

## Density dependent population limitation in dark-bellied brent geese *Branta b. bernicla*

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The dynamics were investigated of the world population of dark-bellied brent geese *Branta b. bernicla*, which winter in western Europe and reproduce on the Siberian tundra. The world population was fluctuating between approximately 220,000 and 315,000 individuals in the last decade of the 20<sup>th</sup> century, after recovering from an extremely low level of about 15,000 in 1955. Cyclical fluctuations are related to the population dynamics of lemmings on the Taymyr Peninsula in Siberia and have been present during the whole study period 1955–1998. We investigated whether, apart from these fluctuations, the population size will level off due to density dependence in reproduction or in survival. This being the case, we also aimed at predicting the approximate equilibrium population size.

Data are provided on the world population since 1955, counted every January, giving details on adult survival and reproduction. A simple discrete-time model was formulated where the reproductive season in Siberia and the winter season in Europe are treated separately allowing for density dependence during either season.

The nature of the density dependence for the model was estimated from the data. Density dependence was significant in reproduction, but not in adult survival. We argue that availability of suitable nesting habitat is an important factor influencing reproduction potential, but the possibility of other factors (e.g. competition for food during spring staging) cannot be excluded.

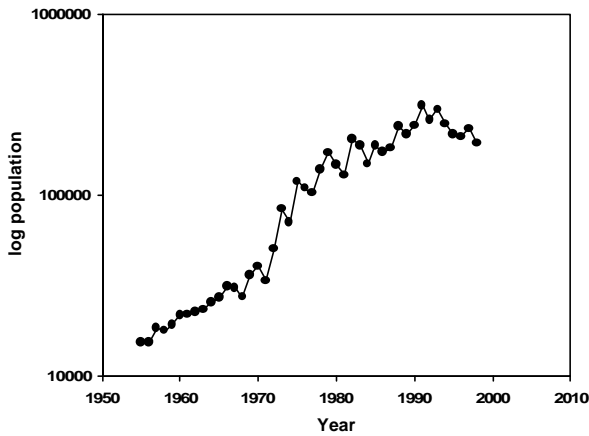
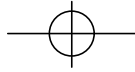
Analysis of the simple model yields a relation between the predicted equilibrium population size and a constant adult death rate estimated at 0.15, which corresponds to a predicted maximum population size of 286,000–332,000 at the time of the January census. Although it is tempting to use such a generic model as a basis to gauge effects of habitat loss on migrating bird species, great care should be taken in formulating rules-of-thumb.

Key words: density dependence, seasonal environment, *Branta b. bernicla*, population modelling, population limitation.

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Detailed data on the entire world population of dark-bellied brent geese *Branta b. bernicla*, which has shown a marked increase from 1955 to the early 1990s, offer an excellent opportunity to study the possible occurrence of density-dependent control in a natural population. A marked change in the rate of increase in

1972 (Fig. 1), which coincided with a hunting ban in Denmark, has often been interpreted as showing that hunting was the key factor reducing the dark-bellied brent goose population level (Prokosch 1984, Ebbinge 1985). Dark-bellied brent geese winter in western Europe, notably along the coasts of western France, Great



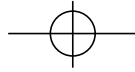
**Figure 1.** The world population of dark-bellied brent geese from 1955 to 1999 on a logarithmic scale using the data from Table 1.

Britain, and in the Dutch Wadden Sea. Range expansion, by moving further north along sea coasts of Britain and into grassland territory inland, has occurred to accommodate the growing numbers of wintering birds (Ebbinge et al. 1999). With this inland shift, the birds cause an increasing amount of agricultural damage, so that to assess the future impact of this population on agriculture, it is important to understand its dynamics.

The number of birds in the world population has risen from about 15,000 in 1955 to between 220,000 and 315,000 in the last decade of the 20<sup>th</sup> century. In earlier work, Prokosch (1984) and Ebbinge (1985) suggested that this increase already showed signs of levelling off in the early 1980s. The latter paper based its conclusion on the observed relation between the number of successful breeding pairs and the number of potential breeding pairs in consecutive years, using the data available at the time. However, a sound statistical analysis of the data was not made. Summers and Underhill (1991) later did undertake a statistical analysis and showed that the relation was not significantly different from a straight line, thus arguing against density dependence controlling the number of breeding pairs. At that time data were available only until 1985. Thirteen years of additional data are now available (until 1998) and we re-address the question whether, with more data, a different method and statistical analysis, the population development of dark-bellied brent geese shows signs of density dependence.

Our method involves a simple mathematical model. Animal populations living in a seasonal environment are usually characterised by a season where resources are plentiful, allowing the animals to reproduce, and a season where resources are scarce, during which the animals may experience great difficulty to survive. Though dark-bellied brent geese reduce the effects of seasonality to a considerable extent by their migratory behaviour, they reproduce only during the short summer in the high arctic, and merely try to survive during their 8-month stay along the coasts of western Europe. To our knowledge, Fretwell (1972) was the first to develop a simple population model like the one we use below, characterised by a season of reproduction, followed by a season with no reproduction and much mortality. From a graphical analysis he concluded that the dynamic behaviour of such models could be quite complex, depending on the form of the curves describing density dependence in reproduction or survival and their intersections. Here, we use a simple two-season model where the curves describing reproduction and survival in different seasons are estimated from the data set for the dark-bellied brent goose. The model allows for equilibrium states and remains simple enough to investigate the relationship between equilibrium population sizes and adult death rate.

