

## XXVIII. THE IMPORTANCE OF SPRING STAGING AREAS FOR ARCTIC-BREEDING GEESE, WINTERING IN WESTERN EUROPE

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In justifying the need to safeguard wintering and spring staging areas for migratory geese, the argument that the condition the geese build up in these areas is of vital importance to their subsequent breeding success, is heard more and more among conservationists.

Examining the value of this argument, we discern two questions:

- is it true that geese can only breed in the Arctic if they have built up sufficient body reserves elsewhere?
- if so, where and when do they build up these necessary reserves?

### 1. The condition hypothesis

#### 1.1 Introduction

The hypothesis that female condition on arrival in the breeding area determines her breeding success has been advanced by several investigators (Ryder, 1967; Harvey, 1971; Newton 1977; Prop et al., 1978). This condition hypothesis could be tested by measuring the condition of individual birds upon arrival in the Arctic and the subsequent breeding performance of these same birds.

So far, only indirect evidence has been accumulated. Positive correlations between mild weather on the wintering grounds and subsequent breeding success in the Arctic have been demonstrated for Barnacle Geese (*Branta leucopsis*) wintering in Ireland (Cabot & West, 1973) and Whooper Swans (*Cygnus cygnus*) wintering in southern Sweden (Nilsson, 1979).

Monitoring Lesser Snow Geese (*Anser caerulescens caerulescens*) at various stages throughout the Arctic summer Ankey & MacInnes (1978), summarized in (Drent & Daan, 1980) revealed that:

- upon arrival on the breeding grounds the geese are heavier than at any other time of the year,
- heavier females would have laid larger clutches,
- during early incubation, weights of females with completed clutches are strikingly similar, even though clutch sizes vary from 2 to 6 eggs,
- the breakdown of both fat and protein reserves results in a 42% weight loss in breeding females at the time of hatching. At that time failed nesters have even lower weights than those whose clutches are about to hatch.

Since in this latter study neither the weights (and therefore condition) at

the onset of breeding of failed breeders nor those of successful ones are known, it is not possible to conclude from these data that the initial body condition of a female goose determines its subsequent breeding performance. Rather, because the weights after laying were so similar, one would favour the explanation that female geese differ in the rate at which they spend their body reserves during incubation. A more subtle approach has been adopted by Lessells & Owen, who used weigh-bridges placed under the nest both in captive Barnacle Geese (*Branta leucopsis*) and in wild Lesser Snow Geese (*Anser c. caerulescens*). In both species similar proportional weight losses were registered in breeding females as those found by Ankney & MacInnes (Lessells *et al.*, 1979, Owen, 1980). However, due to the amount of work involved per nest, this method has not yielded sufficient data to test the condition hypothesis yet.

Recognizing that the Wadden Sea area in western Europe is the only spring staging area for Dark-bellied Brent Geese (*Branta bernicla bernicla*), and that upon return from the breeding grounds in the autumn the breeding success of individual geese can be assessed because parents are accompanied by their recent offspring, we decided to test the condition hypothesis without bothering to go to the Arctic at all.

Brent Geese stay in the Wadden area until late May, feeding on the spring growth on the saltmarshes and thus increasing their body weight from 1250 to 1600 grams on average, in about a month (St. Joseph *et al.*, in prep.). Then they leave on an almost non-stop flight for their breeding grounds in Taymyr, Arctic Siberia. We adopted two different approaches to investigate the condition hypothesis:

- comparing reproductive performance to individual body weight at the point of departure the spring staging areas,
- comparing the mean rate of weight increment in spring to the mean reproductive performance of the whole population.

## 1.2. Methods

Our first approach consisted of cannon netting Brent Geese as close as possible to the date of departure from the Wadden area in spring. Usually mass departure takes place from 20–28 May. The birds caught were measured, weighed, sexed and fitted on each leg with a large plastic ring, each one carrying a single letter or number engraved three times round it for easy observation.

