Abstract

The implementation of a new non-disturbance policy on the Dutch Wadden-Sea island Schiermonnikoog provided an experiment to test ideas concerning the switch between habitats by spring-staging Brent and Barnacle Geese. In the experimental years (2000 and 2001) the farmers desisted from all scaring activities in the embanked pasture area (290 ha) with grasslands intensively managed for dairy farms. The adjoining salt marsh (1635 ha) already was afforded complete protection, and traditionally provided the main goose feeding area in spring. A traditional habitat switch to the marsh coincides with the spring increase of forage production in the marsh habitat, suggesting that forage availability on the marsh is limiting in early spring. Compared to three control years (1997, 98 and 99 with scaring in the pastures) both species of geese extended their usage of the agricultural habitat in the two non-scaring years, where they remained until migratory departure (April for the Barnacle Geese, late May for the Brent). Numbers of geese on the salt marsh did not change, hence non-disturbance triggered an increase of capacity for spring feeding geese at this staging site. The change was most dramatic for the Brent Goose with a doubling of numbers on the island in the years without scaring, and identification of ringed individuals showed that the birds recruiting to this new spring tradition had in previous seasons utilised other sites in the Dutch Wadden Sea.
Introduction

During the spring staging period of Dark-bellied Brent Geese *Branta bernicla bernicla* and Barnacle Geese *Branta leucopsis* along the coasts of western Europe a spectacular switch between foraging habitats occurs as the season progresses (Vickery *et al.* 1995; Rowcliffe *et al.* 2001). Both species of geese utilise agricultural grasslands during winter and early spring, but the majority of geese change to feeding sites on salt marshes prior to departure to their Arctic breeding grounds (Ebbinge *et al.* 1999). Feeding on agricultural land is especially common in Britain and the Netherlands during the winter months up to early March. By then, almost all Barnacle Geese staging in the Netherlands have moved to salt-marsh habitats, and about 80% of the NW European population of Brent Goose forage on salt marshes in May. These spring changes in forage and habitat preferences of massive numbers of *Branta* geese in our coastal ecosystems are intriguing and impinge on management practice (notably where geese conflict with dairy farmers). In the absence of field experiments on a sufficient scale, the causes contributing to the habitat shift are nevertheless still poorly understood. The spring staging period is of exceptional importance for migrant *Branta* geese as accumulated fat reserves are a prerequisite for successful breeding in the Arctic (de Boer & Drent 1989; Ebbinge & Spaans 1995). Understanding the factors governing habitat preference at this time of year is an essential step towards defining the capacity of coastal areas for spring goose grazing.

Previous studies examining the habitat use of geese in spring agree in implicating changes in the relative nutrient content and/or biomass on offer in the competing habitats as the underlying cause to explain the observed habitat switch. Vickery *et al.* (1995) and Rowcliffe *et al.* (2001) illustrate that depletion of forage biomass necessitates a switch of Brent Geese from intertidal flats and salt marshes to agricultural land in Britain during autumn and winter. Increasing primary production in spring allows the geese to return to these habitats. Both studies suppose that agricultural land is less attractive due to lower forage quality. Boudewijn (1984) demonstrates a gradual decline of forage quality of agricultural grassland due to ageing of the sward in the course of spring and argues that the diminishing profitability of this habitat enforces Brent Goose foraging on the salt marshes. Plant production is supposed to start later at the salt marshes. Spring staging Barnacle Geese switch from agricultural pastures to adjacent salt-marsh sites as soon as the nitrogen content of forage plants is on a par between the two habitat types (Prins & Ydenberg 1985). An additional causal factor explaining the habitat shift was put forward by Prins and Ydenberg (1985) who argued that Barnacle Geese utilise the *Festuca rubra* sward on the salt marsh more efficiently than pasture grass species due to lower levels of disturbance on the marsh habitat.

We here analyse spring habitat use of Brent and Barnacle Geese on the Dutch Wadden Sea island of Schiermonnikoog in the light of large-scale changes in goose scaring practices by farmers which provide an experiment to study the influence of disturbance on habitat switches in geese. We studied the use of pasture and salt-marsh habi-
tats by staging geese during five consecutive years (1997, 1998 and 1999 with active scaring of geese on agricultural pastures, and 2000 and 2001 totally without harassment), and collected data on the seasonal characteristics of the main forage plants.