The dynamics of this population are complicated by the fact that almost invariably a virtually complete breeding failure occurs every three years (Roselaar 1979, Summers & Underhill 1987, Greenwood 1987, Ebbinge 1989). These years follow upon peak years for populations of the lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus* in the breeding area of the geese, the Taimyr peninsula. It has been suggested that numbers of the key lemming-predator, the Arctic fox *Alopex lagopus*, increase markedly in lemming peak years and are forced to switch to alternative prey, notably bird eggs and young geese, in the year after the lemming population has collapsed (Summers & Underhill 1987, Spaans et al. 1998). The various explanations for the lemming cycle still lack critical empirical support (Krebs 1993, Stenseth 1999) but its indirect effect on the dynamics of brent geese and waders is substantial and highly predictable. These fluctuations with a more or less tri-annual cycle have been present throughout the whole time series and an underlying trend in growth rate can clearly be discerned. In this paper we analyse whether the overall population growth over a much lon-



**Table 1.** Demographic data for dark-bellied brent geese. Breeding success expressed as percentage of first-winter birds in the winter following year  $x$ . Population size (number) is estimated in January ( $x+1$ ). Average family size = number of offspring per family in winter. Lemming densities are scaled from 1 (virtually no lemmings) to 5 (extremely high densities), according to Kokorev & Kuksov (1990, unpubl. report). 1: no lemmings caught per 100 trap days. 2: <3 lemmings caught per 100 trap days. 3: 10 lemmings caught per 100 trap days. 4: 30 lemmings caught per 100 trap days. 5: 80 lemmings caught per 100 trap days in the best areas. Scores 4-5 are densities as occurring in lemming peak years.

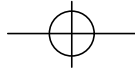
year	number	breeding success	adult survival	average family size	lemming-density Taimyr	year	number	breeding success	adult survival	average family size	lemming-density Taimyr
1955	15500	25,8		?		1977	103400	2,0	0,92	2,8	1
1956	15500	6,5	0,94	?		1978	140000	35,0	0,88	2,8	2
1957	18500	52,8	0,56	?		1979	173000	33,0	0,83	2,4	5
1958	18000	0,4	0,97	?		1980	149000	0,2	0,86	2,8	2
1959	19500	21,6	0,85	?		1981	130000	4,0	0,84	2,8	1
1960	21800	45,0	0,61	?	4	1982	206000	50,0	0,79	3,1	4
1961	22000	5,1	0,96	?	4	1983	190000	3,0	0,89	2,8	3
1962	22800	0,2	1,03	?	1	1984	150000	1,5	0,78	2,8	1
1963	23600	35,0	0,67	?	5	1985	190000	35,0	0,82	2,8	5
1964	25600	34,7	0,71	?	4	1986	174000	0,5	0,91	2,8	1
1965	27300	6,9	0,99	?	2	1987	183000	2,0	1,03	2,6	2
1966	31500	39,7	0,70	?	4	1988	242000	40,0	0,79	3,3	4
1967	31000	5,6	0,93	?	5	1989	219000	0,0	0,90	2,8	1
1968	27600	0,4	0,89	?	1	1990	245000	20,0	0,89	2,8	1
1969	36300	49,7	0,66	2,8	3	1991	314000	35,0	0,83	2,8	4
1970	40800	37,7	0,70	2,8	5	1992	263000	0,0	0,84	2,8	1
1971	34000	0,7	0,83	2,8	2	1993	300000	20,0	0,91	2,8	1
1972	51000	35,5	0,97	2,8	2	1994	250000	7,8	0,77	2,6	4
1973	84500	48,5	0,85	2,8	5	1995	218000	0,4	0,87	2,6	1
1974	71300	0,0	0,84	2,8	1	1996	212000	13,0	0,85	2,3	4
1975	119700	46,3	0,90	2,8	3	1997	235000	14,0	0,95	2,3	2
1976	109900	11,6	0,81	2,5	4	1998	195000	1,0	0,82	2,0	1

ger time span shows any signs of saturation to a constant level.

## Data analysis

The full data set on which our analysis is based is given in Table 1. Population censuses are gathered annually under the auspices of the Goose Specialist Group of Wetlands International (Ebbinge et al. 1999, Delany et al. 1999) in the main brent goose wintering area, which stretches from coastal western France in the southwest (44° northern latitude), along the British south and east coasts and south-western Netherlands, to the Dutch, German and Danish Wadden Sea in the north (56° northern latitude). The Goose Specialist Group also

gathers information on annual productivity by assessing the proportion of first-winter birds in late autumn and early winter. Flocks are scanned by telescope to assess the proportion of first-winter birds, which are readily distinguishable by their plumage from adults. This proportion of first-winter birds, multiplied by the total population census in mid-January, yields an estimate of the number of first-winter birds (Prokosch 1984, Ebbinge 1985, Lambeck 1990). Because first-winter birds tend to stay in family groups throughout the winter, family size can be estimated by counting the number of offspring that accompany an adult pair. Family size has been practically constant over the years (Table 1), showing that no reduction in breeding success per successful pair has taken place. Thus, if we are able to find a reduction in overall reproduction, this must mean



that an ever smaller proportion of pairs are able to reproduce at all.

