

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

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

A lively discussion followed a talk by Ron Summers at the 1988 WSG Annual Meeting at Ipswich (see WSG Bulletin 54: 12-13) about the possible explanations for variations in the breeding success of arctic-breeding waders and geese. The issue concerns the relative contributions to breeding success of such factors as predation by Arctic Foxes on the breeding grounds (linked to population cycles of lemmings), body condition in spring and weather conditions on the breeding grounds. During the Ipswich discussion we heard about recent work by Groningen University showing positive correlations between the breeding success of many species and populations of geese breeding throughout the Arctic. We asked the authors to give this report of their findings to bring the questions to a wider audience than those able to attend the Ipswich meeting since we felt that, although these mainly concerned geese, they are of great relevance to wader-workers involved in the population dynamics of arctic-breeding waders (Eds.)

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%-50% young) and bust years (below 5% young) in an irregular pattern. The Brent population concerned breeds on 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 of this goose population. Roselaar (1979) was the first to point out that there might be a relationship between the 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 has suggested that the fluctuating breeding performance of the Dark-bellied Brent was caused by an annually varying predation rate by Arctic Foxes *Alopex 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 or body condition) for the Taimyr and the Svalbard Brent populations should then be regarded as the cause for the similarity in breeding success.

We briefly review the present state of knowledge of factors which are known to influence the breeding performance of arctic geese, and develop a broader hypothesis for explaining the fluctuating breeding performance of European Dark-bellied Brent. This hypothesis may provide a general framework applicable to other arctic birds particularly waders.

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 (Cramp 1977).

The main sources of data on the breeding performance of the different goose populations were Trooswijk (1974), Ganzenwerkgroep

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.

SPECIES		POPULATION	YEARS OF DATA
Palearctic populations			
Greylag Goose	<i>Anser anser</i>	Iceland	27
Bean Goose	<i>Anser f. fabalis</i>	North-Russia	20
	<i>Anser f. rossicus</i>	North-Russia	22
White-fronted Goose	<i>Anser albifrons</i>	Baltic	33
Pink-footed Goose	<i>Anser brachyrhynchus</i>	Greenland	18
		Svalbard	5
Barnacle Goose	<i>Branta leucopsis</i>	Iceland	32
		Svalbard	28
Dark-bellied Brent	<i>Branta bernicla bernicla</i>	Nova Zembla	25
		Greenland	26
Pale-bellied Brent	<i>Branta bernicla hrota</i>	Taimyr	33
		Svalbard	6
		Greenland	10
Nearctic populations			
White-fronted Goose	<i>Anser albifrons</i>	Pacific flyway	23
		Interior flyway	28
Ross's Goose	<i>Anser rossii</i>	Queen Maud Bay	24
Lesser Snow Goose	<i>Anser caerulescens caerulescens</i>	Central flyway	31
		Pacific flyway	31
Greater Snow Goose	<i>Anser caerulescens atlanticus</i>	Bylot Island	31
Black Brant	<i>Branta bernicla nigricans</i>	Pacific flyway	24
Atlantic Brant	<i>Branta bernicla hrota</i>	Atlantic flyway	18

(1976-1981, 1983, 1984a, 1984b, 1986, 1987a, 1987b), Ogilvie & Boyd (1976), Owen & Norderhaug (1977), Ogilvie (1978, 1980, 1981, 1982a, 1983-1987), Rooth et al. (1981), Owen (1982), Madsen (1984), Ebbinge et al. (1987), and Summers & Underhill (1987).

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 (S_r), percentage of explained variance (R^2), X^2 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 ($X^2=226.19$, d.f.=1, $p<0.001$). Moreover, the 57 positive correlations are significantly more than the only negative one ($X^2=54.07$, d.f.=1, $p<0.001$).

