an on-going increase, there would seem to be room for more geese; 2) levelling off or has been stable over the 30 years, the site could potentially be saturated (i.e. some feature of carrying capacity has been reached); or 3) declining, there could be local issues, such as habitat loss or disturbance affecting goose use of the site. Linear regressions were used to analyse the trend in site use over the last three decades for each site.

Data analyses

The results of all linear regressions are presented with Student *t*-tests of the slope and intercept in the Appendices to this paper. Standard errors (s.e.) and 95% confidence intervals (CI) of the regression parameters were also computed to evaluate the accuracy of the models. Kolmogorov-Smirnoff tests adjusted with the Lilliefors table confirmed that the residuals of each regression were normally distributed.

To facilitate interpretation of trends in: 1) goose numbers, 2) site use, and 3) the relative importance of the main French wintering sites, trends over the whole study period (1982–2012) were measured as an average annual rate of change (*i.e.* Average Annual Growth Rate between 1982 and 2012; hereafter AAGR_{82–12}). TRIM software was used to determine the statistical significance of the trends (van Strien *et al.* 2001; Pannekoek & van Strien 2005). Comparisons between the slopes of regression lines were tested with ANCOVAs which identified the statistical significance of the interaction term. Where necessary, *a posteriori* pair-wise comparisons between slopes were performed using linear contrasts with step-down Bonferroni adjustment in accordance with Holm's method (1979) and further developed by Schaffer (1986) (Milliken & Johnson 2002; Marasinghe & Kennedy 2008).

Modelling and statistical tests were performed using LOGISTIC, GLIMMIX and UNIVARIATE Procedures of SAS software (version 9.2; SAS Institute Inc., Cary, NC, US) and the freeware programme TRIM 3.5 (Pannekoek & van Strien 2005). Means are presented with standard errors throughout.

Results and Discussion

Trends in mid-January goose numbers over the period 1982–2012

Numbers wintering in France in relation to the world population

The world population of Dark-bellied Brent Geese increased by 20.8% between 1982 and 2011 (*i.e.* AAGR₈₂₋₁₁ = + 0.8 ± 0.01%, P < 0.01), comprising a period of continuous increase (since the 1950s) to a historical peak of *c.* 329,000 geese in 1992, followed by a decline and a period of stable numbers at *c.* 220,000 individuals to the present (Fig. 2a). In contrast, the total number of Brent Geese wintering in France has grown faster over the past three decades (*i.e.* AAGR₈₂₋₁₁ = + 2.6 ± 0.01%, P < 0.01), from *c.* 58,000 ± 6,000 individuals (determined from the output of

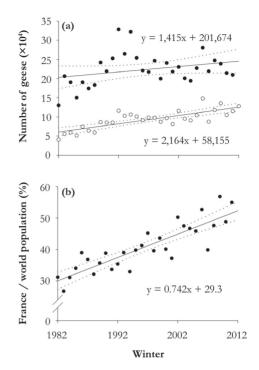


Figure 2. (a) Changes in the numbers of Darkbellied Brent Geese wintering in France (open circles) and in the world population (filled circles) in mid-January over the period 1982–2012; (b) Changes in the percentage of the world population of Dark-bellied Brent Geese wintering in France in mid-January, 1982–2012. Winter was defined by January of that season. Dotted lines indicate 95% confidence intervals (see Appendix 1 for further details on results of statistical analyses).

the linear regression model) in 1982 to *c*. $123,000 \pm 9000$ individuals in 2012 (Fig. 2a).

As a result, the proportion of the world population wintering in France has increased significantly: in 30 years, it increased from $29.3 \pm 1.4\%$ to $51.6 \pm 1.0\%$ (Fig. 2b). This result is consistent with a decrease of *c*. 30% in the number of Dark-

bellied Brent Geese wintering in the UK and the Netherlands between the mid-1990s and the mid-2000s (Musgrove *et al.* 2011; Holt *et al.* 2012; Hornman *et al.* 2012). Thus, France's responsibility for the conservation of this species has further increased.

Numbers in the six main French wintering sites in mid-January

The numbers of Dark-bellied Brent Geese declined moderately at R.N. Moëze-Oléron (AAGR₈₂₋₁₂ = -0.4 ± 0.02%, P < 0.01), showed a very slight increase at Ile de Ré (AAGR₈₂₋₁₂ = + 0.1 ± 0.01%, P < 0.01) and Baie du Mont-Saint-Michel (AAGR₈₂₋₁₂ = + 0.2 ± 0.01%, P < 0.01) and a relatively more pronounced increase at Baie de Bourgneuf (AAGR₈₂₋₁₂ = + 1.5 ± 0.02%, P < 0.01) (Fig. 3).