This marking method, developed by St. Joseph, gave a series of individual combinations which could be read through telescopes at distances of up to 300 metres.

In this way we were able to mark 89 adult females in the period 1976–1979. The next autumn we tried to spot as many as possible of the birds marked the previous spring, and noted whether they were accompanied by young or not.

Secondly, we caught Brent Geese somewhat earlier in the spring, and two or more catches in the same spring allowed us to calculate the regression of body weight on time in the spring of 1977, 1978 and 1979. These were then compared to the overall breeding success the following autumn.

### 1.3. Results

Breeding success turned out to be very poor in 1976 (11.6% juveniles in the autumn) and 1977 (0.01% juveniles). None of our marked birds was accompanied by any offspring the following autumn (see Table 1). With a mean proportion of juveniles of 35% and 33% respectively, 1978 and 1979 were good breeding seasons. In these years a third of the previously marked females was spotted in the autumn and their family size assessed (Table 1). Because the separate samples were too small, we had to combine the 1978 and 1979 samples. In order to compare the weight from these three different catches, weights were adjusted to the level of the 23 May 1978 catch, being the most advanced in the season.

We did this by adding the difference between the means of the catches to the weights of the individual birds concerned. Thus 100 grams was added to the weights of birds resighted from the 18 May 1978 catch and 25 grams to those from the 17 May 1979 catch (See Table 1).

The combined samples (see Fig. 1) indicate that in good breeding seasons the heavier females are more often successful, the mean spring weight of successful females being significantly higher than that of ailed breeders ( $p = 0.02$ ; one-tailed t-test). To find out whether being heavier in spring was simply a result of body size, wing length of successful females were also compared to those of unsuccessful ones, but no significant difference emerged (see Fig. 1). From this we conclude that attaining a heavier spring weight must be due to other factors such as a better feeding technique, or better feeding conditions resulting from better protection against conspecifics by its mate during spring fattening as in the Common Eider (*Somateria mollissima*) (Ashcroft, 1976).

The results of our second approach are given in Fig. 2. The slope of the regression line and thus the rate of body weight increment in 1977 is significantly lower ( $p = 0.1$ ) than in the other two seasons. Accordingly 1977 turned out to be a non-breeding year for these Brent Geese, whereas the other two years were good breeding years (see above, and Fig. 2). We are still very much

*Table XXVIII/1.*

*Numbers of adult female Brent Geese marked at the point of departure from the spring staging areas, and the number resighted the following autumn*

Number caught		Number resighted		
date	mean weight	-	+	
21 - 5 - 76	25 1585 grams	11	11	0
21 - 5 - 77	22 1450 grams	10	10	0
18 - 5 - 78	17 1458 grams	7	4	3
23 - 5 - 78	12 1560 grams	4	2	2
17 - 5 - 79	13 1535 grams	4	2	2