Study area

We conducted our study on the Dutch barrier island Schiermonnikoog (Figure 3.1; 53°30’N, 6°10’E), which features an embanked pasture area (polder, 290 ha), a cattle grazed salt marsh (185 ha) and a large area of ungrazed salt marsh (1450 ha). The pastures, used to produce grass for silage and grazed by cattle between May and November, consist of homogeneous swards of mainly *Lolium perenne* and *Poa* spp.. The pastures are heavily fertilised with approximately 400 kg N.ha⁻¹yr⁻¹ of artificial fertiliser in addition to the application of manure. The salt marsh of Schiermonnikoog is grazed by cattle at a stocking rate of 0.5 cow.ha⁻¹ on 400 ha, from the end of May until October and remained unfertilised since the beginning of the 1990s. The long-term ungrazed salt marsh of Schiermonnikoog is characterised by a declining age of the marsh from West (ca. 100 years old) to East where the island is still extending (detailed description see Olff *et al.* 1997). The European Brown Hare *Lepus europaeus* is a resident grazer of all plant communities frequently used by geese (pers. observation). Hare numbers on the ungrazed salt marsh fluctuate between 300 and 500 animals.

Figure 3.1  Map of the island of Schiermonnikoog, indicating the major habitats utilised by geese (agricultural pastures in the polder, low and high salt marsh) and the focal study site on the ungrazed marsh.
Methods

Spatial distribution of geese

Between 1997 and 2001, we performed regular censuses to assess the total number of Brent and Barnacle Geese on the island and their distribution over the major habitat types. These counts covered the entire island following a fixed route with alternating direction between counts. Counts were independent of the tidal regime. We carried out additional counts in the pasture area at various times during daylight.

On the ungrazed salt marsh, we determined spring habitat use by geese using a range finder (Leica Vector 1000 binocular, 7 x 42), which measured the distance and compass angle between the centre of a goose flock and the observer from fixed observation points. A flock was defined as a cluster of geese of one species, either separated from other geese by at least 50 m, or foraging on a different plant community than other geese present. For groups larger than 200 individuals, multiple measurements were obtained for subgroups of c. 200 individuals. We entered the data in a Geographical Information System (GIS) and combined them with an existing vegetation map of the study site (Kers et al. 1998). The vegetation map (scale 1:5000) dated from 1996 and was based on a comprehensive ground survey guided by aerial photographs. The units of the map legend conform to the classification by Schaminée et al. (1998), and referred to plant communities at the association level. We restricted our analyses to the eastern part of the ungrazed marsh (938 ha), where the fixed observations points had an elevation of at least 5 m above MHT and to a circular area within 650 m of these observation points to prevent bias due to limited visibility. For the purpose of the analyses, we grouped plant communities with a short canopy on the low (Salicornietum, Puccinellietum maritimae and Plantagini-Limonietum) and the high marsh (Armerio-Festucetum, Juncetum gerardii and Artemisietum maritimae). The Artemisietum maritimae is included as the canopy of this plant community is still low and dominated by Festuca rubra in spring in our study area. We calculated the density of geese in these communities with a short canopy for the low and the high salt marsh. The areas of the plant communities, as well as the number of geese observed within these zones were deduced from the GIS database.

Vegetation parameters

We estimated the seasonal development of standing aboveground biomass, primary production and forage quality of food plants for geese using bi-weekly sampling schemes at six sites on the low and the high livestock-ungrazed salt marsh, and five sites in the pasture area in 1998. The sites on the marsh were located on a transect from East to West, within the community dominated by Festuca rubra (Armerio-Festucetum) on the high marsh and the community characterised by Puccinellia maritima (Plantagini-Limonietum) on the low marsh. The distance between each of the sites was approximately 800 m and age of the marsh ranged along the gradient from 10 - 50 years. The sampling sites in the pastures were regularly distributed over the southern half of the pasture area at intervals of approximately 600 m. We sampled Lolium perenne, Poa spp.
in the polder and *Festuca rubra*, *Puccinellia maritima*, *Plantago maritima* and *Triglochin maritima* in the salt marsh, being important forage plants for geese (Prop & Deerenberg 1991; van der Wal et al. 2000). We estimated the net biomass increase of the forage plants (Net Accumulated Primary Production, g dry.m\(^{-2}\).d\(^{-1}\)) from the difference of standing biomass between two sampling periods for plots excluded from grazing. For this purpose, we used mobile exclosures with a surface area of 0.5 m\(^2\) (chicken wire, mesh width 5 cm). Standing live biomass of the forage plants was assessed by clipping all above ground material from 15 cm diameter turves, which we sorted, washed, dried (48 h at 70°C) and weighed to the nearest 10 mg. We determined the nitrogen content of leaf tips (upper 2 cm) of *Festuca rubra*, *Puccinellia maritima* and a mixture of the pasture grasses as a measure of forage quality. Plant samples were collected at all sampling sites during spring 1998. The samples were washed, air-dried at 70°C for 48 h and subjected to an automated CNHS-analysis (Interscience EA 1110).