In contrast, the numbers of Brent Geese wintering in the Bassin d'Arcachon and in the Golfe du Morbihan have increased significantly over the last three decades (Fig. 3). This increase was not the same at the two sites $(F_{1.58} = 34.68, P < 0.0001)$; the average annual increase in number in the Bassin d'Arcachon (*i.e.* $1,355 \pm 198$ individuals) was eight times greater than that of the Golfe du Morbihan (*i.e.* 166 ± 38 individuals). The number of Brent Geese wintering in the Bassin d'Arcachon increased fivefold over the last 30 years, from c. $10,400 \pm 3,600$ individuals in 1982 (determined from the output of the linear regression model) to c. 51,000 \pm 6,000 individuals in 2012 (*i.e.* $AAGR_{82-12} = + 5.4 \pm 0.02\%, P < 0.01)$ whereas the number wintering in the Golfe du Morbihan increased 2.6 times, from c. $3,000 \pm 700$ individuals in 1982 to c. $8,200 \pm$ 1,100 individuals in 2012 (*i.e.* AAGR₈₂₋₁₂ =

+ 4.0 \pm 0.01%, P < 0.01). Therefore, the Bassin d'Arcachon is the French wintering site that has shown the largest increase in goose numbers, both in absolute and in relative terms, over the last three decades.

Relative importance of the main French wintering sites in mid-January

There was substantial variation in the proportion of geese recorded at each of the wintering sites in France in relation to the total numbers wintering in France (Fig. 3):

Four sites showed no trend or a decrease in numbers in relation to total numbers wintering in France over the period 1982–2012: a non-significant decrease at the Baie de Bourgneuf (AAGR₈₂₋₁₂ = $-1.0 \pm$ 0.6%, n.s.), and significant declines at the Baie du Mont-Saint-Michel (AAGR₈₂₋₁₂ = $-2.4 \pm 0.5\%$, P < 0.01), the Ile de Ré (AAGR₈₂₋₁₂ = $-2.5 \pm 0.3\%$, P < 0.01), and the R.N. Moëze-Oléron (AAGR₈₂₋₁₂ = $-3.0 \pm 0.5\%$, P < 0.01). The decline in the three latter sites was of the same order of magnitude ($F_{1.87} = 0.55$, n.s.).

At only two sites have the numbers of geese been growing faster than the national number over the last 30 years: the Golfe du Morbihan (AAGR₈₂₋₁₂ = +1.4 ± 0.6%, P < 0.05), which attained a level at the end of the period (*i.e. c.* 6.8% of the French total) similar to that of the Ile de Ré (*c.* 7.9%), and R.N. Moëze-Oléron (*c.* 6.8%). However, although the difference from the latter site was not significant ($F_{1,58} = 2.15$, n.s.), Bassin d'Arcachon had the highest growth (AAGR₈₂₋₁₂ = +2.7 ± 0.5%, P < 0.01); it now hosts 43.2 ± 3.9% of the total number of Brent Geese wintering in France, that is, 22.3 ± 2.2% of the world population (Fig. 4).

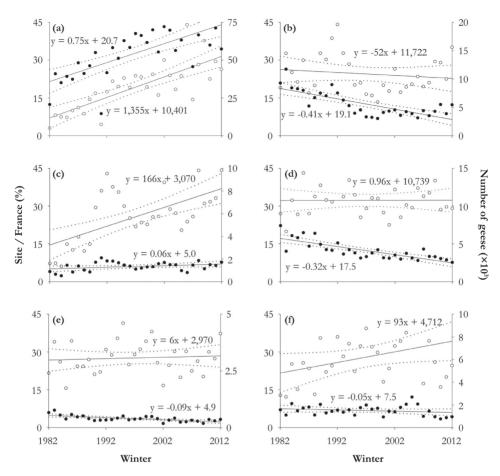


Figure 3. Trends in the proportion of geese counted in mid-January at each of the main French wintering sites compared to the total numbers wintering during the same month in France over the period 1982–2012 (black dots, left y-axis) and trends in mid-January number of geese for each site over the same period (white dots, right y-axis): (a) Bassin d'Arcachon; (b) R.N. Moëze-Oléron; (c) Golfe du Morbihan; (d) Ile de Ré; (e) Baie du Mont-Saint-Michel; and (f) Baie de Bourgneuf. Winter was defined by January of that season. Dotted lines indicate 95% confidence intervals (see Appendices 2 and 3 for further details on results of statistical analyses).