We count years starting just after the breeding season and let  $k$  denote the year, such that  $k = 0, 1, \dots$ , where 0 corresponds to 1955. Annual survival rates in Table 1 were calculated as the number of adult birds in year  $k + 1$  divided by the total population size in year  $k$ . This requires the assumption that adult survival rate equals survival rate of first-winter birds, at least after January, when these first-winter birds are older than six months. First-winter birds that do not reach that age are not taken into account at all, because they do not live long enough to be included in the mid-January census (Ebbing et al. 1991). Overestimation of the total population size in one year leads to an underestimation of the death rate, and even impossible negative death rates such as in 1961 and 1986. However, this underestimation in one year is directly compensated for by an overestimation of the death rate in the next year. The population trend of dark-bellied brent geese from 1955 to 1999 is given in Figure 1.

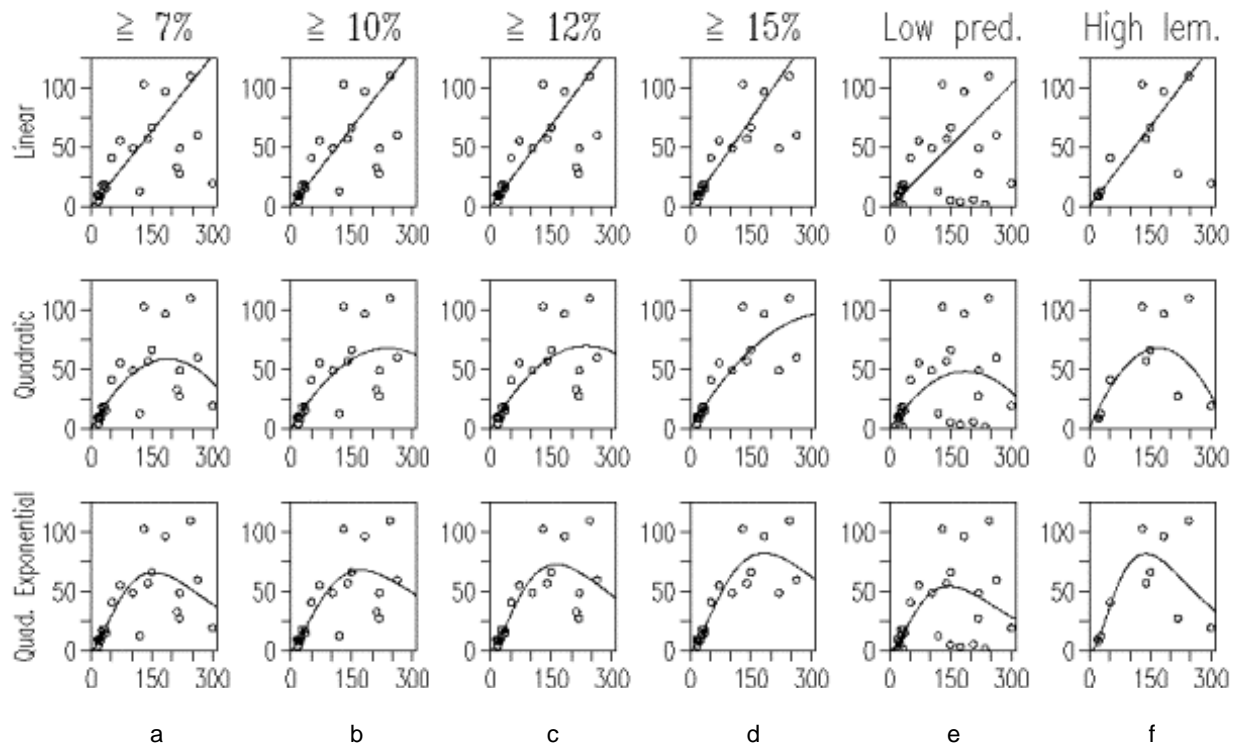
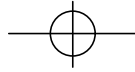
We differentiate between two seasons in the same year and express this in the notation. By  $N_{2k}$  we denote the population size of dark-bellied brent geese in August of year  $k$ , and ignore all young that are doomed to die before January. By  $N_{2k+1}$  we denote the population size in January, after the autumn migration. So, for example, year 0 has the population sizes  $N_0$  just after the breeding season in 1955 and a population size reduced by mortality  $N_1$  at the start of the wintering season in 1955–56). Likewise  $N_3$  denotes the population size just after the breeding season in year 1 (1956) and  $N_4$  the winter population in 1956–57, etc. The data points are interpreted as values for odd indices of the discrete variable  $N$  (i.e. as estimates for consecutive values of  $N_{2k+1}$ ,  $k = 0, 1, \dots$ ).

Counts were analysed by means of a log-linear model with overdispersion (McCullagh & Nelder 1989). The overdispersion parameter was estimated by means of Pearson's statistic. Deviance differences, adjusted for overdispersion, were employed for significance testing.