We used data from the weather station of the Free University Amsterdam on Schiermonnikoog to assess precipitation on the island for the period of January through April to obtain the date at which a temperature sum of 180°C was reached in the years 1997 to 2001. The temperature sum reflects the sum of positive averages of minimum and maximum air temperature per day from 1 January onwards and is used as an indication for the starting date of grass growth.

**Scaring regime - a large-scale experiment**

During the first three years of our study (1997-1999) an active scaring policy was effective on Schiermonnikoog to prevent geese feeding on the agricultural pastures (Bazuin & van der Wal 1991). In the attempt to drive geese from the pastures to the adjacent salt-marsh sites in order to protect the first spring harvest of grass, farmers scared geese daily using flares in addition to more traditional techniques, such as scarecrows and flags. On average, 160 flares were used each spring (pers. comm. J.B. Bazuin). Apart from normal agricultural activities there was little further disturbance except for low-intensity search for the first Lapwing *Vanellus vanellus* eggs during March and the first week of April following local tradition.

For the spring seasons of 2000 and 2001, the government implemented a new goose management scheme, which incurred increased financial compensation of goose damage to local farmers, under the stringent condition that no goose scaring of any sort was to be undertaken. From January 2000 onwards, the shooting of flares was banned and the presence of people other than the farmer himself on the pastures was restricted to the late afternoon (after 16:30, pers. comm. T. Talsma). According to our observations the local people obeyed the rules strictly. To quantify the effect of the different scaring regimes we compared data on disturbances collected in the pasture habitat during the spring seasons 1998 to 2001. Focal goose flocks foraging on agricultural pastures were selected randomly and followed during at least 1 hour. We noted all disturbances with an identifiable human related cause. We defined an event as disturbance when more than 50% of the flock flew up. The number of tourists visiting
Schiermonnikoog, another potential source of disturbance for geese, varied by less than 10 % between the five years of our study (pers. comm. Administration Wageningen Ferry Service) and we, therefore, assume that this factor did not influence the large-scale scaring experiment related to the pasture area. In the pasture area the activities of tourists were virtually restricted to passing by on bicycle, keeping to the paved paths, and generally ignored by the geese. From 15 April onwards, each year the eastern salt marsh (a breeding bird reserve) was closed to the public entirely.

**Movements of individual birds**

To analyse switches of individual geese between staging sites and between habitat types, we used sightings of ringed Brent Geese. From the 1970s onwards, Brent Geese are marked individually with coded colour leg bands within the Brent Goose ringing scheme either on the Siberian breeding grounds or at the European wintering sites and data on re sightings are available through the ring data base maintained by Bart Ebbing and Gerard Müssens (Alterra, Wageningen, The Netherlands). On Schiermonnikoog, Brent Goose flocks in the pasture and the salt-marsh habitat were scanned regularly for the presence of ringed individuals during the entire staging period. For the purpose of this study, we analysed sightings of Brent Geese on the island from May 2000 and May 2001 (the two seasons when scaring was banned) and deduced the staging history of these individuals during previous years from the long-term data base.

**Data analyses**

Census results were averaged for bi-weekly periods for the years 1997-1999 (active scaring) and 2000-2001 (no scaring), thereby combining data from different years according to the scaring regime. For the pastures and the salt marsh, we tested differences of goose numbers between years with and without scaring using Mann-Whitney U tests for each species and each period. To test differences of the distribution of colour-ringed Brent Geese between habitat types and between years with different scaring regimes, we applied chi square statistics.

For the salt marsh, differences in goose density between plant communities with short canopy on the low and the high salt marsh were tested per month using General Linear Modelling (GLM) with species and salt-marsh zone as well as the interaction term as fixed factors. Variation in forage quality, standing biomass and production of forage plant species was analysed using GLM, with plant species as a fixed factor and day number as well as day number-squared as co-variates. We accounted for possible interactions between the independent variables. Any non-significant factors were removed stepwise from the model and final models were defined through a post-hoc Tukey’s test. When appropriate, data were square root transformed \( y' = \sqrt{(y+0.5)} \) for count data or log-transformed \( y' = \lg_{10}(y+1) \) for vegetation parameters to obtain homogeneity of variances before entering statistical testing, however, untransformed data are given in the graphs. Statistical analyses were carried out with SPSS 10.1 (SPSS Inc.).
Results

Habitat use in years with and without scaring

Table 3.1 reviews human related disturbances for the pasture habitat during years with differing scaring regime. We recorded hardly any human disturbances that caused flocks to fly up after the ban on active scaring from spring 2000 onwards.