- returning without offspring

+ returning with offspring

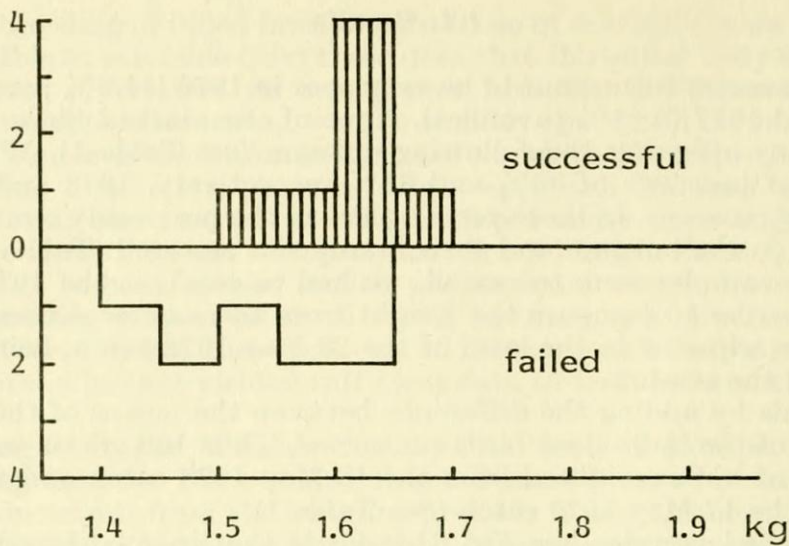


Figure XXVIII/1: Breeding success and spring departure weights in adult female *B. b. bernicla*. The mean spring weight of successful females (1618 grams,  $n = 7$ ) differed significantly from that of failed breeders (1536 grams,  $n = 8$ ) ( $p = 0.02$ ,  $t = \text{test}$ ). Mean wing lengths of both groups (332 mm against 334) did not differ significantly ( $t$  test)

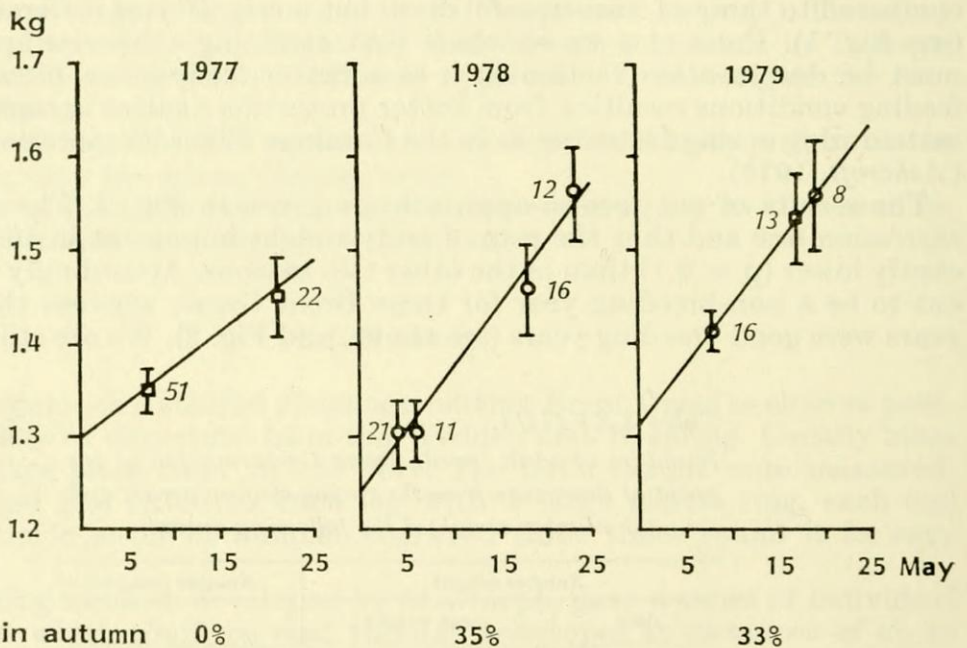


Figure XXVIII/2: Rate of increase in body weight in adult female *B. b. bernicla* in May in three years with the subsequent breeding success of the whole population. Squares are samples from the Dutch part of the Wadden Sea, and circles from the German Wadden Sea. These symbols indicate the mean, whereas vertical bars indicate the 95% confidence interval. Numbers indicate sample size. The slope of the regression line in 1977 differs significantly from that in 1978 ( $p = 0.005$ ) and 1979 ( $p = 0.01$ ), but the slopes of 1978 and 1979 do not differ significantly ( $p = 9.005$ ,  $t$  test)

in the dark as to the cause of this reduced rate of body weight increment in 1977. *Ebbinge* (1977) suggested strong winds as a possible factor reducing intake of food, or resulting in a higher energy expenditure to maintain body temperature.

## 2. The spring staging areas

### 2.1. Introduction

Our second question as to when and where the apparently important body condition is built up, will be treated in this section.