We did not find a significant density dependence in survival during the non-reproductive season, i.e. the number surviving was found to be directly proportional to the population size. In a log-linear model with only a constant and an offset for  $\log(\text{population size})$ , the constant represents the proportionality parameter. We indicate this parameter by  $d$ , the fraction of the popula-

tion that does not survive the non-reproductive season (which includes mortality during the migration from Siberia to Europe). The estimate of  $d$  over the 1955–1997 period equals 0.15 with 95 % confidence interval (0.13, 0.17). The years 1961 and 1986 had to be excluded from the analysis because they showed 'negative mortality'. Though theoretically this leads to an overestimation of the mean mortality rate ( $d$ ), the amount of this overestimation is negligible. We tested this by setting the mortality rate in 1961 and 1986 at 0 %, and 'adding' the 'negative mortality' rates to the subsequent years 1962 and 1987. This led to a value for  $d = 0.14$  (0.12–0.16). Several alternative ways of dealing with the 'negative' years gave the same result to two decimal places. An independent estimate for the adult annual death rate based on re-sightings of individual colour-ringed brent geese over the period 1973–1989 using a Jolly-Seber approach yielded the value of 0.16 (Ebbing 1992), which falls within the confidence interval above. We also tested whether survival differed in the period before and after the hunting ban in Denmark in 1972. This resulted in the estimates  $d = 0.18$  for the period 1955–1972 and  $d = 0.15$  for 1973–1997. The variance for 1955–1972 is seven times greater than the variance for 1973–1997. The two estimates are not significantly different.

For the analysis of the data on reproduction a number of choices had to be made, because we were interested only in establishing whether the trend in population development shows density dependence. When Ebbing (1985) analysed the brent goose data set for the period 1960–1984 there was a clear dichotomy in 'good' and 'bad' years. There were either years with at least 33 % first-winter birds, averaging 40.8 %, or years with less than 12 % first-winter birds, averaging 3.2 %. There were no years with values between 12 % and 33 %. More recently this dichotomy has been less clear, because more intermediate values have occurred, e.g. 20 % in 1990 and 1993, 13 % in 1996 and 14 % in 1997, at the expense of years with high productivity. This in itself can be seen as an indication for density dependence starting to operate. However, we prefer an objective approach, by defining criteria to exclude those years when breeding success was low, because of other reasons than density dependence. In other words, we wish to filter out the years when, on an almost regular basis, complete to almost complete breeding failure occurred. We took two approaches.



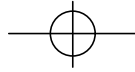
**Figure 2.** Plot of linear, quadratic and a quadratic  $\times$  exponential function  $N_f(N)$  describing the number of first-winter birds as a function of total population size when only the years are considered in which (a–d) the proportion of first-winter birds is larger than 7 %, 10 %, 12 % and 15 %, respectively; (e) when years with an inferred high predation pressure (see text) are excluded; and (f) when only years when inferred low predator numbers coincide with a high abundance of lemmings are included.

Because breeding failure is associated with years when predation pressure is high as a result of the three-year lemming cycle, our first approach was to exclude these 'high predation years' from the analysis. For most years we do not have direct observations on predation pressure, which has to be inferred from the available data on lemming density (Table 1). High predation pressure on the geese by arctic foxes and snowy owls *Nyctaea scandiaca* is expected when predator abundance has increased as the result of a lemming peak in the previous year, and when this lemming peak year is followed by a crash in lemming numbers. We would thus exclude years when lemming abundance is scored as 1–2 immediately following upon years with a lemming score of 4–5 (Fig. 2e). A more stringent criterion is to include in the analysis only those years when predator levels are supposed to be low, i.e. when lemming abundance is high (scale 4–5) immediately following a lemming low (1–2; Fig. 2f).

Because we do not know exactly what causes these

perturbations (or indeed the precise lemming cycle), we also adopted a second approach by including only years in which breeding success exceeded a predetermined percentage. We tested several cut-off points: 7 %, 10 %, 12 % and 15 %. In Figure 2a–d we show estimates for the dependence of the number of first-winter birds on the total winter population size for these cut-off points and lemming years.

For the reproduction counts a generalised linear model with both Poisson and gamma distributions was employed. Plots of standardised residuals against fitted values were in favour of the gamma distribution and we therefore chose the gamma distribution for the analysis. We tested a linear relationship through the origin (i.e. no density dependence) against a quadratic relationship, and both of these against a quadratic multiplied by a negative exponential. The differences between these nested models were tested by approximated F-tests. The P-values for these comparisons are given in Table 2. One can see that using supposedly high predator levels



**Table 2.** P-values for comparison of (1) linear, (2) quadratic and (3) quadratic times exponential for four values of the cut-off point for reproduction and for the cases in which predator peak years are ignored, and when only lemming peak years coinciding with low predator levels are included. P-values less than 0.05 are considered significant.

Including years with	1–2	2–3	1–3
>7 % first-winter birds	0.005	0.153	0.008
>10 % first-winter birds	0.044	0.214	0.063
>12 % first-winter birds	0.028	0.046	0.012
>15 % first-winter birds	0.156	0.024	0.027
predator levels not high	0.072	0.406	0.144
low predator + high lemming	0.035	0.167	0.046

as a selection criterion for excluding years of poor reproduction does not give any insight. There are apparently too many years that also result in a low breeding success for other reasons, e.g. adverse headwinds during spring migration (Ebbinge 1989, Ebbinge 2000). However, using the stricter criterion of including only peak lemming years that coincided with supposedly low predator levels (inferred by also having had low lemming levels the previous year) does yield a significant density dependent effect (Table 2, columns 1–2 and 1–3).