The patterns of habitat use by Brent and Barnacle Geese during spring are summarised in Figure 3.2, which compares the scaring years with the non-scaring experimental years. Almost the entire local populations of both goose species foraged in pasture habitat until the second half of February. From then on, large numbers of Barnacle Geese were observed on the salt marsh (Figure 3.2D), and numbers on the agricultural pastures started to decrease (Figure 3.2C). Brent Goose numbers on the marsh increased gradually during March and April (Figure 3.2B), reaching the maximum in May just prior to departure for the breeding grounds.

The use of the agricultural habitat differed markedly between years with an active goose scaring regime (1997-1999) and years when goose scaring was banned (2000-2001). Barnacle Goose numbers in the agricultural habitat declined sharply during February in years with active disturbance, but showed a delayed decline in the absence of scaring, considerable numbers remaining until the end of April (Figure 3.2C). During March and the beginning of April, the number of Barnacle Geese in the pasture habitat differed by more than a factor three between the two scaring regimes. It will be noted that the total contingent of Barnacle Geese staging on the island was higher in the non-scaring years. Brent Goose numbers in the pasture habitat increase until the beginning of March, as new birds arrive from wintering grounds in France and Great Britain (Figure 3.2A). In years with active scaring, Brent Goose numbers decline after mid-March in the pasture habitat (Figure 3.2A), as birds switch to the salt-marsh habitat (Figure 3.2B). While in these years Brent Geese were almost absent from the agricultural habitat by the beginning of May, Brent numbers remained high (with on aver-

Table 3.1  Frequency of human disturbances in the pasture habitat 1998-2001; observation periods were corrected for the number of geese observed and are then given as goose hours.

<table>
<thead>
<tr>
<th>Year</th>
<th>scaring</th>
<th>observation effort (hrs)</th>
<th>observation effort in goose hrs.</th>
<th>human disturbances per 10,000 goose hrs.</th>
<th>observation period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>yes</td>
<td>24</td>
<td>30800</td>
<td>6.5</td>
<td>9 March till 15 April</td>
</tr>
<tr>
<td>1999</td>
<td>yes</td>
<td>40</td>
<td>14724</td>
<td>6.8</td>
<td>23 March till 10 May</td>
</tr>
<tr>
<td>2000</td>
<td>no</td>
<td>14</td>
<td>15000</td>
<td>0</td>
<td>2 May till 4 May</td>
</tr>
<tr>
<td>2001</td>
<td>no</td>
<td>39</td>
<td>72000</td>
<td>0.3</td>
<td>5 May till 27 May</td>
</tr>
</tbody>
</table>
Figure 3.2  Spring numbers of Brent (panel A and B) and Barnacle Geese (panel C and D) on the polder (agricultural pasture) and salt marsh of Schiermonnikoog for years with (1997-99) and without (2000-01) active disturbance by farmers. Bars represent periods of two weeks and comprise several goose counts as indicated on top of the graphs. Asterisks indicate significant differences in goose numbers between the two scaring regimes ($P < 0.05$).

Table 3.2  The average number of Brent and Barnacle Geese on Schiermonnikoog during March, April and May 1997-2001 and spring temperature and precipitation as a proposition of growth conditions for forage plants; $T_{sum}$ 180 indicates the date at which the sum of positive averages of minimum and maximum daily air temperature reaches 180°C (starting from 1 January) and is used as a reference for the start of grass growth.

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean number of Barnacle Geese</th>
<th>Mean number of Brent Geese</th>
<th>Number of counts</th>
<th>$T_{sum}$ 180</th>
<th>Precipitation until 1 May (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>March April May</td>
<td>March April May</td>
<td>March April May</td>
<td>1 May</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>4627 1959 2</td>
<td>2056 1681 1755</td>
<td>6 10 11</td>
<td>1 March</td>
<td>117</td>
</tr>
<tr>
<td>1998</td>
<td>4567 3341 26</td>
<td>2289 2385 1615</td>
<td>6 7 9</td>
<td>11 February</td>
<td>239</td>
</tr>
<tr>
<td>1999</td>
<td>6875 3048 12</td>
<td>1689 2237 1624</td>
<td>3 4 4</td>
<td>no data</td>
<td>226</td>
</tr>
<tr>
<td>2000</td>
<td>7333 3513 188</td>
<td>2462 3918 5273</td>
<td>5 5 3</td>
<td>5 February</td>
<td>187</td>
</tr>
<tr>
<td>2001</td>
<td>13012 2946 570</td>
<td>3322 3302 3889</td>
<td>1 1 1</td>
<td>8 March</td>
<td>194</td>
</tr>
</tbody>
</table>
age 2,000 birds in May) after the ban of active scaring by farmers. The total population of Brent Geese on the island in May was thus doubled after scaring was banned in the pasture habitat (Table 3.2).