Since a positive correlation between winter temperature and subsequent breeding success was found in two studies (*Cabot & West*, 1973; *Nilsson*, 1979), one might think that achieving the right breeding condition is a rather slow process continuing through the winter.

However, data on annual fluctuations in body weight in Brent Geese (*Branta bernicla bernicla*) (*St. Joseph et al.*, in prep.) and Lesser Snow Geese (summarized by *Owen*, 1980) show that the lowest weights occur shortly after the winter is over. This finding made it more likely that spring feeding conditions in themselves determine whether sufficient body reserves can be accumulated, irrespective of feeding conditions in the preceding winter.

Virtually the entire dark-bellied Brent Goose population (*Branta bernicla bernicla*) is concentrated in the Wadden area (*St. Joseph*, 1979) throughout the spring (April – May). To find out whether other Arctic-breeding goose species were concentrated on special spring staging areas too, we analyzed the available ringing recoveries of Barnacle Geese (*Branta leucopsis*), White-fronted Geese (*Anser albifrons*) and Bean Geese (*Anser fabalis*) ringed in the Netherlands.

### 2.2 Method

We restricted the analysis to shot birds, to avoid any bias inherent in the category of birds "found dead".

The analysis covers the period 1955–1978, but the majority of our material stems from the sixties. In the fifties very few birds were ringed, and in the seventies spring hunting in the U.S.S.R. was no longer permitted (*Rutschke*, 1976). We grouped the recoveries in five 10-day periods (decades) from 10 April until the end of May.

Because the last two periods included many recoveries from the breeding grounds, these were combined.

One duck species, the Wigeon (*Anas penelope*), was included in the analysis, because, ecologically speaking, it is the "goose" among the ducks. For each species and each period the mean position was calculated. The significance of the differences between these mean positions was tested using the Mardia test ( $p < 0.05$ , *Mardia*, 1972).

### 2.3 Results

In Table 2 the mean positions (in tenths of degrees) are given for all different species and periods except the Barnacle Goose (*Branta leucopsis*). Too few recoveries of the latter species were available to calculate its mean position in all ten-day periods. From recent counts (Ebbinge, 1981) we know that the entire Russian population of this species from mid-April to mid-May is concentrated in the Baltic in Gotland and in the Estonian S.S.R.

This is in agreement with the six recoveries of *Branta leucopsis* in mid-spring (20–30 April) (see Fig. 3).

In Fig. 3 the actual distribution of the recoveries of all four species in mid-spring is depicted.

It is obvious that in spring all goose species are virtually separated from each other. Only White-fronts (*Anser albifrons*) and Wigeon (*Anas penelope*) overlap during one ten-day period (20–30 April).

Whereas both *Branta* species stay the entire spring period within a well defined area, the data on the other species (Table 2) indicates a gradual shift in a northeastward direction.

This gradual shift to the north while accumulating body reserves is apparently also typical in Lesser Snow Geese (*Anser c. caerulescens*) staging at James Bay (Wypkema & Ankney, 1979).