Trends in wintering phenology over the period 1982–2012

Changes in the arrival and departure dates of Dark-bellied Brent Geese over the 30year period varied between the six main French wintering sites, with three main patterns of change identified (Table 1, Fig. 5). Two sites – the Bassin d'Arcachon and the Baie de Bourgneuf – were the only sites that showed a significant change in both the arrival and the departure dates for the Brent

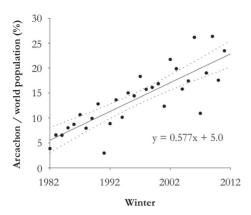


Figure 4. Changes in the percentage of the world population of Dark-bellied Brent Geese counted at Arcachon in mid-January during 1982–2012 inclusive. Winter was defined by January of that season. Dotted lines indicate 95% confidence intervals (see Appendix 4 for further details on results of statistical analyses).

Geese (Fig. 5a,f). This shift of the order of a month was the same for arrivals and departures, with the geese both arriving earlier and leaving earlier, so the overall duration of their wintering period at these two sites remains unchanged (Arcachon: $F_{1.58} = 0.25$, n.s.; Bourgneuf: $F_{1.58} = 0.15$, n.s.; Table 1). Elsewhere, at R.N. Moëze-Oléron (median departure date = c. 20January), Ile de Ré (c. 25 February) and the Baie du Mont-Saint-Michel (c. 7 March) Brent Goose departure dates have not changed significantly over the last three decades. However, they now arrive 2-3 weeks earlier (Fig. 5b,d,e) and show a rate of advancement that does not differ significantly from those at Bassin d'Arcachon and Baie de Bourgneuf ($F_{4,145}$ = 1.75, n.s.). Thus, they have increased the duration of their winter stay at these sites. Thirdly, at Golfe du Morbihan, Brent Goose

arrival dates did not change during 1982–2012 (*i.e.* mid-October) but the departure date is now delayed by an average of 40 \pm 14 days (*i.e.* 1982: 23 Dec. \pm 8 days vs. 2012: 1 Feb. \pm 6 days), which also increases the duration of their winter stay at a site which was formerly considered to be a pre-wintering area (Mahéo 1991).

Trends in numbers of goose-days over the period 1982–2012

The number of goose-days remained stable at four of the six main French wintering sites over the last three decades, suggesting possible saturation at these sites (Fig. 6): Baie du Mont-Saint-Michel (AAGR₈₂₋₁₂ = $+0.5 \pm$ 0.01%, n.s.), Golfe du Morbihan (AAGR₈₂₋₁₂ $= + 0.4 \pm 0.01\%$, n.s.), Ile de Ré (AAGR₈₂₋₁₂ $= + 0.4 \pm 0.01\%$, n.s.), and R.N. Moëze-Oléron (AAGR₈₂₋₁₂ = + 0.5 \pm 0.01%, n.s.). The number of goose-days at Baie de Bourgneuf rose significantly (AAGR₈₂₋₁₂ = + 2.8 \pm 0.01%, P < 0.01) and more than doubled over the whole period, while at Bassin d'Arcachon, numbers increased at a greater rate (AAGR₈₂₋₁₂ = + 5.7 \pm 0.01%, P < 0.01) ($F_{1.58} = 77.72$, P < 0.0001), increasing 4.6 fold between 1982 and 2012. These graphs show that the numbers of goose-days registered at Golfe du Morbihan, Bassin d'Arcachon and, to a lesser extent, the Ile de Ré and the R.N. Moëze-Oléron peaked at the same time as the peak in numbers of the world population (i.e. in 1992–1994).