**Movements of individually marked Brent Geese**

Figure 3.3 summarises the staging history of individually marked Brent Geese observed in the pasture habitat and on the salt marsh during the spring seasons of 2000 and 2001 when active scaring was banned on Schiermonnikoog. While 25 out of 32 rings recorded on the salt marsh had been regular visitors of that distinct site during previous years, only 12 out of 28 rings recorded on the agricultural pastures had been previously observed there ($\chi^2 = 6.44$, Yate's corrected, $P = 0.011$). In the agricultural habitat, 16 individuals had not been recorded on Schiermonnikoog at all prior to the cessation of active scaring. Eight of these were sighted as staging birds along the Groningen mainland coast in other years, while three individuals had previously staged on the island of Texel, Terschelling or Ameland, respectively. For the remaining five individuals no staging records were available for previous years. Our pasture records do not allow us to judge whether the same individuals were present in both non-scaring years as there are only few records for May 2000. On the salt marsh, four out of seven newcomers stem from mainland staging sites at Groningen coast, one from Texel and two from the Friesian mainland coast. Out of the salt-marsh group, on average 74% of the ringed individuals seen in one year had been recorded at that distinct site the year before. No Brent Geese that were seen in the pasture habitat in May had a record of staging on the salt marsh of Schiermonnikoog. Similar staging histories account for the salt-marsh group: none of the Brent Geese recorded at our focal salt-marsh site was observed at the pasture site in May, during any of the study years.

![Figure 3.3](image)

**Figure 3.3** Spring history of individually marked Brent Geese recorded on the eastern salt marsh and on the agricultural pastures during May 2000 and 2001, after goose scaring was banned from the island.
Habitat differences concerning food availability

Biomass production of plant species common in the diet of Brent and Barnacle Geese (*Festuca rubra*, *Puccinellia maritima*, pasture grasses) strongly increased during spring (Figure 3.4A). On the agricultural pastures, this increase was significantly steeper than on either high or low salt-marsh habitats (GLM: interaction between plant community

![Figure 3.4](image_url)

**Figure 3.4** Spring phenology of forage plants during 1998. A) Increase in primary production (g dry-weight.m\(^{-2}\).day\(^{-1}\)), B) Increase in above-ground living biomass of forage plant species (g dryweight.m\(^{-2}\)) and C) Development of the nitrogen content of grasses in the polder (pasture grasses), on the high (*Festuca rubra*) and the low (*Puccinellia maritima*) salt marsh, calculated as mean + SE. Different letters indicate significant differences between regression lines. Lines drawn by eye.
and day number $F_{2,63} = 4.3, P = 0.018, R^2 = 0.62$, simple contrasts). Biomass production on the low salt marsh started only in the second half of April and overall production was low (less than $2 \text{ g.m}^{-2}\text{.d}^{-1}$). The high salt marsh was intermediate in terms of primary production when compared to the low marsh and the pasture habitat, still plant growth started early and values exceeded $1 \text{ g.m}^{-2}\text{.d}^{-1}$ during the second half of March already. Standing biomass followed the same pattern as primary production with lowest amounts of biomass ($0-10 \text{ g.m}^{-2}$) on the low marsh and highest values (over $200 \text{ g.m}^{-2}$) in the pasture habitat at the end of spring (Figure 3.4B; GLM, interaction between plant community and day number $F_{2,91} = 4.19, P < 0.001, R^2 = 0.82$).

The seasonal development of forage quality, measured as nitrogen content of leaf tissues, followed similar trajectories for all forage species sampled (Figure 3.4C). Nitrogen content first increased slightly during early April and then decreased, as the growing season proceeded. The data are best described by a regression model with day number ($F_{1,99} = 0.029, P < 0.001$), day number-squared ($F_{1,99} = 0.052, P < 0.001$) and forage species ($F_{2,99} = 40.8, P < 0.001$) as independent variables ($R^2 = 0.764$). *Festuca rubra* showed the lowest nitrogen content compared to pasture grasses and *Puccinellia maritima* during the entire spring season.