We conclude that there is clear evidence for density dependence. There is also clear evidence that reproduction decreases with increasing population size. For cut-off points at 12 % and 15 % the declining exponential function performed better than the declining quadratic. This is not true, however, for all cut-off points and therefore both the quadratic and the exponential model are used in the subsequent analysis.

Therefore, we denote the estimated curves by  $Nf_q(N)$  and  $Nf_e(N)$  for the quadratic and exponential function as, respectively

$$Nf_q(N) = aN + bN^2$$

$$Nf_e(N) = (cN + dN^2)e^{-kN}$$

and estimate parameters for a cut-off at 12 %. These are:  $a = 0.5897$  (s.e. 0.0783),  $b = -0.000001244$  (s.e. 0.000000443),  $c = 0.221$  (s.e. 0.199),  $d = 0.00001767$  (s.e. 0.00000872), and  $k = 0.00001187$  (s.e. 0.00000221).

## The model and its analysis

We use a discrete time mathematical model that divides the year into two seasons: a reproductive and a non-reproductive season (akin to models in Fretwell 1972 and Goss-Custard & Sutherland 1997). We assume that in the reproductive season there is no mortality. We had to simplify the real world in order to be able to use the existing population data, which are based on annual censuses in mid-January (see above and Discussion). In the model, therefore, the population size just after reproduction in August is estimated by including only those newly born geese that survive to January. Thus, part of the mortality of young-of-the-year is included in the estimated reproduction. Our reproductive season therefore runs from January to August, and the non-reproductive season from August till January. In the model all mortality occurs only during this non-reproductive season, which includes the period of autumn migration and coincides with the hunting season.

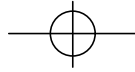
We assume that the number of first-winter birds in year  $k$ , is given by

$$N_{2k-1}f(N_{2k-1})$$

where  $f$  is a function that describes the possible density dependence in reproductive success (i.e. any density dependence is assumed to arise from the numbers of birds present in the breeding season). Similarly, we assume that the number of birds that do not survive the autumn season in year  $k$  is given by

$$N_{2k}h(N_{2k})$$

where  $h(N_{2k})$  is the fraction of birds that does not sur-



vive the non-reproductive season, which could possibly also be density dependent.

Our basic model becomes

$$N_{2k} = N_{2k-1}(1 + f(N_{2k-1}))$$

$$N_{2k+1} = N_{2k}(1 - h(N_{2k})).$$

From the data analysis we found that  $h(N_{2k}) = \mathbf{d}$  for all  $k$ , and for both choices for the reproductive function given in the previous section. The model with the quadratic reproduction function therefore becomes

$$N_{2k} = N_{2k-1}(1 + a + bN_{2k-1})$$

$$N_{2k+1} = N_{2k}(1 - \mathbf{d})$$

with regression parameters  $a$  and  $b$  given in the previous section, and with the current per capita death rate  $\mathbf{d} = 0.15$ . In the model with the exponential reproduction function the first equation is replaced by

$$N_{2k} = N_{2k-1}(1 + (c + dN_{2k-1})e^{-kN_{2k-1}})$$

with  $c$ ,  $d$ , and  $k$  as above.

The technical details of the analysis of the dynamic behaviour of the model are given in the Appendix, where we also show that the behaviour is generic for a wider class of functions  $f$  with similar properties to the forms chosen for best fit in Figure 2. The model allows one or more steady states, depending on reproduction function and the value of  $\mathbf{d}$ . The current best estimate for  $\mathbf{d} = 0.15$  gives a steady state population size of 332,000 birds in January, using the quadratic reproduction function (see Appendix).

If we use the exponential function for reproduction the situation is more complicated. Because of the exponential term more steady states can exist than in the quadratic case (see Appendix). We find for  $\mathbf{d} = 0.15$  that the exponential model predicts a steady state population size of 286,000 birds in January. Because, given our assumptions, the model overestimates various factors (e.g. survival, age at first reproduction), the predicted numbers are probably an overestimate of the maximum population size.

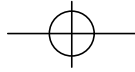
In the model, birds are assumed to reproduce starting in the first breeding season after they were born, whereas in reality brent geese are only capable of reproducing from their second breeding season onwards. The data on the number of first-winter birds in Table 1 have

not been corrected for non-breeding one-year-olds (yearlings) but have been calculated, as is usual, using the total population count and the proportion of first-winter birds in the wintering flocks. A correction for non-breeding yearlings was proposed by Ebbinge (1989), since dark-bellied brent geese do not breed successfully when one year old (B. Ganter in prep.) and the number of yearlings varies strongly between years. However, as most brent geese are born in peak lemming years, which are usually followed by years without any breeding success, the first opportunity to nest does usually not arise before brent geese are at least in their third year. In our 44-year data-set there are only eight exceptions to this rule: 1960, 1964, 1970, 1973, 1976, 1979, 1991 and 1997. For the sake of simplicity, therefore, we do not differentiate between age classes in the model.