Conclusion and perspectives

The importance of France as winter quarters for the world population of the Dark-bellied Brent Goose has increased from supporting c. 30% of the total

Sites	A/D	Date in 1982 ± CI 95% (days)		Date in 2012 ± CI 95% (days)		Δ 1982–2012 <i>n</i> days ± days	∆ wintering <i>n</i> days ± days	
Bassin	Arrival	27 Nov.	± 7	29 Oct.	± 3	-29 ± 19	n.s.	
d'Arcachon	Departure	26 Feb.	± 7	1 Feb.	± 7	-25 ± 14		
R.N. Moëze-	Arrival	24 Oct.	± 6	13 Oct.	± 3	-11 ± 10	$+11 \pm 10$	
Oléron	Departure	30 Jan.	± 15	14 Jan.	± 9	n.s.		
Ile de Ré	Arrival	10 Nov.	± 11	17 Oct.	± 3	-24 ± 14	$+24 \pm 14$	
	Departure	26 Feb.	± 8	23 Feb.	± 5	n.s.		
Golfe du	Arrival	17 Oct.	± 2	15 Oct.	± 1	n.s.	$+40 \pm 14$	
Morbihan	Departure	23 Dec.	± 8	1 Feb.	± 6	$+40 \pm 14$		
Baie du	Arrival	13 Dec.	± 7	23 Nov.	± 2	-20 ± 10	$+20 \pm 10$	
Mt-St-Michel	Departure	10 Mar.	± 7	4 Mar.	± 6	n.s.		
Baie de	Arrival	15 Nov.	± 9	11 Oct.	± 5	-35 ± 14	n.s.	
Bourgneuf	Departure	1 Mar.	± 12	23 Jan.	± 11	-37 ± 24		

Table 1. Trends in arrival/departure dates and in the duration of wintering of Dark-bellied Brent Geese on the six main French wintering sites over the period 1982–2012 (based on outputs of linear regression analysis).

numbers in 1982 to just over half in 2012. Out of the six most nationally important wintering sites, mid-January numbers at Bassin d'Arcachon increased fivefold and at Golfe du Morbihan more than doubled in the same period. Bassin d'Arcachon has become a major wintering site, now hosting nearly 25% of the world population. The wintering phenology has changed at each of the six main sites. These have been grouped according to three major patterns of change determined by the arrival and departure dates, although Brent Geese now arrive at five of these sites three to four weeks earlier than 30 years ago. At Golfe du Morbihan, the arrival date, which was already the

earliest, remained constant; Brent Geese arrived at this site in mid-October in 2012 as was the case in 1982. Numbers of goosedays as an index of intensity of site use increased substantially at Baie de Bourgneuf and especially Bassin d'Arcachon.

It is not clear whether these changes are the results of intrinsic or extrinsic factors acting upon the geese. However, these preliminary results provide the basis for future work. It would be particularly interesting to identify local or regional factors explaining the differences in the numerical and phenological changes in the birds' use of the different sites, for instance by analysis of re-sightings of ringed birds to determine movements

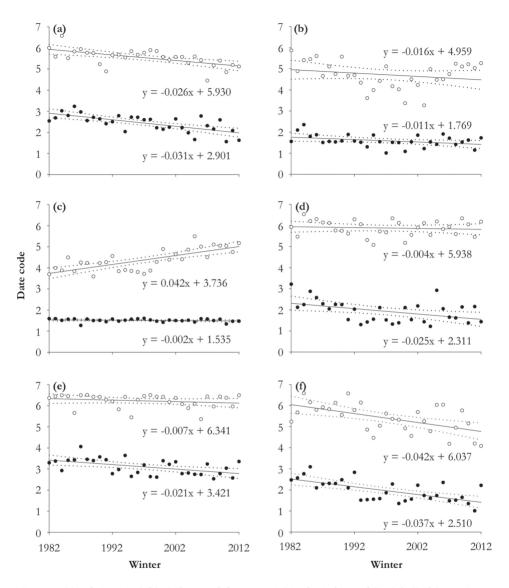


Figure 5. Trends in arrival (black dots) and departure (white dots) dates of Dark-bellied Brent Geese on the six main French wintering sites over the period 1982–2012: (a) Bassin d'Arcachon; (b) R.N. Moëze-Oléron; (c) Golfe du Morbihan; (d) Ile de Ré; (e) Baie du Mont-Saint-Michel; and (f) Baie de Bourgneuf. Dates are coded as follows: 0 = 1 September; 1 = 1 October; 2 = 1 November; 3 = 1 December; 4 = 1 January; 5 = 1 February; 6 = 1 March; 7 = 1 April (cf. Methods, for details). Winter was defined by January of that season. Dotted lines indicate 95% confidence intervals (see Appendix 5 for further details on results of statistical analyses).

