A MATTER OF EATING OR BEING EATEN? THE BREEDING PERFORMANCE OF ARCTIC GESE AND ITS IMPLICATIONS FOR WADERS

W. F. de Boer & R. H. Drent

INTRODUCTION

Breeding success of the European Black-bellied Brent Goose Branta bernicla bernicla, generally expressed as the percentage of young in the total population, has been assessed from counts in the wintering area of NW Europe since 1954 (Ogilvie & St Joseph 1976). These data show that breeding performance is highly variable, including both boom years (between 20% and young) and bust years (below 5% young) in an irregular pattern. The Brent population is known to nest in the Taimyr peninsula on the arctic shores of Siberia. Next to nothing is known from direct observation in the breeding area but there has been speculation about the cause of the wide fluctuations in breeding performance. Roselaar (1979) was the first to point out that variable breeding performance of the Dark-bellied Brent and the fluctuating population of Lemmings in the arctic. He reasoned that some overall factor must be involved since there was a correlation between breeding performance of the Brent and that of the Curlew Sandpiper Calidris ferruginea a species known to nest in the same area. Summers (Summers 1986, Summers & Underhill 1987) has further elaborated the hypothesis and suggested that the fluctuating breeding performance of the Dark-bellied Brent was caused by an annually varying predation rate by Arctic Foxes Alopec lagopus. Lemmings are a favourite prey of the foxes. In years with a small Lemming population foxes will necessarily have to change their diet, switching to the eggs of the Brent Geese. This prey-switching-hypothesis should explain the positive correlation found between the breeding performance of the Brent Goose and the population size of the Lemming each year on the Taimyr peninsula. Although Summers & Underhill had no information on the supposed fluctuating predation rate of the Arctic Foxes on Brent eggs, the correlation between the breeding success and the Lemming population was striking and has been the source of much debate (see e.g. Boyd 1987, Dhondt 1987, Ebbinge 1987, Owen 1987).

There are a number of difficulties in accepting the evidence of correlations in validating the prey-switching hypothesis. These will be discussed more fully in the final section of this paper. It is important to bear in mind that the overall success of breeding is likely to be influenced by a series of successive factors rather than being determined by some single overriding event. Our approach in widening the field of search for casual factors influencing the breeding success of arctic goose populations has been to investigate the fluctuation of the European Dark-bellied Brent in more detail. In this paper we examine the extent to which the breeding performances of other arctic-breeding geese show similarity with each other over the years. If for example the breeding performance of the Pale-bellied Brent on Svalbard (where there are no Lemmings) is positively correlated with the Taimyr-breeding Brent then it is doubtful that the prey-switching-hypothesis can be correct in explaining the fluctuating breeding performance of the Taimyr Brent. Other similar factors such as climate, circumstances at the wintering areas, body condition and body plumage of the geese involved in the population dynamic of arctic-breeding waders (Eds.)

METHODS

Species and sub-populations

The species covered in the analyses are listed in Table 1. For the distinction of the different populations and their breeding areas, wintering areas and flyways we refer to Ogilvie (1978), Cramp (1977) and Bellrose (1980).

Breeding performance data

Breeding performance measured as the percentage of young in the population, is determined on the wintering grounds after the geese have returned from their breeding areas. Young geese can at this time of the year easily be distinguished in the flock by their different plumage.

The main sources of data on the breeding performance of the different goose populations were Trooßwijk (1974), Ganzenwerksgroep
Table 1. Species, names, populations and total years of available breeding performance data of the Palearctic and Nearctic goose populations covered by the analyses in this paper.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>POPULATION</th>
<th>YEARS OF DATA</th>
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<tbody>
<tr>
<td><strong>Palearctic populations</strong></td>
<td></td>
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<tr>
<td>Greylag Goose</td>
<td>Anser anser</td>
<td>Iceland 27</td>
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<tr>
<td>Bean Goose</td>
<td>Anser f. fabalis</td>
<td>North-Russia 20</td>
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<tr>
<td>White-fronted Goose</td>
<td>Anser albifrons</td>
<td>North-Russia 22</td>
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<tr>
<td>Pink-footed Goose</td>
<td>Anser brachyrhynchus</td>
<td>Baltic 33</td>
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<tr>
<td>Barnacle Goose</td>
<td>Branta leucopsis</td>
<td>Greenland 18</td>
</tr>
<tr>
<td>Dark-bellied Brent</td>
<td>Branta bernicla bernicla</td>
<td>Svalbard 5</td>
</tr>
<tr>
<td>Pale-bellied Brent</td>
<td>Branta bernicla hrota</td>
<td>Iceland 32</td>
</tr>
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<tr>
<td><strong>Nearctic populations</strong></td>
<td></td>
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<tr>
<td>White-fronted Goose</td>
<td>Anser albifrons</td>
<td>Pacific flyway 23</td>
</tr>
<tr>
<td>Ross’s Goose</td>
<td>Anser rossii</td>
<td>Queen Maud Bay 24</td>
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<tr>
<td>Lesser Snow Goose</td>
<td>Anser caerulescens caerulescens</td>
<td>Central flyway 31</td>
</tr>
<tr>
<td>Greater Snow Goose</td>
<td>Anser caerulescens atlanticus</td>
<td>Pacific flyway 31</td>
</tr>
<tr>
<td>Black Brant</td>
<td>Branta bernicla nigricans</td>
<td>Bylot Island 31</td>
</tr>
<tr>
<td>Atlantic Brant</td>
<td>Branta bernicla hrota</td>
<td>Pacific flyway 24</td>
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We used data only from between 1954 and 1986. At times several authors have reported different data for the breeding performance of the same population for the same year. In these cases we have used the average of the data available.