## Discussion

### Density dependence

Density dependence is a widely accepted concept in population ecology (e.g. Sinclair 1989), but data at the level of an entire (closed) population are extremely rare in birds (Newton 1998). Such data exist for bird populations confined to a few small islands, like the Seychelles Warbler *Acrocephalus sechellensis* (Komdeur 1994) and migratory waders and waterfowl which concentrate, often in large numbers, in a few local areas during the non-breeding season. Owen (1984) emphasised density-dependent depression of recruitment rate in the Svalbard population of barnacle geese *Branta leucopsis* as the key factor setting a limit on future population growth. Yet further growth was observed in later years due to the establishment of new colonies, that each went through a cycle of increasing productivity followed by a decline as carrying capacity was reached and the inhabitants became older (Black 1998). Larsson & Forslund (1994; see also Van der Jeugd & Larsson 1998) convincingly demonstrated density dependent effects on reproduction in recently established breeding colonies of barnacle geese on Gotland, Sweden. In dark-bellied brent geese local density-dependent effects on spring staging grounds have been demonstrated (Ebbinge 1992, Ganter & Ebbinge 1997). However, this seemed to have consequences only for the spatial distribution of the geese in spring, and not for the size of



the world population as a whole, because goose numbers still increased on the more recently colonised inland areas, whereas numbers levelled off on the salt marshes that traditionally had been used by brent for many decades.

The present analysis shows that there are now also significant repercussions on the world population level of brent geese, particularly through a reduction in the rate of reproduction. Increasing competition on the spring staging sites in the Wadden Sea or in the White Sea could be a factor responsible for this decline in reproduction. It is well known that the geese must accumulate sufficient body reserves to complete their migration within a limited time and arrive with sufficient reserves to breed successfully (Ebbinge & Spaans 1995). However, up to the year 2000 there has been no detectable decline in spring departure body-mass of birds caught at the end of May in the Wadden Sea (Ebbinge unpubl.).

#### Effects on the breeding grounds

Several studies on the breeding grounds, from 1990 to 1995, showed that there are different nesting options open to brent geese: on small islands in between gull colonies (Spaans et al. 1993, Ebbinge 2000), on very remote offshore islands, within nesting territories of snowy owls and, although in much lower numbers, scattered over low-lying delta areas (Ebbinge et al. 1999). In general these are areas that are – at least temporarily – inaccessible to Arctic foxes, either because of surrounding water after the ice has melted, or because of fierce defence by snowy owls. The first option (gull colonies) was successfully used during nesting in five out of six years in the Pyasina delta (Spaans et al. 1998), and is probably the most predictable type of nesting habitat for brent. During the same six years two lemming peak years occurred (1991 and 1994) and only in such years were brent geese observed to nest in association with snowy owls elsewhere on the Taymyr Peninsula (Underhill et al. 1993, Summers et al. 1994). We can only speculate about where brent geese mostly nested when the population was still in the increasing phase, but the limited number of gull islands seem to be the most likely candidates. Though documented for black brant *B. bernicla nigricans* on Wrangel Island in the far east of Siberia, nesting within territories of snowy owls is a new phenomenon for dark-bellied brent

on the Taymyr Peninsula. The fact that this occurs at the present population level is probably an indication that nesting habitat is now really a limiting factor. We interpret the observed decline in breeding success mainly as a result of limited safe nesting possibilities. Even within the gull colonies, though still relatively safe during the egg-stage, successful reproduction is extremely difficult for brent geese at the current nesting densities. Only a few brent geese remain on the islands to raise their goslings, and the majority leave these islands with their goslings in the first week after hatching. Despite this, a high proportion of the newly hatched goslings is still taken by gulls (Ebbinge 2000). Therefore we consider crowding on the limited safe nesting sites in Siberia a much more likely explanation for the observed decline in productivity, than competition for food on the spring staging areas. Since there are indications that the total number of juvenile birds is now declining, however, this cannot be the only explanation. If reaching the limitations of the breeding territory were the only factor operating we would expect the yearly total of juveniles to saturate, rather than decline.

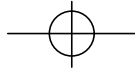
The fact that the mean family size has remained virtually constant at about 2.7 offspring per pair (over a period of 25 years in which the population size increased by sevenfold) also indicates that lack of suitable nesting sites is probably the main limiting factor. Those pairs that still have access to those sites are still as productive as at lower population levels.

Adverse headwinds in the Baltic during spring migration that have an impact on reproduction (Ebbinge 1989) cannot explain the observed reduction in breeding success, because in the period 1970 to 1996 adverse wind conditions in spring occurred only in 1971, 1976, 1984, 1987 and 1992. In all other seasons wind conditions were favourable for spring migration. There is thus no discernable trend in the frequency of these adverse conditions.

#### Hunting

Hunting is usually mentioned as the key factor that reduced brent goose numbers so dramatically in the 20<sup>th</sup> century (Salomonsen 1958, Prokosch 1984, Ebbinge 1991). In our analysis survival prior to the Danish hunting ban in 1972 is also on average 3 % (= 0.18–0.15) lower than later on, but this difference is not significant. From the published Danish game statistics (Strand-





gaard & Asferg 1980) one can work out that in the period 1955–1971 on average 10 % of the total population was shot annually in Denmark alone. There are large differences between years (varying from 4 % to 18 %) with a particularly high hunting pressure after good breeding seasons with many young birds. Though the estimated 3 % difference is in the right direction, the lack of significance shows that the available census data do not allow very precise estimates. The variance in the data before the hunting ban is seven times greater than the variance after the ban. This does not necessarily mean that the hunting ban in 1972 in Denmark was not the key factor allowing the dark-bellied brent goose population in western Europe to recover. Theoretically one could expect that increased population levels would also lead to increased mortality through increased competition. Among Svalbard barnacle geese mortality during autumn migration increased from 2 % to 8 % when the overall population size increased from 3,000 to 11,000 (Owen & Black 1991). In our case, however, this is probably impossible to ascertain with the available data, because of the simultaneous reduction in hunting pressure. This will have lowered the overall mortality rate, thus masking any increase in natural mortality.