**After the switch - goose distribution on the marsh**

Densities of Barnacle Geese were significantly higher on the high marsh as compared to the low marsh for both March and April, although the species also frequently used low marsh sites in March (Figures 3.5A, B). Barnacle Geese leave for their breeding quarters by the last week of April (Figure 3.5 C). Brent Goose densities tended to be

![Figure 3.5](image)

*Figure 3.5* The average density of Brent and Barnacle Geese visiting plant communities with a short canopy on the low and the high salt marsh during March (A), April (B) and May (C). Different letters indicate significant differences between mean goose densities. The number of goose counts is indicated as n. Data comprise the years 1997-2000.
higher on the low as compared to the high marsh during all months although this difference was only significant for the month of May. During March and April, there is considerable overlap in the use of the two zones of the salt marsh by both goose species at this level of scale. For each month the interaction between goose species and salt-marsh zone explained significant variation (GLM, interaction term March: $F_{1,80} = 15.90, P < 0.001$, $R^2 = 0.47$, April: $F_{1,80} = 10.01, P < 0.005$, $R^2 = 0.137$, May: $F_{1,80} = 9.20, P < 0.005$, $R^2 = 0.67$).

Discussion

The nature of the habitat switch and the trigger effect of scaring

In all five years of our study, we have observed that large numbers of Barnacle and Brent Geese gradually shift the focus of their foraging activities from the agricultural pasture habitat to the salt marsh (Figure 3.2). In years when farmers were scaring the geese to protect the first cut of grass, Barnacle Goose usage of the pasture habitat declined from mid-February onwards. Brent Goose numbers started to decline in the same area from mid-March, one month later. Without scaring activities in the years 2000 and 2001, the average number of geese in the agricultural area was significantly higher towards the end of the staging period for both species when compared to years with scaring (Figures 3.2A & C). We conclude that scaring contributed substantially to an early departure from the pasture habitat in spring. It is striking that total goose numbers utilising the salt marsh were closely similar for both species over the entire spring period, suggesting that this habitat was used to capacity. Geese foraging in the pasture in years without active scaring during late spring represent additional immigrants from other staging sites. Our information from reading coded legbands casts some light on this problem, at least for the Brent Geese, which received intensive study each spring season. In keeping with our long-term data base, individuals observed out on the eastern salt marsh tended to return each year both with and without scaring, and represent a stable staging strategy centred on the traditional habitat. By contrast, the ringed birds feeding in the pasture habitat in the past two (non-disturbed) years have a different history. In contrast to the marsh contingent, where a minority (7/32) were new sightings, a majority of the individuals in the pasture area (16/28) were new to the island. We assume that normally these Brent Geese would have passed by, but now were induced to stay for a prolonged period. Hence, the cessation of scaring has been the starting point for the Brent Geese to form a novel staging strategy utilising the pasture habitat during the entire spring period. We commenced systematic goose watching on the island in 1973, and never before observed a concentration of Brent Geese present in the enclosed pasture land right up to departure for the breeding grounds in late May. That the complete absence of harassment by flares is a necessary prerequisite to this new tradition does not mean that this is the only condition to apply. We will argue in the next section that the pasture can only be exploited effectively by Brent Geese if they are able to exert a concentrated (and unbroken)
grazing regime and thus maintain a portion of the pasture habitat in the early growth stage conducive to efficient goose usage. Freedom from disturbance sets the stage as it were.

It is intriguing to compare our data with the results of experimental implementation of refuges set-aside from hunting disturbance in Denmark (Fox & Madsen 1997; Madsen et al. 1998). In these experimental reserves, a large and rapid increase in the number of dabbling ducks following protection from hunting was observed. This showed that the ducks could increase their length of stay at the Danish staging sites, if habitat conditions were adequate. In contrast, Ganter et al. (1997) presented a case study from a Brent Goose staging site at the German Wadden Sea coast of Schleswig-Holstein, where salt-marsh habitat was lost due to embankment. Ganter et al. (1997) detected frequent long-distance movements of individually marked Brent Geese, displaced by the loss of their staging habitat. In their study, human activities negatively affected the conditions of the spring staging site, destroying a staging tradition and forcing geese to look for new opportunities elsewhere.