Figure 2 shows that the breeding performances of Greylag and Pink-footed Geese 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

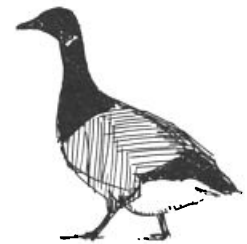
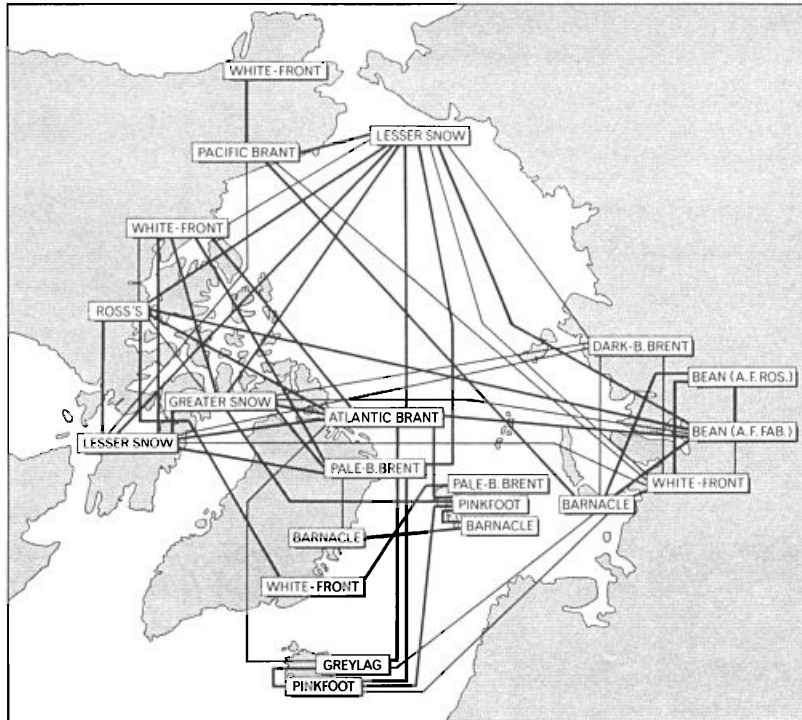


Figure 1. Correlations in the breeding performance of arctic goose populations. In this polar projection, populations between which breeding performance is significantly correlated ($p < 0.05$) are connected by lines. Thick lines represents a correlation coefficient larger than 0.5, thin lines a coefficient smaller than 0.5 (for breeding areas and subpopulations see Cramp (1977) and Bellrose (1980)).

Iceland ($r = -0.644$, $N = 36$, $p < 0.005$); Barnacle Goose in Svalbard ($r = -0.335$, $N = 28$, $p < 0.05$); Pacific Brant in Alaska ($r = -0.412$, $N = 24$, $p < 0.05$). These goose populations are responsible for only four of the significant correlations, so this effect cannot be the only explanation for the positive significant correlations.

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.

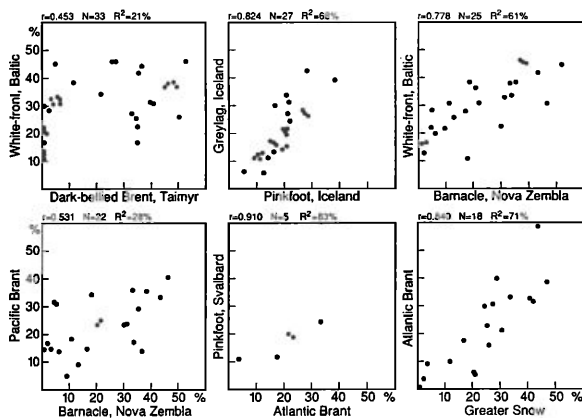


Figure 2. Relationships between the breeding performance of pairs of selected arctic goose populations in the same year. Each point is the breeding performance of the two populations in one year. Characteristics of the linear regression are given in the headings (all are significant at $p < 0.01$).

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 1978, Ebbinge et al. 1982, Thomas 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 predictor of their 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, Ryder 1972, Green et al. 1977, Newton 1977, Cooper 1978, 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 years 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 1978, 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 (Byrkjedal 1980). After hatching and raising the young, adult geese moult. Early snowstorms and decreasing temperature can jeopardize the survival of the moulting geese. Hence early nesting and moulting is favoured.