#### Predicting the effects of habitat loss

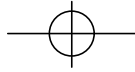
It is not the aim of this paper to study the effects of habitat loss for migratory populations as did Fretwell (1972) and Sutherland (1996), based on intersections of curves representing the relationships between population density and, respectively, mortality and reproduction. In the analyses presented in Sutherland (1996) and Goss-Custard & Sutherland (1997), only the steady state population density changed as a result of habitat loss. The reason for this is that the form of the two curves leads to a unique steady state. This corresponds in our case to the quadratic reproduction function, for which a similar intersection study (see Appendix) would result in the intersection of two straight lines. Theoretically, of course, the dynamics can become more complicated if the curves behave differently so as to give rise to multiple steady states. Biologically speaking our model with the exponential reproduction function suggests (see Appendix) that one has to be careful that  $d$  is not increased significantly from its present value (e.g. due to renewed hunting). At some point one enters a region where multiple steady states can exist and the following

phenomenon (hysteresis) could occur: in theory the population might collapse completely over a short time period, after which re-establishment is unlikely even if the unfavourable conditions are improved. These more complicated situations can indeed occur in real systems of migrating birds, as when the curves are estimated from our data (see e.g. Sinclair 1989 for a broader ecological context). Consequently the effects of habitat loss can be more dramatic than a gradual shift in expected steady state densities to adapt to new conditions. This makes clear that one has to be careful when deriving rules-of-thumb from postulated curves that do not fully reflect realistic dynamics, as exemplified by the brent geese data. This becomes particularly relevant if one realises that the brent geese data are among the longer and more detailed time series available for any species.

#### Practical implications

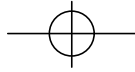
The present conclusion that the world population of dark-bellied brent geese is likely to remain below about 330,000 individuals (and probably below 300,000) has great implications for the management of this subspecies. If correct, it would imply that governments and nature protection societies can now plan for sufficient nature reserves to accommodate this population of high arctic migrants, and that farmers do not have to fear for a further substantial increase in this subspecies and increasing economic loss.

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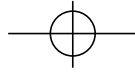
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## Appendix

### Analysis of the models

We first analyse the more difficult case, i.e. the model with exponential reproduction function (repeated for convenience from the main text).

$$N_{2k} = N_{2k-1} (1 + (c + dN_{2k-1})e^{-kN_{2k-1}})$$

$$N_{2k+1} = N_{2k} (1 - \mathbf{d})$$

Since the time-unit of one year has been divided into two half-year seasons, we look for steady state pairs  $(N, M)$  such that

$$N = M (1 + (c + dM)e^{-kM})$$

$$M = N (1 - \mathbf{d})$$

i.e. a steady state is a pair  $(N, M)$  such that in each consecutive year there will be  $N$  birds in August and  $M$  birds at the time of the winter counts in January. Since we only observe the population in January we are interested in the value of  $M$ . One can immediately see from the second equation that  $M = N(1 - \mathbf{d})$ . We can then find  $N$  by solving

$$N = N(1 - \mathbf{d}) + (c(1 - \mathbf{d})N + d(1 - \mathbf{d})^2 N^2)e^{-k(1 - \mathbf{d})N}.$$

This leads to  $N = 0$ , or, for positive  $N$ , the possible solution of

$$\frac{\mathbf{d}}{1 - \mathbf{d}} = (c + d(1 - \mathbf{d})N)e^{-kN(1 - \mathbf{d})}.$$

We cannot solve the latter equality for  $N$  analytically, but we can analyse it graphically by plotting the right-hand side, which we denote by  $g(N) = f(N(1 - \mathbf{d}))$ , and the left-hand side, a horizontal line, in one graph as functions of  $N$  (see Figure 3a–c). This amounts to plotting re-scaled per capita growth and re-scaled per capita death in one graph. Intersection points are values of population size where, when multiplied by population size, increase over one year equals decrease over one year, i.e. values of  $N > 0$  for which the system is in equilibrium. This is also done in Fretwell (1972) and Goss-Custard & Sutherland (1997). As Fretwell points out,

one has to be careful in doing this since the fact that growth and decline happen in different seasons in the model makes it impossible simply to plot the functions  $f$  and  $h$  directly: the arguments of  $Nf(N)$  and  $Nh(N)$  are different. The re-scaling takes this into account for  $f$  (the re-scaling of  $h$  in our case is not strictly necessary since it is a constant function).

The intersection points  $N^*$  correspond to positive steady state pairs  $(N^*, N^*(1 - \mathbf{d}))$  of our system. We study the various possibilities for intersections of the curves as we vary the only parameter with a clear biological interpretation, i.e.  $\mathbf{d}$ , the per capita probability of not surviving the winter season. The other parameters  $(c, d, k)$  are set to the values estimated for them from the reproduction data. One can numerically calculate the steady state value for  $N$  as a function of the parameter  $\mathbf{d}$ . There are three possibilities for increasing values of  $\mathbf{d}$  (and one degenerate case between the first and the second), see Figure 3a–c: one positive steady state (stable), two positive steady states (one unstable, one stable), or no positive steady state (and zero is the only equilibrium of the system). For  $\mathbf{d} = 0.15$  and the parameters relevant for the cut-off point of 12 % one finds a unique stable positive steady state  $N^* \approx 336,000$ . This leads to a steady state size at the January of  $M^* \approx 286,000$  birds.