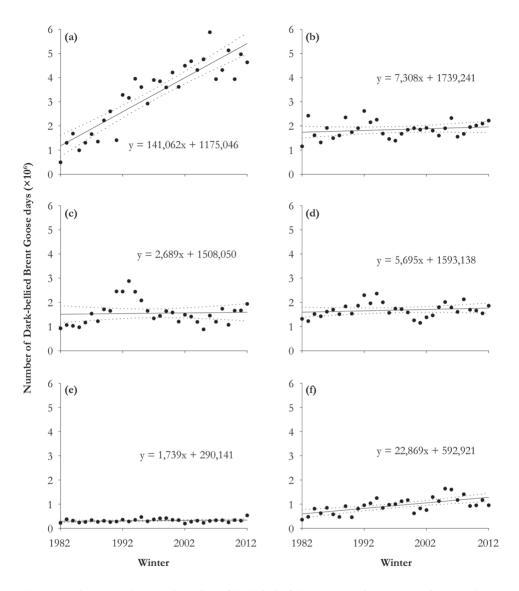


Figure 6. Changes in the annual number of Dark-bellied Brent Goose-days (expressed in cumulative goose-days $\times 10^6$ over the whole wintering period) registered at each of the six main wintering sites in France over the period 1982–2012: (a) Bassin d'Arcachon; (b) R.N. Moëze-Oléron; (c) Golfe du Morbihan; (d) Ile de Ré; (e) Baie du Mont-Saint-Michel; and (f) Baie de Bourgneuf. Winter was defined by January of that season. Dotted lines indicate 95% confidence intervals (see Appendix 6 for further details on results of statistical analyses).

between sites. This could usefully be extended to take into account wintering areas in the UK and in the Netherlands. Some attempts to quantify the carrying capacity of the different sites should focus firstly on the Bassin d'Arcachon where the site use by Brent Geese has increased dramatically, despite the fact that the extent of the eelgrass beds – an important food source for the geese – has declined substantially over the past 30 years (Plus *et al.* 2010).

Acknowledgements

We would like to thank Sophie Le Dréan-Ouenec'hdu and Roger Mahéo who, as the heads of the French Brent Goose Network, have coordinated the censuses and compiled the count data for more than 35 years. We acknowledge the numerous observers who have participated in censuses each winter over many years, sometimes in freezing temperatures! We would like to extend special thanks to Valérie Monbet from IRMAR (Mathematics Research Institute of Rennes) who kindly provided statistical advice for this paper. We also thank J.-M. Paillisson and F. Fonteneau for their comments on earlier versions of this manuscript. Finally, we are grateful to Aldyth Nys, who helped to improve the English, and are thankful to the reviewers, Preben Clausen and Abel Gyimesi, as well as the two co-editors, Eileen Rees and Tony Fox, for their constructive comments.

References

- Charman, K. & Macey, A. 1978. The winter grazing of saltmarsh vegetation by Darkbellied Brent Geese. Wildfowl 29: 153–162.
- Clausen, P. 1998. Choosing between feeding on Zostera and salt marsh: factors affecting

habitat use by Brent geese in spring. In F. Mehlum, J.M. Black & J. Madsen (eds.), Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, 23–26 September 1997, Norsk Polarinstitute Skrift 200: 277–294.

- Delany, S. & Scott, D. 2006. Waterbird Population Estimates – Fourth Edition. Wetlands International, Wageningen, the Netherlands.
- Desmonts, D., Fritz, H., Cornulier, T. & Mahéo, R. 2009. Rise in human activities on the mudflats and Brent Geese (*Branta bernicla*) wintering distribution in relation to *Zostera* spp. beds: a 30-year study. *Journal of Ornithology* 150: 733–742.
- Ebbinge, B., Berrevoets, C., Clausen, P., Ganter, B., Günther, K., Koffijberg, K., Mahéo, R., Rowcliffe, J.M., St Joseph, A.K.M., Südbeck P. & Syroechkovsky Jr., E.E. 1999. Darkbellied 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 Publication No. 48, Wageningen, the Netherlands.
- Ebbinge, B.S., Blew, J., Clausen, P., Klaus Günther, K., Hall, C., Holt, C., Koffijberg, K., Le Dréan-Quénec'hdu, S., Mahéo, R. & Pihl, S. 2013. Population development and breeding success of Dark-bellied Brent Geese *Branta h. bernicla* from 1991–2011. *Wildfowl* (Special Issue No. 3): 74–89.
- Fox, A.D., Ebbinge, B.S., Mitchell, C., Heinicke, T., Aarvak, T., Colhoun, K., Clausen, P., Dereliev, S., Farago, S., Koffijberg, K., Kruckenberg, H., Loonen, M.J.J.E., Madsen, J., Mooij, J., Musil, P., Nilsson, L., Pihl, S. & Van der Jeugd, H. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. Ornis Svecica 20: 115–127.
- Ganter, B. 2000. Seagrass (Zostera spp.) as food for Brent geese (Branta bernicla): an overview. Helgoland Marine Research 54: 63–70.

- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65–70.
- Holt, C.A., Austin, G.E., Calbrade, N.A., Mellan,
 H.J., Hearn, R.D., Stroud, D.A., Wotton, S.R.
 & Musgrove A.J. 2012. Waterbirds in the U.K.
 2010/11: The Wetland Bird Survey. BTO/ RSPB/JNCC, Thetford, UK.
- Hornman, M., Hustings, F., Koffijberg, K., Kleefstra, R., Klaassen, O., Van Winden, E., SOVON Ganzen- en Zwanenwerkgroep & Soldaat L. 2012. Watervogels in Nederland in 2009/2010. SOVON report 2012/02, Waterdienst rapport BM 12.06. SOVON Vogelonderzoek Nederland, Nijmegen, the Netherlands. [In Dutch with English summary and figures captions.]
- Inger, R., Ruxton, G.D., Newton, J., Colhoun, K., Robinson, J.A., Jackson, A.L. & Bearhop, S. 2006. Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *Journal* of *Animal Ecology* 75: 1190–1200.
- Mahéo, R. 1991. Bernache cravant Branta bernicla. In D. Yeatman-Berthelot (ed.), Atlas des oiseaux de France en biver, pp.100–101. Société Ornithologique de France, Paris, France.
- Marasinghe, M.G. & Kennedy, W.J. 2008. SAS for Data Analysis – Intermediate Statistical Methods. Springer Science, New York, USA.
- Milliken, G.A. & Johnson, D.E. 2002. Analysis of Messy Data – Vol. 3: Analysis of Covariance. Chapman & Hall/CRC, New York, USA.
- Musgrove, A.J, Austin, G.E., Hearn, R.D., Holt, C.A., Stroud, D.A. & Wotton, S.R. 2011. Overwinter population estimates of British waterbirds. *British Birds* 104: 364–397.
- Pannekoek, J. & van Strien, A. 2005. TRIM 3 Manual (Trends & Indices for Monitoring data). Statistics Netherlands, Voorburg, the Netherlands.
- Plus, M., Dalloyau, S., Trut, G., Auby, I., de Montaudouin, X., Emery, E., Noël, C. &

Viala C. 2010. Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). *Estuarine, Coastal and Shelf Science* 87: 357–366.

- Rowcliffe, J.M., Watkinson, A.R., Sutherland, W.J. & Vickery, J.A. 2001. The depletion of algal beds by geese: a predictive model and test. *Oecologia* 127: 361–371.
- Schaffer, J.P. 1986. Modified Sequentially Rejective Multiple Test Procedures. *Journal of* the American Statistical Association 81: 826–831.
- Schricke, V. 2004. La Bernache cravant à ventre sombre Branta bernicla bernicla. In ONCFS (ed.), Connaissance des espèces de la Faune sauvage et gestion de leurs babitats. CD-rom. Office National de la Chasse et de la Faune Sauvage, Paris, France.
- Schricke, V. 2010. La gestion des herbus de la baie du Mont-Saint-Michel. In Maison de la baie de Somme et de l'Oiseau (ed.), Actes de la Conférence 'Zones humides, chasse et conservation de la nature', 17–19 Juin 2009. Aestuaria, pp. 97–110.
- Scott, D.A. & Rose, P.M. 1996. Atlas of Anatidae populations in Africa and Western Eurasia. Wetlands International Publication No. 41, Wageningen, the Netherlands.
- Valéry, L., Schricke, V., Fritz H. & Lefeuvre, J.-C. 2008. A synthetic method to assess the quality of wintering sites for the Dark-bellied Brent Goose *Branta bernicla bernicla* – The case study of the salt marsh of Vains in the Mont-Saint-Michel Bay, France. *Vogehvelt* 129: 221–225.
- Van Strien, A.J., Pannekoek, J. & Gibbons, D.W. 2001. Indexing European bird population trends using results of national monitoring schemes: a trial of a new method. *Bird Study* 48: 200–213.
- Vickery, J.A., Sutherland, W.J., Watkinson, A.R., Lane, S.J. & Rowcliffe J.M. 1995. Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499–508.