This general breeding biology scheme for arctic geese is summarised in Figure 3. Condition is seen as the focal factor and there is often a relationship between spring weight and observed breeding performance the following autumn. The second most important factor is probably the timing 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 acting on body condition at that time to determine breeding outcome.

Does this short review help in identifying the cause of the positively correlated breeding performances? The general breeding biology scheme (Figure 3) gives some possible indications. Suppose that the correlations are partly caused by the same factor. Such a causal factor must then operate on a global scale because of the dispersed habitats of arctic geese.

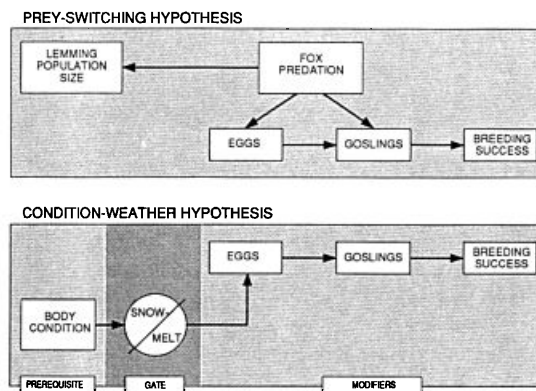


Figure 3. Scheme of the breeding biology of arctic geese according to two hypotheses: the prey-switching hypothesis (Summers 1986), and the condition-weather hypothesis (see text for further details).

Climate is a candidate for this causal factor (see also Boyd 1982). It is a factor that could operate at a world-wide scale with a potentially large impact on breeding performance. The relationship between snow-melt and breeding success described earlier, is highly suggestive. If there is some widespread synchrony in the timing of snow-melt, then this could explain the correlations in breeding performance. Little is known however, of the snow-melt in the breeding areas. Most areas are not well known and uninhabited by man.

Owen & Norderhaug (1977) (extended in Prop et al. 1984) provide snow-melt data from West Spitsbergen. These authors demonstrated a strong relationship between snow-melt and the breeding performance of the Barnacle Goose; the later the snow-melt the poorer the breeding success. The breeding performance of the other two goose populations in this area, the Pink-footed Goose and the Pale-bellied Brent, fit precisely on the graph of the Barnacle data (Figure 4). This supports the hypothesis that snow-melt is an important factor with a potentially 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 (Matson & 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 & Bhanu Kumar 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

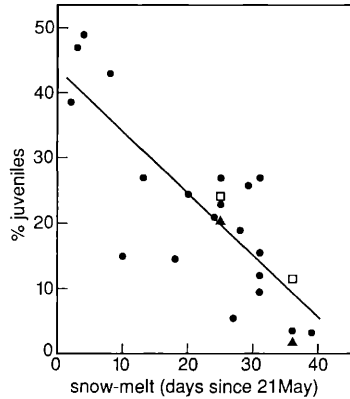


Figure 4. The relation between the breeding performance on West Spitsbergen (% juveniles measured of the Barnacle Goose (O)) and the date of snow-melt there (date in Owen & Norderhaug (1977) and Prop *et al.* (1984)). The two years for which both melt data and breeding performance is available for the 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 ($t_{18}=-5.7$, $p<0.001$). For every 10 days delay in snow-melt, the percentage juveniles drops by 9.6.

indistinguishable from that for the Barnacle Geese and snow-melt on West Spitsbergen ($t_{12}=1.749$, n.s.). The similarity in the slope of this relationship is striking: in Spitsbergen breeding success declines by 0.96% per day of delay in snow-melt compared to 0.63% for the Canadian data. This may provide one indication that climate, and especially snow-melt, is the factor responsible for the positive correlations we have found in breeding performance on the goose populations.

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 (in *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 highly 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.