One can compute in a straightforward way, by looking at the maximum of  $g$ , the values for  $\mathbf{d}$  where two steady states exist, and the value of  $\mathbf{d}$  above which no positive steady state exists. Because the precise form of the reproduction function is unknown, these details have little merit and we do not carry out this calculation.

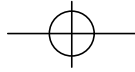
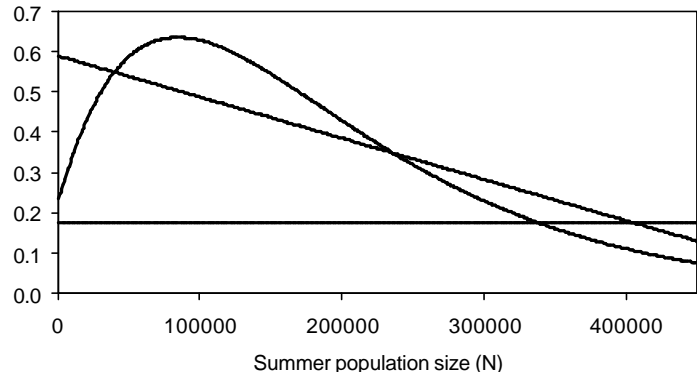
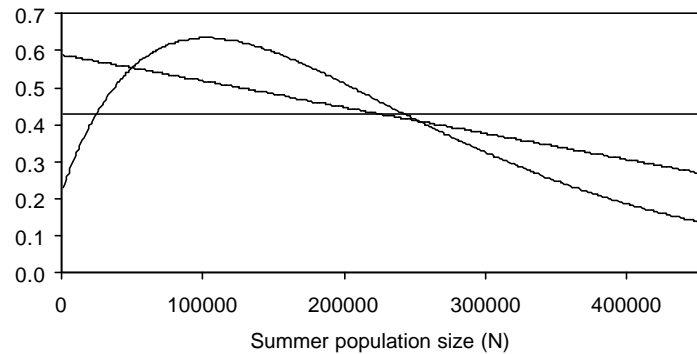
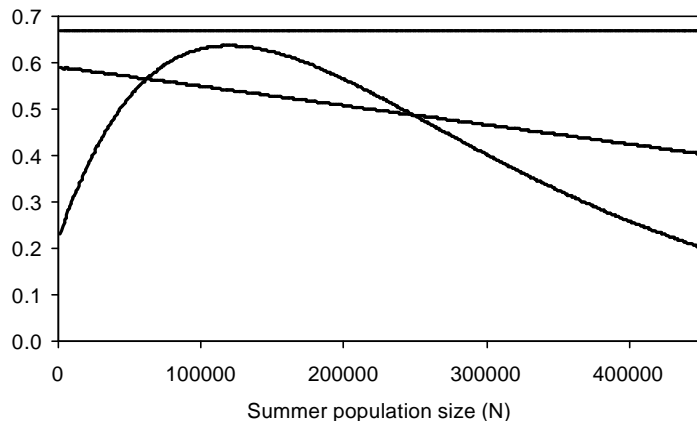
For the quadratic reproduction function we obtain (see Figure 3a) with similar reasoning that either  $N = 0$  or  $N$  is the solution of

$$\frac{\mathbf{d}}{1 - \mathbf{d}} = a + bN$$

We then find a unique positive steady state

$$N^* = \frac{\mathbf{d}}{(1 - \mathbf{d})^2 b} - \frac{a}{(1 - \mathbf{d})b},$$

which exists for all  $\mathbf{d} < a/(1 + a) = 0.37$ . The parameter values corresponding to the cut-off point of 12 % and  $\mathbf{d} = 0.15$  yield  $N^* \approx 390,000$ . This results in a steady state value  $M^* \approx 332,000$  birds at the January census.

Figure 3a,  $d = 0.15$ Figure 3b,  $d = 0.30$ Figure 3c,  $d = 0.40$ 

**Figure 3.** Plot of constant scaled mortality  $d/(1-d)$  (horizontal line) and the scaled per capita reproduction functions  $f(N(1-d))$  against total population size  $N$  (in August). Intersections of the horizontal line and each of the two curves correspond to positive steady states of the corresponding models. (a)–(c) are for  $d = 0.15, 0.30$  and  $0.40$  respectively. The scaled per capita quadratic reproduction function is a straight line with negative slope, giving one or no intersection with the scaled mortality. The re-scaled per capita exponential reproduction function is the unimodal curve with one, two or no intersections.

In the case of the quadratic reproduction function we therefore find a unique steady state, whereas the exponential reproduction function leads to more complicated dynamic behaviour. These findings are rather robust to the precise choice of the two functions in the sense that functions having the same qualitative

features as the ones chosen will give the same generic picture. For example, in the case of the exponential reproduction function, behaviour will be the same as long as the curve  $Nf(N)$  is S-shaped for small values of  $N$  and is unimodal, or monotonically increasing to a level of saturation.