CREATING NEW FORAGING OPPORTUNITIES FOR DARK-BELLIED BRENT *BRANTA BERNICLA* AND BARNACLE GEESE *BRANTA LEUCOPSIS* IN SPRING - INSIGHTS FROM A LARGE-SCALE EXPERIMENT

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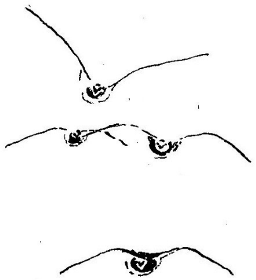

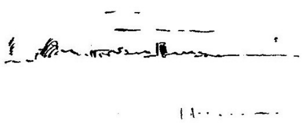

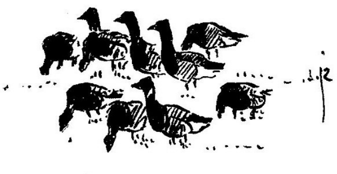

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The implementation of a new non-disturbance policy on Schiermonnikoog (Dutch Wadden Sea islands) provided an experiment to test ideas concerning the switch between habitats by spring-staging Dark-bellied Brent Geese *Branta bernicla* and Barnacle Geese *B. leucopsis*. In the experimental years (2000 and 2001) the farmers desisted from all scaring activities in the enclosed 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 (Apr for the Barnacle Geese, late May for the Dark-bellied 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 Dark-bellied 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.

Keywords: *Branta bernicla* – *Branta leucopsis* - salt marsh - agricultural grassland – herbivory – forage quality - disturbance

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INTRODUCTION

During the spring staging period of Dark-bellied Brent Geese *Branta 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 Mar. 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 Dark-bellied 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 (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 Dark-bellied 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 Dark-bellied 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 Red Fescue *Festuca rubra* sward on the salt marsh more efficiently than pasture grasses due to lower levels of disturbance on the marsh habitat. Following this line of reasoning, it can be expected that staging geese extend their period of use of agricultural swards in spring under circumstances when the influence of human disturbances is minimized in this habitat type.

We here analyse spring habitat use of Dark-bellied 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 habitats 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.

METHODS

Our study was conducted on the Dutch barrier island Schiermonnikoog (53º30’N, 6º10’E; Fig. 1), 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 Nov, consist of homogeneous swards of mainly Perennial Ryegrass *Lolium perenne* and Meadow-grass *Poa spp.*. The pastures are heavily fertilised with approximately 400kg N $ha^{-1}yr^{-1}$ of artificial fertiliser in addition to the application of manure. The western part of the salt marsh of Schiermonnikoog is grazed by cattle at a stocking rate of 0.5 cow ha^{-1} from the end of May until Oct and has 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 in all plant communities frequently used by geese (pers. observation).

Spatial distribution of geese

Between 1997 and 2001, weekly counts of the total number of Dark-bellied Brent and Barnacle Geese on the island were performed and the distribution of geese over the major habitat types was assessed. These counts followed a fixed route with alternating direction between counts. Counts were independent of the tidal regime. Up to three additional counts in the pasture area were carried out every week at varying moments during daylight.

On the ungrazed salt marsh, spring habitat use by geese was determined using a range finder (Leica Vector 1000 binocular, 7 x 42) measuring 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 50m, 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. In a Geographical Information System (GIS) this information was combined with an existing vegetation map of the study site (Kers *et al.* 1998). The units of the legend refer to plant communities at the association level (Schaminée *et al.* 1998). The analyses were restricted to the eastern part of the ungrazed marsh (938 ha), where the fixed observations points had an elevation of at least 5 m above Mean High Tide and to a circular area within 650 m of these observation points to prevent bias due to limited visibility. 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) were pooled. We calculated the density of geese in these short-canopy communities for the low and the high salt marsh. The Artemisietum maritimae is included as the canopy of this plant community is still low and dominated by Red Fescue in spring in our study area. The surface areas of the plant communities as well as the number of geese observed within these zones were deduced from the GIS database.

Vegetation parameters

The seasonal development of standing above ground biomass, primary production and forage quality of food plants for geese was estimated at the eastern part of the salt marsh, and in the pasture area in 1998. The sites on the marsh were located within the community dominated by Red Fescue (Armerio-Festucetum) on the high marsh (n = 6) and the community characterised by Common Salt-marsh Grass *Puccinellia maritima* (Plantagini-Limonietum) on the low marsh (n = 6). The sites in the pasture were located in the southern half of the pasture area. We measured the net biomass increase (Net Accumulated Primary Production NAPP in g dryweight m^{-2} d^{-1}) of the main forage plants (Prop & Deerenberg 1991, van der Wal *et al.* 2000): Perennial Ryegrass, Meadow-grass, Red Fescue, Common Salt-marsh Grass, Sea Plantain *Plantago maritima* and Sea Arrow Grass *Triglochin maritima*. 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 turfs, followed by sorting, washing, drying (48 h at 70^{o}C) and weighing of the plant material to the nearest 10 mg. As a measure of forage quality, the nitrogen content of leaf tips (upper 2 cm) was determined for Red Fescue, Common Salt-marsh Grass and the pasture grasses through an automated CNHS-analysis (Interscience EA 1110). With the help of data from the weather station of the Free University Amsterdam on Schiermonnikoog we assessed precipitation on the island for the period of Jan through Apr and obtained the date at which a temperature sum of 18º C is 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 Jan onwards and is used as an indication for the starting date of grass growth.