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

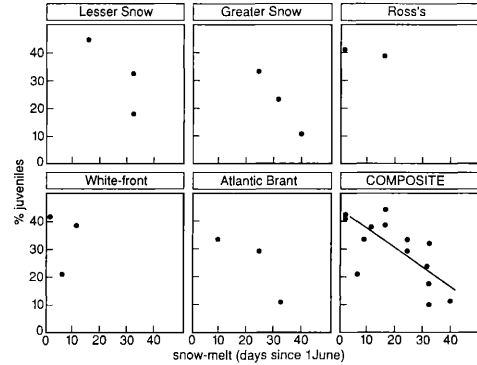


Figure 5. The breeding performance of 5 Nearctic goose populations in 1975-1977 compared with the date of snow-melt at their breeding area. All data points are plotted in the composite-graph, which shows the significant regression-line ($t_{12}=-3.37$, $p<0.01$). In the composite-graph, the percentage 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, Dey *et al.* 1979; breeding area, Bellrose 1980.

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 concentration of nests on snow free patches in late melt years. In the case of geese, direct effects on the food supply are likely to be more important in mediating nesting success.

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 on the scene is the only satisfactory approach, to discovering precisely at what stage in the breeding (*e.g.* non-nesting, low egg productivity, non-hatching or loss of goslings) it occurs.