The two sub-populations of Bean Goose Anser fabalis (A. f. fabalis and A. f. rossicus) are difficult to recognize in the field. For the breeding performance data of these two populations we used catch-data from the Nature Research Institute (Arnhem) for which the identity and the age of the geese in the sample is known.

Statistical tests

The methods we used were: Pearson product-moment correlation coefficient (r), Spearman rank correlation coefficient (Sr), percentage of explained variance (R²), X² analyses and t-tests.

RESULTS

The breeding performance records of the 21 goose populations concerned vary in length from 5 to 33 years (Table 1). The 21 goose populations give us 210 possible comparisons between pairs of populations in bivariate correlations. In 58 cases of the 210 combinations Pearson product moment correlation coefficient was significantly different from zero. Only one correlation had a negative coefficient, the other 57 had a positive coefficient. The geographical distribution of the positive correlations is shown in a polar projection (Figure 1) by connecting the populations concerned by lines.

It is clear from Figure 1 that Nearctic goose populations are much more strongly linked with each other with respect to breeding performance than are populations monitored on the European wintering grounds: 64% of the combinations in North America are positively correlated, compared with only 23% of the combinations in Europe.

A total of 5% (11) of the 210 combinations would be correlated on the basis of chance. The 58 combinations significant at the 5% level are more than expected at random (X²=226.19, d.f.=1, p<0.001). Moreover, the 57 positive correlations are significantly more than the only negative one (X²=54.07, d.f.=1, p<0.001).

Figure 2 shows that the breeding performances of Greylag and Pink-footed Goose breeding in Iceland are particularly strongly correlated, with 68% of variance explained over 27 years of data. In some other combinations of species, for example the Taimyr-Brent and the Baltic White-fronted Goose, the breeding performance is less strongly correlated. We could find no evidence that the strength of the relationship between two breeding populations is influenced by the distance between their breeding grounds (unpublished data).

One explanation for the many positive correlations of breeding performance is the possibility that all goose populations are increasing and that their breeding performance is decreasing because of a density-dependant factor. This has been proposed for the Pink-footed Goose in Iceland (Ogilvie 1982b, Ebbinge 1985) and for the Barnacle Goose on Svalbard (Owen 1984). However, the breeding performance of only four populations has declined during the years for which data are available. These are: Greylag Goose in Iceland (r=-0.578, N=27, p<0.005); Pink-footed Goose in...
Figure 1. Correlations in the breeding performance of arctic goose populations. In this polar projection, populations between which breeding performance is significantly correlated (p<0.05) are connected by lines. Thick lines represent a correlation coefficient larger than 0.5, thin lines a coefficient smaller than 0.5 (for breeding areas and subpopulations see Cramp (1977) and Bellrose (1980)).

Figure 2. Relationships between the breeding performance of pairs of selected arctic goose populations in the same year. Each point is the breeding performance of the two populations in one year. Characteristics of the linear regression are given in the headings (all are significant at p<0.05).

We have found a surprisingly large number of positive correlations in breeding performance between several dispersed breeding goose populations. The breeding success of the European Dark-bellied Brent Goose is significantly, and positively correlated with the breeding success of five other goose populations. The percentage of explained variance by the linear regression is, however, lower than 25% in all of the five cases. No correlation was found between the Taimyr-Brent and other Branta subspecies. The breeding success of the Taimyr Brent is positively correlated with that of its closest neighbours, the Barnacle and White-fronted Goose in northern Russia. Our results do not exclude the lemming hypothesis as the major explanation for the fluctuating breeding performance of the European Dark-bellied Brent. It is clear, however, that the breeding performance of the Taimyr Brent is not totally independent of the breeding performance of other goose populations. The 57 positively correlated goose combinations pose a problem in determining the cause of this phenomenon. We discuss this below.

DISCUSSION

Is there a single factor that can explain why the breeding performance of so many goose populations all over the world are positively correlated?