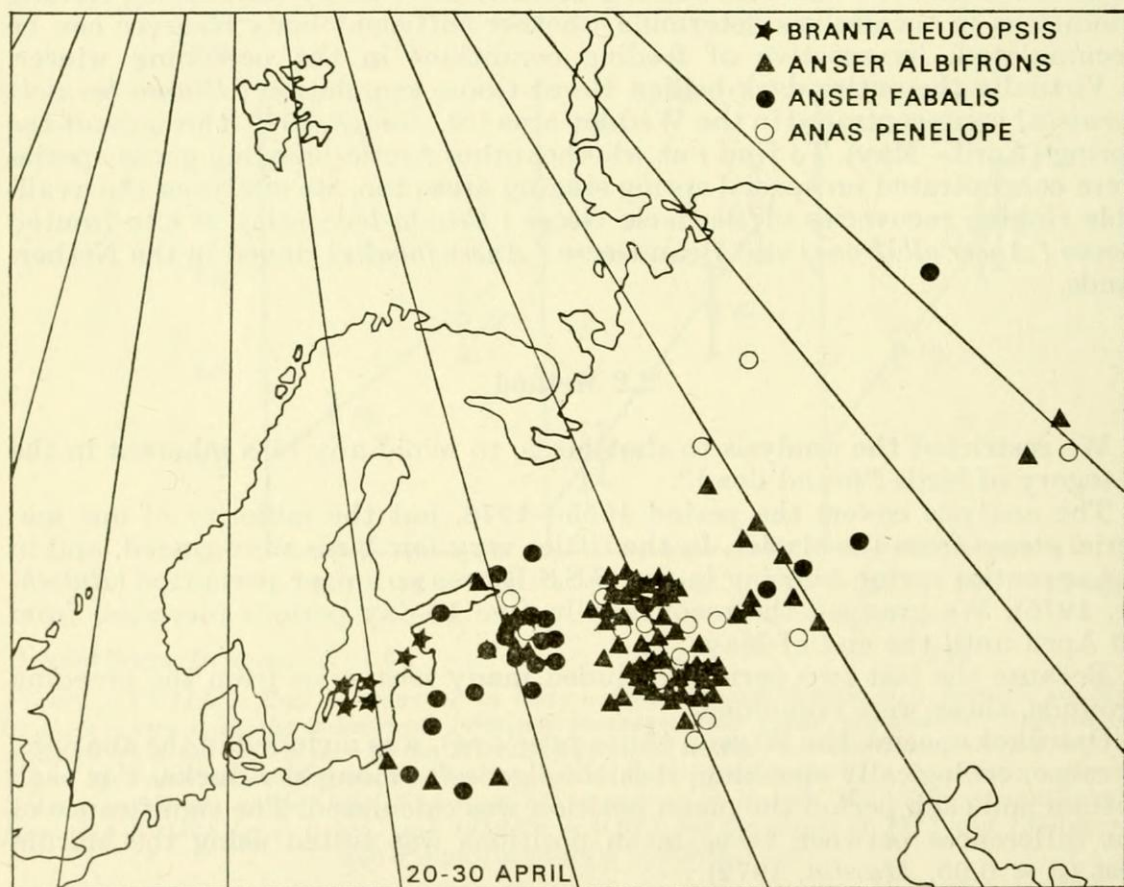


Figure XXVIII/3: Positions of geese and Wigeon (*Anas penelope*) shot between 20–30 April in the period 1955–1978, ringed in the Netherlands (see Table 2)

Table XXVIII/2.

Mean positions of spring recoveries of *Anser albifrons*, *Anser fabalis* and *Anas penelope*, ringed in the Netherlands (up to 1978)

Period	<i>Anser albifrons</i>	<i>Anser fabalis</i>	<i>Anas penelope</i>
	n: Mean position	n: Mean position	n: Mean position
10 - 20 April	88 54.7 N 39.7 E	11 55.3 N 26.1 E	30 53.6 N 39.1 E
20 - 30 April	112 56.1 N 40.1 E	23 58.1 N 31.0 E	18 56.1 N 49.9 E
1 - 10 May	54 60.2 N 44.0 E	38 64.3 N 40.1 E	51 62.0 N 54.2 E
10 - 30 May	144 67.0 N 47.2 E	107 66.7 N 49.6 E	147 64.5 N 61.8 E

Except for the positions of *Anser albifrons* and *Anas penelope* in the period 20-30 April all these positions differ significantly from each other (Mardia test,  $p < 0.05$ )

### 3. Discussion

From data on family size and the overall proportion of juveniles in the wintering population, it can be inferred that in very good breeding seasons (with a mean of 3 juveniles per family and almost 50% juveniles in the wintering population), two-thirds of the adult birds raise their young successfully. In moderately good years (30-35% juveniles) only a third of the adults are doing so. Our results after good breeding seasons with 7 out of 15 returning females being successful do not depart significantly from what one would have expected.