ACKNOWLEDGEMENTS

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

REFERENCES

- Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- Barry, T.W. 1962. Effects of late seasons on Atlantic Brant reproduction. *Journal of Wildlife Management* 26: 19-26.
- Bellrose, F.C. 1980. *Ducks, Geese and Swans of North America*. Third edition. Stackpole Books, Harrisburg.
- Boyd, H. 1982. Influence of temperature on arctic-nesting geese. *Aquila* 89: 259-269.
- Boyd, H. 1987. Do June temperatures affect the breeding success of Dark-bellied Brent Geese *Branta b. bernicla*? *Bird Study* 34: 155-159.
- Byrkjedal, I. 1980. Nest predation in relation to snow-cover - a possible factor influencing the start of breeding in shorebirds. *Ornis Scandinavica* 11: 249-252.
- Cabot, D. & West, B. 1973. Population Dynamics of Barnacle Geese, *Branta leucopsis*, in Ireland. *Proc. Royal Irish Acad.* 73: 415-443.
- Cooch, G. 1961. Ecological aspects of the Blue-snow Goose complex. *Auk* 78: 72-89.
- Cooper, J.A. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. *Wildlife Monographs* no. 61. Wildlife Society Inc.
- Cramp, S. & Simmons, K.E.L. (eds.). *The birds of the Western Palearctic*. Volume I: Ostrich to Ducks. Oxford University Press, Oxford.
- Davies, J.C. & Cooke, F. 1983. Annual nesting productivity in Snow Geese: prairie droughts and arctic springs. *Journal of Wildlife Management* 47: 291-296.
- Dey, B., Moore, H. & Gregory, A.F. 1979. Application of satellite images for monitoring snow-line in the Yukon and Northwest Territories. *Polar Record* 19(122): 473-483.
- Dey, B. & Kumar, B.S.R.U. 1982. An apparent relationship between spring snow cover and the advance period of the Indian summer monsoon. *Journal of Applied Meteorology* 21: 1929-1932.
- Dhondt, A.A. 1987. Cycles of lemmings and Brent Geese *Branta b. bernicla*: a comment on the hypothesis of Roselaar and Summers. *Bird Study* 34: 151-154.
- Drent, R.H. & Prins, H.H.T. 1987. The herbivore as prisoner of its food supply. In: J. van Aniel, Bakker, J.P. and Snaydon, R.W. (Eds.). *Disturbance in Grasslands; species and population responses*. Dr. W. Junk Publishers, Dordrecht.
- Ebbinge, B.S. 1985. Factors determining the population size of arctic-breeding geese wintering in western Europe. *Ardea* 73: 121-128.
- Ebbinge, B.S. 1987. In Hoeverre bepalen lemmingen het broedresultaat van Rotganzen *Branta bernicla*? *Limosa* 60: 147-149.
- Ebbinge, B., St Joseph, A., Prokosch, P., & Spaans, B. 1982. The importance of spring staging areas for arctic-breeding geese wintering in western Europe. *Aquila* 89: 249-258.
- Ebbinge, B., van den Berg, L., van Haperen, A., Lok, M., Philippona, J., Rooth, J. & Timmerman, A. 1987. Numbers and distribution of wild geese in the Netherlands, 1979-1984. *Wildfowl* 37: 28-34.
- Ely, C.R. & Raveling, D.G. 1984. Breeding biology of Pacific White-fronted Geese. *Journal of Wildlife Management* 48: 823-837.
- Findlay, C.S. & Cooke, F. 1982. Breeding synchrony in the Lesser Snow Goose *Anser caerulescens caerulescens*. I: Genetic and environmental components of hatch date variability and their effects on hatch synchrony. *Evolution* 36: 342-351.
- Ganzenwerkgroep Nederland van het IWRB 1976, 1977, 1978, 1979, 1980, 1981. Resultaten van de Ganzentellingen in Nederland in het winterhalfjaar van 1974-1980, first-sixst message. *Watervogels* 1: 91-102, 2: 102-115, 3: 145-163, 4: 73-91, 5: 65-95, 6: 119-142.
- Ganzenwerkgroep Nederland/Belgie. 1983, 1984a, 1984b, 1986, 1987a, 1987b. Ganzentellingen in Nederland en Vlaanderen in het seizoen 1980-1985. *Ardea* 56: 9-17, 57: 7-16, 57: 147-152, 59: 25-31, 60: 31-39, 60: 137-146.
- Green, G.H., Greenwood, J.J.D. & Lloyd, C.S. 1977. The influence of snow conditions on the date of breeding of wading birds in North-East Greenland. *Journal of Zoology* 183: 311-328.
- Greenwood, J.J.D. 1987. Three-year cycles of lemmings and arctic geese explained. *Nature* 328:577.
- Houston, D.C., Jones, P.J. & Sibly, R.M. 1983. The effects of female body condition on egg laying in Lesser-Backed Gulls *Larus fuscus*. *Journal of Zoology* 200: 509-520.
- Lemieux, L. 1959. The breeding biology of the Greater Snow Goose on Bylot Island, Northwest territories. *Canadian Field Naturalist* 73: 117-128.
- Meltofte, H. 1985. Population and breeding schedules of waders, *Charadrii*, in high arctic Greenland. *Meddelelser om Gronland, Bioscience*, no. 16.
- Madsen, J. 1984. Status of the Svalbard population of Light-bellied Brent *Branta bernicla hrota* wintering in Denmark 1980-1983. In: Mehlum, F. and Ogilvie, M. (Eds.). *Current Research on Arctic Geese*. Norsk Polarinstittutt, Oslo, Skrifter no. 181: 119-124.
- Matson, M. & Wiesnet, D.R. 1981. New data base for climatic studies. *Nature* 289: 451-456.
- Murton, R.K. & Westwood, N.J. 1977. *Avian Breeding Cycles*. Clarendon Press, Oxford.
- Newton, I. 1977. Timing and success of breeding in Tundra-nesting geese. In: Stonehouse, B. and Perrins, C.M. (Eds.). *Evolutionary Ecology*. MacMillan Press, London.
- Nilsson, L. 1979. Variation in the production of young of Swans wintering in Sweden. *Wildfowl* 30: 129-134.
- Ogilvie, M.A. 1978. *Wild Geese*. T. and A.D. Poyser, Berkhamsted.
- Ogilvie, M.A. 1981, 1982a, 1983, 1984, 1985, 1986, 1987. Numbers of geese in Britain and Ireland, 1979, 1985. *Wildfowl* 31: 172, 32: 172, 33: 172, 34: 173-174, 35: 180, 36: 152, 37: 176.
- Ogilvie, M.A. 1982b. The status of the Pink-footed Goose *Anser brachyrhynchus*. *Aquila* 89: 127-131.
- Ogilvie, M.A. & Boyd, H. 1976. The numbers of Pink-footed and Greylag Geese wintering in Britain: observations 1969-1975 and predictions 1976-1980. *Wildfowl* 27: 63-83.