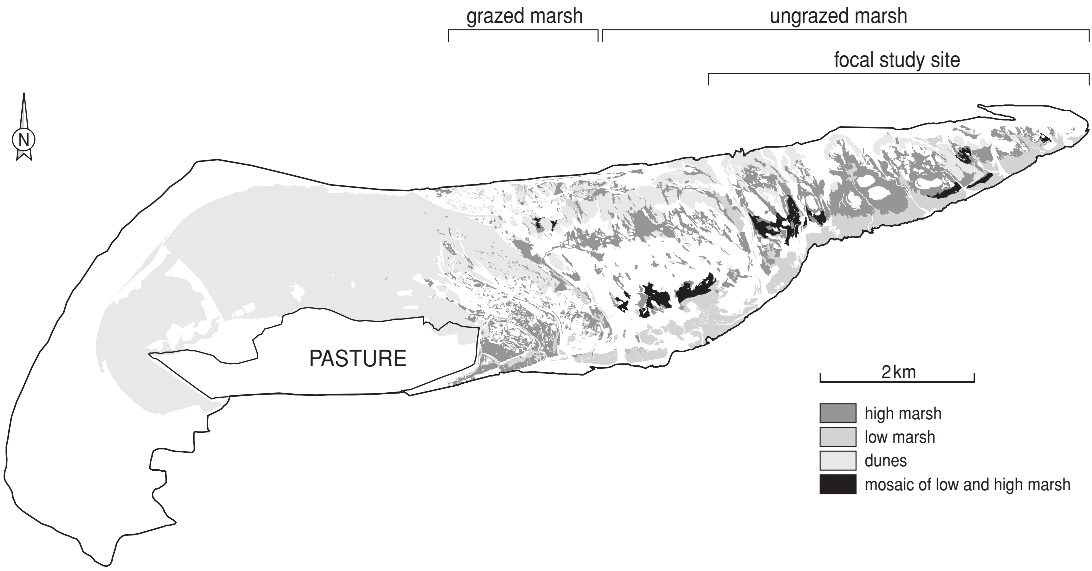

Fig. 1. Map of Schiermonnikoog, indicating the major habitats (agricultural pastures, low and high salt marsh) and the focal study site on the ungrazed marsh.

Scaring regime - a large-scale experiment

During the first three years of our study (1997-99) an active scaring policy was effective on Schiermonnikoog to prevent geese feeding on the agricultural pastures. In the attempt to drive geese from the pastures to the adjacent salt-marsh sites, farmers scared geese daily using flares, scarecrows and flags. On average, 160 flares were used each spring (B. Bazuin, pers. comm.). Apart from normal agricultural activities there was little further disturbance except for low-intensity search for Lapwing *Vanellus vanellus* eggs during Mar and the first week of Apr, 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 Jan 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 , T. Talsma, pers. comm.). According to our observations the local people obeyed the rules strictly. 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 Wagenborg Ferry Service) and it is therefore assumed 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. Each year, the eastern salt marsh is closed to the public entirely from 15 Apr onwards. To quantify the effect of the different scaring regimes, data on disturbance events were compared 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. All disturbances with an identifiable human related cause were noted. An event was defined as disturbance when more than 50% of the flock took off.

Movements of individual birds

With the help of sightings of ringed Dark-bellied Brent Geese, switches of individual geese between staging sites and between habitat types were analysed. From the 1970s onwards, Dark-bellied Brent Geese are marked individually with coded colour leg bands within the Dark-bellied 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 Ebbinge (Alterra, The Netherlands). On Schiermonnikoog, Dark-bellied 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 Dark-bellied 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 Dark-bellied Brent Geese between habitat types and between years with different scaring regimes, we applied χ^2statistics. For the salt marsh, differences in goose density between plant communities with short canopy on the low and the high salt marsh were tested for each 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. Regression lines were deduced from the parameter estimates given in the model and significant differences between the levels of the regression lines analysed with $P < 0.05$ using contrast estimates. When appropriate, data were square-root transformed ($y' = \sqrt{(y+0.5)}$ for count data) or log-transformed ($y' = \log10(y+1)$ for vegetation parameters) to obtain homogeneity of variances before entering statistical testing. Non-transformed 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 1 reviews human-related disturbances for the pasture habitat during years with differing scaring regime. It has to be acknowledged that observation periods differ between years. Never-

Table 1. Frequency of human disturbances in the pasture habitat 1998–2001; observation periods were corrected for the observation effort and the number of geese observed (goose hours).