There were still sources of disturbance in the pasture area in the ‘non-scaring’ years, related to tourism (including traffic) and normal agricultural activities. Both increase in intensity over spring. However, the birds seemed to adapt quickly to the new situation and flew up less frequently in reaction to these ordinary sources of disturbance as compared to years with scaring (Table 3.1). Finally, we must emphasise the role of tradition and local knowledge. Although geese are obviously opportunistic and able to respond quickly to the presence of newly available habitat (van Eerden 1984; Zijlstra et al. 1991; this study), it has also been demonstrated that many individuals are very faithful to their staging sites. Brent Geese utilising the eastern part of the salt marsh at our study site form a very distinct group and it is interesting to note that none of these birds opted for spring staging in the pasture habitat. This gives rise to the speculation that individuals making what amount to last-minute site decisions recruited to the newly available pasture site. It would be interesting to know the previous history of these geese in more detail, in particular if they had experienced unfavourable conditions the previous year. In Pinkfooted Geese Anser brachyrhynchus for example, Madsen (2001) showed that individuals not attaining the abdominal profile index corresponding to breeding condition were more prone to shift spring staging site the next year.

In contrast to the situation described by Prins & Ydenberg (1985) for Barnacle Geese, the switch to the marsh was not an absolute departure from the polder habitat at a specific moment in recent years, but took place more slowly. In connection with this more gradual course of the habitat shift, it is interesting to note that Barnacle Geese tend to prolong their total staging period at Dutch staging sites during recent years and flocks can be observed at the mainland coast as late as mid-May (Koffijberg et al. 1997). Brent Goose numbers also build up gradually on the marsh over spring. We have discussed several processes that can explain such a gradual change, notably an increasing primary production on the marsh allowing for an increase in grazing pressure over time, a decreasing nutrient intake rate on the polder and increasing recreational pressure in the course of spring. The order in which the two habitats are
utilised coincides with the seasonal development of primary production at each site, supporting the idea that forage availability is limiting on the marsh in early spring. This shows a clear analogy with the winter situation, where the same switch is observed in the opposite direction (Vickery et al. 1995; Rowcliffe et al. 2001).

**The goose grazing cycle in the pasture habitat**

With increasing age or standing biomass of the sward, a decline in forage quality is often observed (van Soest 1994). This effect of forage maturation occurs on the salt marsh (Stahl et al. 2001) as well as in the pasture habitat (Boudewijn 1984; chapter 5). Additionally, there are clear indications that small species of waterfowl, such as the Brent Goose, suffer from a declining intake rate of matter when grass swards grow tall (chapter 5). For Wigeon *Anas penelope*, this phenomenon is well established (Durant 2001). A declining rate of biomass intake, in combination with declining forage quality, leads to a preference of Brent Geese for swards with intermediate values of standing crop (Vickery & Sutherland 1992; Riddington et al. 1997; Hassall et al. 2001; chapter 5). Under undisturbed conditions the geese will cope with increasing primary production of their forage plants in spring by means of aggregation of their foraging activities in one sub-area. Through an increase of the frequency of grazing visits to one area, they are able to maintain a short, suitable sward in part of the available habitat (Spaans & Postma 2001; chapter 5). In the years without scaring on Schiermonnikoog, all grazing was concentrated on a single field by the end of May and the average number of birds on this field had increased by more than a factor two in comparison to March (chapter 5). At this site, the consumption of the major part of primary production maintained a short sward, while the vegetation grew tall in the remainder of the pastures (Figure 3.6A). An exclosure experiment at the Brent Goose reserve on Texel, demonstrated that this pattern was consistent with the hypothesis that Brent Geese have a preference for short swards. In that experiment, geese preferred patches with a short canopy over patches with a tall canopy, experimentally established using short-term exclosure in the same field (chapter 5). Without continuous grazing, the profitability of highly productive agricultural grassland as feeding habitat for Brent Geese diminishes quickly. This applied for example during the years with scaring and in the study by Boudewijn (1984).

These observations during the phase of rapid spring growth underline the importance of facilitation in maintaining the sward in a close-cropped stage, permitting efficient harvest by the geese. On the Dutch barrier island of Ameland, we observed a concentration of goose grazing towards the end of May, in pastures that were also grazed by sheep (chapter 4). Figure 3.6 illustrates the close analogy in development of the canopy for swards that are maintained by Brent Geese until May, and for ungrazed swards, at the three islands mentioned. Ungrazed pastures at each study island quickly developed a tall sward, while intensive grazing maintained a short sward. On Ameland sheep grazing assisted the Brent Geese in doing so (chapter 4). Recent grazing experiments with Brent and Barnacle Geese at salt-marsh sites on Schiermonnikoog demonstrated that Brent Geese show a strong feeding preference for swards of *Festuca rubra,*
Figure 3.6  The seasonal development of canopy height in agricultural grass swards when continuously grazed by geese as compared to ungrazed swards. A) Schiermonnikoog spring 2000 (this study, chapter 5), B) Texel spring 2000, ungrazed plots were experimentally fenced from the beginning of March (chapter 5), C) Ameland spring 1998, ungrazed plots were left aside by the geese from April onwards; maintained plots were grazed by geese as well as sheep (chapter 4). The grey bar indicates a range of canopy heights, for which it is assumed that it can be most efficiently grazed by Brent Geese, as derived from experimental data presented in chapter 5.
previously grazed (and thereby maintained at higher forage quality) by Barnacle Geese within the same staging season (Stahl et al. 2001). Further exclosure experiments are called for to ascertain the presumed facilitative effect of the heavy spring grazing by Barnacle Geese on pastures preceding usage by the Brent on the same fields.