Appendix 1. Results of linear regressions on trends in numbers for the world population of Dark-bellied Brent Geese and for numbers wintering in France as well as on trends in the ratio between number of Brent Geese in France and in the world population over the period 1982–2012 (based on January counts).

Sites	Y = ax + b	Value	<i>s.e.</i>	t	Р	CI (95%)	n
World	а	1,415	873	1.620	n.s.	-374 - 3,203	30
	b	201,674	15,501	13.011	< 0.0001	169,923 – 233,426	30
France	а	2,164	313	6.911	< 0.0001	1,524 - 2,805	31
	b	58,155	5,740	10.131	< 0.0001	46,415 - 69,895	31
France vs.	а	0.742	0.081	9.195	< 0.0001	0.577 - 0.907	30
world	b	29.3	1.432	20.446	< 0.0001	26.3 - 32.2	30

Appendix 2. Results of linear regressions on trends in numbers of Dark-bellied Brent Geese in the six main French wintering sites over the period 1982–2012.

Sites	Y = ax + b	Value	<i>s.e.</i>	t	Р	CI (95%)	n
Bassin	а	1,355	198	6.830	< 0.0001	949 – 1,761	31
d'Arcachon	b	10,401	3,638	2.859	0.008	2,961 – 17,841	31
R.N. Moëze-	а	-52	66	-0.782	n.s.	-188 - 84	31
Oléron	Ь	11,722	1,219	9.615	< 0.0001	9,289 – 14,216	31
Ile de Ré	а	0.96	45	0.022	n.s.	-90 - 92	31
	b	10,739	819	13.110	< 0.0001	9,064 - 12,414	31
Golfe du	а	166	38	4.393	< 0.0001	89 - 243	31
Morbihan	b	3,070	692	4.437	< 0.0001	1,655 – 4,486	31
Baie du	а	6.0	14	0.421	n.s.	-23 - 35	31
Mt-St-Michel	Ь	2,970	261	11.381	< 0.0001	2,436 - 3,503	31
Baie de	а	93	49	1.911	n.s.	-7 - 193	31
Bourgneuf	Ь	4,712	896	5.261	< 0.0001	2,881 - 6,544	31

Appendix 3. Results of linear regressions on trends in the proportion of each main wintering site compared to the total number of Dark-bellied Brent Geese wintering in France over the period 1982–2012.

Sites	Y = ax + b	Value	<i>s.e.</i>	t	Р	CI (95%)	n
Bassin	а	0.75	0.13	5.609	< 0.0001	0.48 - 1.0	31
d'Arcachon	Ь	20.74	2.46	8.446	< 0.0001	15.7 - 25.8	31
R.N. Moëze-	a	-0.41	0.07	-6.149	< 0.0001	-0.550.27	31
Oléron	Ь	19.13	1.23	15.607	< 0.0001	16.6 - 21.6	31
Ile de Ré	а	-0.32	0.05	-7.024	< 0.0001	-0.420.23	31
	Ь	17.46	0.84	20.746	< 0.0001	15.7 - 19.2	31
Golfe du	а	0.06	0.03	1.897	n.s.	-0.005 - 0.1	31
Morbihan	Ь	5.00	0.61	8.144	< 0.0001	3.7 - 6.2	31
Baie du	а	-0.09	0.02	-4.847	< 0.0001	-0.120.05	31
Mt-St-Miche	l b	4.91	0.33	15.062	< 0.0001	4.2 - 5.6	31
Baie de	а	-0.05	0.04	-1.227	n.s.	-0.13 - 0.03	31
Bourgneuf	Ь	7.53	0.74	10.233	< 0.0001	6.0 - 9.0	31

Appendix 4. Result of the linear regression on trend in the ratio between number of Brent Geese wintering in Arcachon and the world population of Dark-bellied Brent Geese over the period 1982–2012.