- Ogilvie, M.A. & St Joseph, A.K.M. 1976. Dark-bellied Brent Geese in Britain and Europe, 1955-1976. *British Birds* 69: 422-439.
- Orlov, V.A., Sarancha, D.A. & Shelepova, O.A. 1986. Mathematical models of the numerical dynamics of Lemmings *Lemmus dicrostonyx* and its applications of West Taimyr. *Soviet Journal of Ecology* 17: 97-104. Plenum Publishing Corp.
- Owen, M. 1982. Population dynamics of Svalbard Barnacle Geese 1970-1980. *Aquila* 89: 229-247.
- Owen, M. 1984. Dynamics and age structure of an increasing goose population - the Svalbard Barnacle Goose *Branta leucopsis*. In: Mehlum, F. and Ogilvie, M. (Eds.). *Current Research on Arctic Geese*. Norsk Polarinstitut, Oslo, Skrifter no. 181: 37-47.
- Owen, M. 1987. Brent Goose *Branta b. bernicla* breeding and lemmings - a re-examination. *Bird Study* 34: 147-149.
- Owen, M. & Norderhaug, M. 1977. Population dynamics of Barnacle Geese *Branta leucopsis* breeding in Svalbard, 1948-1976. *Ornis Scandinavica* 8: 161-174.
- Prop, J., van Eerden, M.R. & Drent, R.H. 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. In: Mehlum, F. and Ogilvie, M. (Eds.). *Current Research on Arctic Geese*. Norsk Polarinstitut, Oslo, Skrifter no. 181: 87-117.
- Raveling, G. 1978. The timing of egg laying by northern geese. *Auk* 95: 294-303.
- Rooth, J., Ebbinge, B., van Haperen, A., Lok, M., Timmerman, A., Philippona, J. & van der Lek, L. 1981. Numbers and distribution of wild geese in the Netherlands, 1974-1979. *Wildfowl* 32: 146-155.
- Roselaar, C.S. 1979. Fluctuaties in aantallen kromekstrandlopers *Calidris ferruginea*. *Watervogels* 4: 202-211.
- Ryder, R.P. 1972. Biology of nesting Ross's Geese. *Ardea* 60: 185-215.
- Summers, R.W. 1986. Breeding production of Dark-bellied Brent Geese *Branta bernicla* in relation to lemming cycles. *Bird Study* 33: 105-108.
- Summers, R.W. & Underhill, L.G. 1987. Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders *Charadrii* on the Taimyr Peninsula. *Bird Study* 34: 161-171.
- Teunissen, W., Spaans, B. & Drent, R.H. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea* 73: 109-119.
- Thomas, V.G. 1983. Spring migration: the prelude to goose reproduction and a review of its implications. In: Boyd, H. (Ed.). *Western Hemisphere Waterfowl and Waterbird Symposium*. Canadian Wildlife Service, Ottawa.
- Troostwijk, W.J.D. 1974. Ringing data on White-fronted Geese *Anser a. albifrons* in the Netherlands. *Ardea* 62: 98-110.
- W.F. de Boer* & R.H. Drent, Zoologisch Laboratorium, Rijksuniversiteit Groningen, PO Box 14, 9750 AA Haren, The Netherlands.
- * Present address: S.N.V.-Ati, Association Neerlandaise d'Assistance au Developpement, B.P. 1135, n'Djamena, Tchad.

KNOTS IN SOUTHERN MOZAMBIQUE

Alan Vittery

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 135 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.

Winter 1977/78

Three or four birds at Inhaca Island on 12/13 November and 12 birds at Costa do Sol on 1 December were the only sightings.

The apparent decline in numbers over the three years is probably more a reflection of the increasing difficulty of making observations during that time than of any marked change in status. The records from the first winter based on the largest number of visits to the coast, suggest a late autumn build-up, and then a move to other feeding areas in mid-winter (southern summer) and an early spring passage.

REFERENCES

- Summers, R.W., Underhill, L.G., Pearson, D.J. & Scott, D.A. 1987. Wader migration systems in southern and eastern Africa and western Asia. *Wader Study Group Bull* 49, Suppl./IWRB Special Publ. 7: 15-34.

Alan Vittery, *The Saltings, Cley-next-the-Sea, Norfolk NR25 7RZ, U.K.*