**Habitat use on the salt marsh**

The two species of geese studied differ in their use of the salt marsh. Barnacle Geese start using the marsh earlier in the season than Brent, and are recorded in higher numbers on the high marsh. Brent Geese, on the other hand, concentrate most of their grazing on the low salt marsh (Figure 3.5). On the high marsh, Barnacle Geese mainly consume *Festuca rubra* (Prop & Deerenberg 1991), with the effect of quality enhancement of the forage through repeated grazing (Prins & Ydenberg 1985; Stahl et al. 2001). Nevertheless, the nitrogen content is lowest for *Festuca* in comparison to all forage species sampled (Figure 3.4C). Standing biomass and forage production, by contrast, are higher on the high marsh (Figure 3.4A & B) as compared to the low marsh. This may explain why grazing pressure by geese is higher on the high than on the low marsh in early spring.

**Pasture and marsh as alternative foraging habitat**

It is infeasible to appoint a single parameter as main trigger for the habitat decision in staging geese. So far, we discussed the role of disturbance regimes, staging traditions and facilitative grazing by conspecifics or other herbivores and its influence on plant phenology. Differences in forage characteristics (plant availability and the nutrient mix) between the two habitat types directly interact with intake rates and can form a prime key for habitat decisions. The main forage species on the marsh (*Festuca rubra* and *Puccinellia maritima*) contained less nitrogen than the pasture grasses, and this relative difference in forage quality between habitat types even increased over time. As we measured forage quality in terms of nitrogen content only, we cannot exclude plant fibre content, amino-acid composition or contents of other nutrients in leaf tissue as parameters differentiating habitats. Our data showed that nitrogen content of salt-marsh grasses alone cannot explain the attractiveness of the marsh habitat during the years of our study. The presence of the plant species *Triglochin maritima* and *Plantago maritima* increases attractiveness of the marsh for Brent Geese. The nitrogen content of both plant species is prominent as compared to the grass species (May: *Plantago maritima* 3.6% ± 0.22 s.e., n = 7; *Triglochin maritima* 4.7% ± 0.18 s.e., n = 6) and intake rates are high for these plants (Prop & Loonen 1989; Prop 1991; Prop & Deerenberg 1991).

The overall standing biomass of food is lower on the salt marsh, and the translation of this parameter into intake rates remains to be studied in detail. Preliminary studies with captive geese did not reveal higher rates of biomass-intake for Barnacle Geese on either *Puccinellia maritima* or *Festuca rubra* swards when compared to pasture grasses,
but our first data on Brent Geese point to higher rates of intake on the marsh (Heuer-mann 2001). As primary production is limited on the marsh, goose numbers can only increase gradually in this habitat, following the increase in biomass production during the season. Although the pasture habitat has been largely unattractive in the past due to scaring by farmers, an early habitat switch of the majority of geese was restricted by limited forage production on the marsh. The cessation of scaring allowed an increased utilisation of agricultural grassland through the aggregation of geese in space and time, as a response to the high primary production here.

In conclusion of our analyses, we want to emphasise that the best choice between alternative staging habitats remains above all an individual choice for birds differing in their needs and prospects (e.g. concerning subsequent breeding) as well as their ability to cope with habitat characteristics (e.g. disturbance). The case study of Schiermonnikoog demonstrated that the creation of new spring foraging opportunities for geese in an agricultural habitat mainly attracted birds from other staging sites, obviously eager to explore new sites, while birds with an island pedigree kept with their traditional habitat switch to the salt marsh. The study of the repercussions of these individual decisions in terms of reproductive benefits remains duty of continued investigation during the coming years.

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References


de Boer WF, Drent RH (1989) A matter of eating or being eaten? The breeding performance of Arctic geese and its implications for waders. WSG Bull. 55: 11-17

Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anatidae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle


Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese Branta b. bernicla in the high Arctic. J. Avian Biol. 26: 105-113


Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. Ardea 89: 427-440


Young sheep on the "Nieuwlandsreid", the livestock-grazed salt marsh on Ameland (photo A.J. van der Graaf).