Sites	Y = ax + b	Value	<i>s.e.</i>	t	Р	CI (95%)	n
Arcachon	а	0.577	0.074	7.798	< 0.0001	0.425 - 0.728	30
vs. world	Ь	5.0	1.312	3.786	< 0.001	2.3 - 7.7	30

Sites	A/D	Y = ax + b	Value	s.e.	t	Р	CI (95%)	n
Bassin	Arrival	а	-0.031	0.006	-5.129	< 0.0001	-0.040.02	31
d'Arcachon		b	2.901	0.110	22.056	< 0.0001	2.69 - 3.12	31
	Departure	а	-0.026	0.007	-4.058	< 0.0001	-0.040.01	31
		Ь	5.930	0.119	45.742	< 0.0001	5.70 - 6.16	31
R.N. Moëze-	Arrival	а	-0.011	0.005	-2.116	< 0.05	-0.02 - 0.00	31
Oléron		Ь	1.769	0.100	12.747	< 0.0001	1.57 - 1.96	31
	Departure	а	-0.016	0.013	-1.254	n.s.	-0.04 - 0.01	31
		b	4.959	0.235	19.049	< 0.0001	4.50 - 5.42	31
Ile de Ré	Arrival	а	-0.025	0.010	-2.682	< 0.02	-0.040.01	31
		b	2.311	0.174	10.541	< 0.0001	1.97 - 2.65	31
	Departure	а	-0.004	0.007	-0.545	n.s.	-0.02 - 0.01	31
		b	5.938	0.137	39.616	< 0.0001	5.67 - 6.21	31
Golfe du	Arrival	а	-0.002	0.002	-1.147	n.s.	-0.005 - 0.001	31
Morbihan		b	1.535	0.028	37.495	< 0.0001	1.48 - 1.59	31
	Departure	а	0.042	0.007	5.911	< 0.0001	0.03 - 0.06	31
		b	3.736	0.131	24.338	< 0.0001	3.48 - 3.99	31
Baie du	Arrival	а	-0.021	0.007	-3.172	< 0.01	-0.030.01	31
Mt-St-Michel		Ь	3.421	0.123	23.942	< 0.0001	3.18 - 3.66	31
	Departure	а	-0.007	0.006	-1.103	n.s.	-0.02 - 0.01	31
		b	6.341	0.116	50.233	< 0.0001	6.11 - 6.57	31
Baie de	Arrival	а	-0.037	0.008	-4.645	< 0.0001	-0.050.02	31
Bourgneuf		Ь	2.510	0.145	14.127	< 0.0001	2.23 - 2.79	31
	Departure	а	-0.042	0.012	-3.661	< 0.001	-0.070.02	31
		b	6.037	0.211	26.414	< 0.0001	5.62 - 6.45	31

Appendix 5. Results of linear regressions on trends in arrival/departure dates of Darkbellied Brent Geese on the six main French wintering sites over the period 1982–2012.

Sites	Y = ax + b	Value	<i>s.e.</i>	t	Р	CI (95%)	n
Bassin	а	141,062	12,473	11.309	< 0.0001	115,551 – 166,572	31
d'Arcachon	Ь	1175,046	217,834	5.394	< 0.0001	729,526 - 1620,566	31
R.N. Moëze-	а	7,308	6,870	1.064	n.s.	-6,743 - 21,359	31
Oléron	b	1739,241	119,979	14.496	< 0.0001	1493,856 - 1984,626	31
Ile de Ré	а	5,695	5,905	0.965	n.s.	-6,381 - 17,771	31
	Ь	1593,138	103,121	15.449	< 0.0001	1382,232 - 1804,043	31
Golfe du	а	2,689	10,096	0.266	n.s.	-17,960 - 23,338	31
Morbihan	Ь	1508,050	176,322	8.553	< 0.0001	1147,431 – 1868,669	31
Baie du	а	1,739	1,447	1.201	n.s.	-1,222 - 4,699	31
Mt-St-Miche	l b	290,141	25,280	11.477	< 0.0001	238,437 - 341,845	31
Baie de	а	22,869	4,916	4.652	< 0.0001	12,814 - 32,924	31
Bourgneuf	b	592,921	85,862	6.905	< 0.0001	417,313 – 768,529	31

Appendix 6. Results of linear regressions on trends in the number of goose-days recorded at the six main wintering sites in France over the period 1982–2012.