A drawback of the method we applied to investigate the condition hypothesis is that the body reserves Dark-bellied Brent Geese (*Branta bernicla bernicla*) build up each spring are not only used in egg formation and subsequent breeding. The birds have to migrate over 4000 km to reach the breeding grounds. It would be very interesting indeed to have information on body weights upon arrival in Taymyr.

However, because mass migration in a very short period of time is the general pattern in this species, it is unlikely that the migration effort, and thus the amount of weight loss due to it, will vary much between individuals. Thus the impressive spread in body weights at the point of departure from the spring staging areas is not likely to be altered much during spring migration.

In some years all Brent Geese (*Branta b. bernicla*) may have to invest a much greater proportion of their body reserves into migration because of adverse weather conditions (especially continuing strong headwinds). This, of course, might have serious repercussions on breeding success.

Another more serious drawback of our method is that, theoretically, parents arriving in good condition may hatch their eggs successfully, but yet lose their young to predators before these young have become fully fledged. Such parents would, of course, be classified as failed breeders by us. In part, however, the capacity to avoid predation may depend on the individual condition of the parents, as well.

Thus our method does not distinguish in which phase of the breeding season body condition determines reproductive performance.

The frequent occurrence of non-breeding years in Dark-bellied Brent Geese (*Branta b. bernicla*) is usually ascribed to adverse weather during the predation pressure resulting from lemming cycles (*Meltofte*, pers. comm.). The fact that the rate of body weight increment in spring is significantly lower in one of our three years of study, which turned out to be a non-breeding year, indicates that Brent Geese may not always leave these spring staging areas in the same condition each year. This possibly results in non-breeding years even if the weather during the breeding season is favourable.

Another indication of the extreme importance of these spring staging areas is the clear spatial separation between the different species (Fig. 3). We consider this a result of the need to avoid inter-specific competition in this critical period in the annual cycle of Arctic-breeding geese. That different species of geese and Wigeon (*Anas penelope*) are potential competitors food is borne out by observations at other times of the year. Both Wigeon (*Anas penelope*) and Brent Geese (*Branta bernicla*) feed in autumn on eelgrass (*Zostera*). As a result *Zostera* beds in several areas are rapidly eaten out (*Charman*, 1979), and then Brent Geese are occasionally observed to chase away feeding Wigeon from the remaining patches of *Zostera*.

Following the reclamation of the Lauwersmeer area in the Netherlands both Wigeon (*Anas penelope*) and Barnacle Geese (*Branta leucopsis*) eagerly harvested the same rich resource, glasswort (*Salicornia*), which completely covered about 3300 ha of the vast recently drained mudflats. In this latter case direct interspecific interactions were largely avoided because Wigeon visited the plains during the night, whereas Barnacle Geese came in the daytime (*Prop & van Eerden*, 1981). Nevertheless they were feeding on exactly the same resource.

In midwinter, mixed flocks of White-fronted Geese (*Anser albifrons*) and Barnacle Geese (*Branta leucopsis*) are a common sight in the Dutch province of Friesland, while in other parts of the Netherlands mixed flocks of Bean Geese (*Anser fabalis*) and White-fronted Geese (*Anser albifrons*) also occur (*Rooth et al.*, 1981). In these cases too, it is likely that the different species overlap in their food choice.

Therefore separation between these species, either ecologically or spatially, as has been suggested by *Lack* (1974), is not always the case.

When these Arctic-breeding species arrive in the autumn, abundant summer growth in the temperate zone has produced plenty of food to harvest. Because of this abundance, interspecific competition has probably not been severe enough for the different species to evolve exclusive feeding strategies in the autumn and winter. In spring not only are the demands of the birds building up their body reserves much higher, but also food, though high in quality, becomes available day by day only in small amounts.

In such a situation competition for food is more likely to occur, and this, we suggest, resulted in the evolution of segregated spring staging areas for these potentially competitive species.

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