The most important within-season variable that has been shown to be responsible for differences in breeding performance is the body
condition of geese (Newton 1977, Ankney & MacInnes 1982, Ebbinge et al. 1982, Teunissen et al. 1983, Drent & Prins 1987, Ebbinge 1987, Teunissen et al. 1987). (Body condition here is the state of the reserves of fat, protein, calcium, phosphorus, etc.) Female geese arriving in their breeding area with a low body mass are, on average, less successful in breeding than heavier geese. Feeding conditions at the wintering, staging and breeding areas largely dictate changes in body condition. Differences in foraging behaviour and status or rank are also responsible for changes in foraging efficiency and therefore in condition. Weather, especially temperature and rainfall, influences the quality and the amount of vegetation available on offer (Cabot & West 1973, Nilsson 1979, Davies & Cooke 1983). Condition upon arrival on the breeding grounds is also partly dependent on temperature and the direction and the speed of wind while migrating (Ebbinge et al. 1982).

Once birds are on their breeding area, the most sensitive to the eventual breeding success is probably the date at which egg laying starts. A relationship between clutch size and the date on which the first egg is laid has been found for almost every goose species (Lemieux 1959, Cooch 1961, Barry 1962, Cooper 1978, Ryder 1972, Findlay & Cooke 1982, Davies & Cooke 1983, Ely & Raveling 1984, Prop et al. 1984). This clutch initiation date is dependent partly on the timing of arrival but in many extensive snow-cover precludes nesting immediately after arrival. Hence snow-cover and date of snow-melt have a large impact on clutch initiation and indirectly on condition, clutch size and breeding performance. The condition and weight of the female geese decreases when snow-cover delays clutch initiation and at the same time prevents foraging. The potential clutch size a female can lay decreases because of follicle resorption (Barry 1962, Murton & Westwood 1977, Raveling 1976, Findlay & Cooke 1982, Houston et al. 1983). Successful hatching of the eggs depends on weather factors (freezing, flooding) and on predation (Cooch 1961, Cooper 1978), which can be influenced by snow-cover (Mynkjeidal 1980). After hatching and raising the young, adult geese moult. Early snowstorms and decreasing temperature can jeopardize the survival of the mouling geese. Hence early nesting and mouling is favoured.

This general breeding biology scheme for arctic geese is summarised in Figure 3. Condition on the date of snow-melt and clutch initiation. A delayed season increases the non-foraging period and results in a loss of condition of the geese. This in turn results in more atretic follicles and a lower breeding success. This chain of events explains the correlation found between the timing of snow-melt and breeding success, e.g. for Barnacle Geese in Svalbard (see Owen & Norderhaug 1977, Prop et al. 1984). We view snow-melt phenology as a screen or gate before the moult or breeding. The potential overriding role in the breeding biology of the arctic geese.

A more extended data set of snow-melt can be found at the National Oceanic Atmospheric Administration (NOAA) in the USA. NOAA satellites have photographed the snow-cover of the northern Hemisphere on a weekly basis since 1966 (Watson & Wiesnet 1981). Snow-cover charts are drawn using these photographs. These snow-cover data are used in climatology studies, because of the large impact of the snow-cover on the world climate (see e.g. Dey & Shresta 1982). Snow-melt data are not directly available for all breeding areas but the date of snow-melt is available for 1975-1977 in Northern Canada. This information together with the exact location of the breeding areas (Bellrose 1980) and the breeding performance of the populations concerned in the years 1975-1977, is combined in Figure 5. The Lesser Snow Goose, the Greater Snow Goose and the Atlantic Brant do have a lower breeding performance in years with a delayed snow-melt. The White-fronted Goose breeds over a much larger area and hence experiences a variable snow-melt. This may account for a less clear pattern in this species. Plotting data for all species together shows a negative correlation between snow-melt date and breeding performance (Figure 5). The relationship is statistically

Figure 3. Scheme of the breeding biology of arctic geese according to two hypotheses: the prey-switching hypothesis (Summers 1986), and the condition-weather hypothesis (see text for further details).
Geese and snow-melt on west Spitsbergen by Arctic Foxes should be the main determining factors on the goose populations. Positive correlations we have found in breeding performance on West Spitsbergen (% juveniles measured of the Barnacle Goose (O)) and the date of snow-melt there (date in Owen & Norderhaug (1977) and Prop et al. (1984)). The two years for which both melt data and breeding performance is available for the Pink-footed Goose () and the Pale-bellied Brent (X) breeding in the general breeding area are also plotted in the graph. The regression line is based on the Barnacle Goose data (t₁₋=−5.7, p<0.001). For every 10 days delay in snow-melt, the percentage juveniles drops by 9.6.

Identifying a relationship between snow-melt and productivity does not however, tell us how a late year is translated into poor success. Theoretically, a complex interaction with predation (by foxes or other agents) is a possible contributory cause. For example Meltofte (1985) has shown that in late melt years waders breeding in Greenland suffer a proportionally higher egg loss to ground predators, which he attributed to the higher predation pressure. Worldwide synchrony in the fluctuations of lemming populations has never been observed and cannot therefore be regarded as the cause of a worldwide fluctuating predation pressure. Some goose species (such as the Greater Snow Goose) are thought to be able to protect their nests against fox predation, but they too have a higher fluctuating breeding performance; one which is positively correlated with the breeding performance of the Taimyr Brent. It is very unlikely that predation is the causal factor for the positive correlations in breeding performance because of the limited scale at which predation operates.

According to the lemming-hypothesis predation by Arctic Foxes should be the main determining factor for the breeding success of the European Dark-bellied Brent. It is known that predation can have a devastating effect on the production of young of a breeding colony, as demonstrated by several observations (e.g. Summers & Underhill 1987). We believe that population fluctuations or fluctuations in breeding performance of arctic geese are not, however, caused by predation alone. Worldwide synchrony in the fluctuations of lemming populations has never been observed and cannot therefore be regarded as the cause of a worldwide fluctuating predation pressure. Some goose species (such as the Greater Snow Goose) are thought to be able to protect their nests against fox predation, but they too have a higher fluctuating breeding performance; one which is positively correlated with the breeding performance of the Taimyr Brent. It is very unlikely that predation is the causal factor for the positive correlations in breeding performance because of the limited scale at which predation operates.

We hope that we have shown that predation is an unlikely single cause of the fluctuations in breeding success. Body condition is probably the most important causal factor. Delayed snow melt prolongs the non-nesting period and decreases weight and condition. The cause of the positive correlations in breeding performance is as yet, not well understood, but climate is a possible candidate because it has both world-wide influence and a potentially large role in the breeding biology of the arctic geese.

It is interesting to note that Orlov et al. (1986) believed that predation plays a minor role in lemming fluctuations in Taimyr. They found that lemming mortality was highest in the spring period and partly dependant on the date of snow melt. This could be an alternative explanation for the synchrony in fluctuations of lemming population and in the production of young by the Dark-bellied Brent: both arise for the same climatic reason.

With the current state of knowledge, deductions about the causal factor behind fluctuations in the breeding performance of Dark-bellied Brent have all the elements of a detective mystery. Clearly investigation of the scene is the only satisfactory approach, to discovering precisely at what stage in the breeding cycle (e.g. non-nesting, low egg productivity, non-hatching or loss of goslings) it occurs.

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**Figure 4.** The relation between the breeding performance on West Spitsbergen (% juveniles measured of the Barnacle Goose (O)) and the date of snow-melt there (date in Owen & Norderhaug (1977) and Prop et al. (1984)). The two years for which both melt data and breeding performance is available for the Pink-footed Goose () and the Pale-bellied Brent (X) breeding in the general breeding area are also plotted in the graph. The regression line is based on the Barnacle Goose data (t₁₋=−5.7, p<0.001). For every 10 days delay in snow-melt, the percentage juveniles drops by 9.6.

**Figure 5.** The breeding performance of 5 Nearctic goose populations in 1975-1977 compared with the date of snow-melt at their breeding area. All data points are plotted in the composite-graph, which shows the significant regression-line (t₁₋=−3.37, p<0.001). In the composite-graph, the percentage of juveniles drops by 6.3% for every 10 days in snow-melt. The regression is not significantly different from the relationship shown in Figure 4. Sources are: snow-melt, Bey et al. 1979; breeding area, Bellrose 1980.
ACKNOWLEDGEMENTS

We thank H. Boyd and V. Thomas who helped us with data on the breeding success of North American goose and D. Visser who made the drawings.

REFERENCES


Little is known of migrant waders in Mozambique (see Summers et al. 1987). The Knot Calidris canutus is known to winter in South Africa on the western seaboard but there are few records from the eastern coast of southern Africa. I was based at Maputo (formerly Lourenco Marques) in Mozambique from October 1975 until April 1978 and saw Knots in each of the three winters, on the sand flats to the north of the city (Costa do Sol) and at Inhaca Island on the seaward side of the Bay of Maputo (formerly Delagao Bay). The records are as follows:

Winter 1975/76
First recorded on 8 November, when 52 birds were at Costa do Sol. A total of 75 were there on 27 November but there were fewer in December/January (maximum 9 on 14 December). Numbers increased again to 45 on 8 February and at least 120 were present from 15 February to 20 March, with 30 at Inhaca Island on 27 February. The last birds seen were 20 at Costa do Sol on 10 April.

Winter 1976/77
Three birds were at Maputo as early as 11 September. A total of 25 were seen at Costa do Sol on 2 October, with 50 at Inhaca Island from 21-28 November. One bird at Costa do Sol on 19 December was the last seen.