Year	scaring	observation effort (h)	observation effort (goose h)	human disturbances per 10 000 goose h	observation period
1998	yes	24	30 800	6.5	9 Mar-15 Apr
1999	yes	40	14 724	6.8	23 Mar-10 May
2000	no	14	15 000	0	2 May-4 May
2001	no	39	72 000	0.3	5 May-27 May

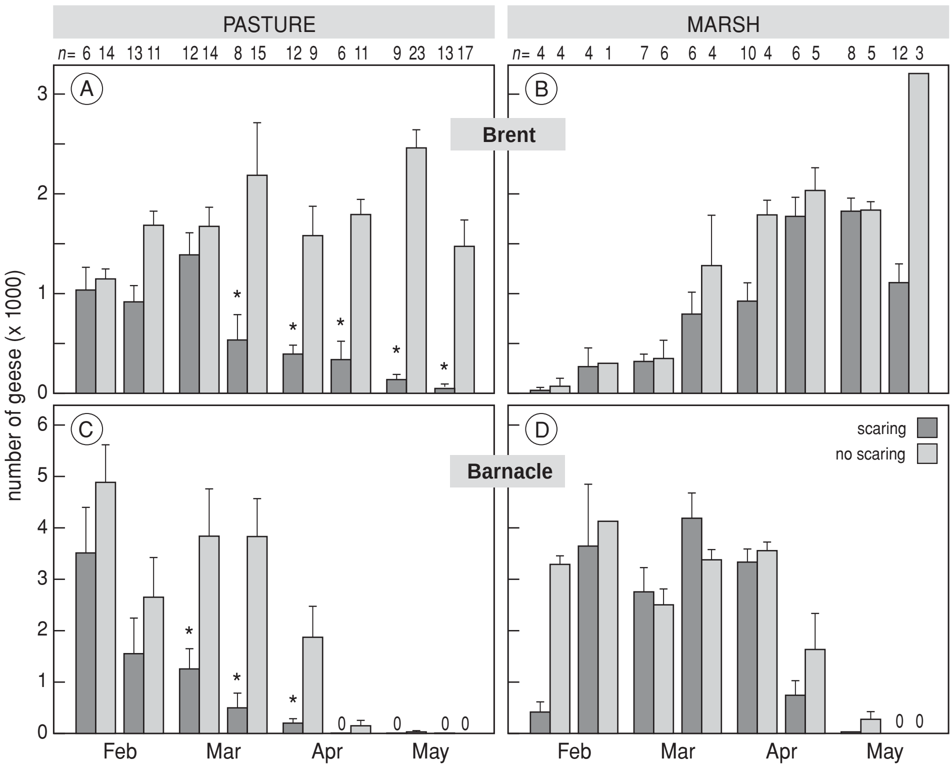

Fig. 2. Spring numbers of Dark-bellied Brent (panel A and B) and Barnacle Geese (panel C and D) on the agricultural pasture and salt marsh of Schiermonnikoog for years with (1997-99) and without (2000-01) active disturbance by farmers. Bars represent periods of two weeks(mean ± SE) and comprise several goose counts as indicated on top of the graphs. Asterisks indicate significant differences in goose numbers between the two scaring regimes ($P < 0.05$).

theless, it becomes clear that hardly any human disturbances causing flocks to fly up were recorded after the ban on active scaring from spring 2000 onwards. The patterns of habitat use by Dark-bellied Brent and Barnacle Geese during spring are summarised in Fig. 2, comparing years of active scaring with the non-scaring experimental years. In general, almost the entire local populations of both goose species forages in the pasture habitat until the second half of Feb. From then on, large numbers of Barnacle Geese can be observed on the salt marsh (Fig. 2D), and numbers on the agricultural pastures start to decrease (Fig. 2C). Dark-bellied Brent Goose numbers on the marsh increase gradually during Mar and Apr (Fig. 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 (1997-99) and years when goose scaring was banned (2000-01). Barnacle Goose numbers in the agricultural habitat declined sharply during Feb in years with active disturbance, but showed a delayed decline in the absence of scaring, with considerable numbers remaining until the end of Apr (Fig. 2C). During Mar and the beginning of Apr, 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 population of Barnacle Geese staging on the island was higher in the non-scaring years. In all years, Dark-bellied Brent

Table 2. The average number of Dark-bellied Brent and Barnacle Geese on Schiermonnikoog during Mar, Apr and May 1997–2001 and spring temperature and precipitation as a proposition of growth conditions for forage plants; Tsum 180 indicates the date at which the sum of positive averages of minimum and maximum daily air temperature reaches 180º C (starting from 1 Jan) and is used as a reference for the start of grass growth.

Year	Barnacle Geese			Dark-bellied Brent Geese			Counts (*n*)			Tsum 180	Precipitation until 1 May (mm)
	Mar	Apr	May	Mar	Apr	May	Mar	Apr	May		
1997	4627	1959	2	2056	1681	1755	6	10	11	1 Mar	117
1998	4567	3341	26	2289	2385	1615	6	7	9	11 Feb	239
1999	6875	3048	12	1689	2237	1624	3	4	4	*no data*	226
2000	7333	3513	188	2462	3918	5273	5	5	3	5 Feb	187
2001	13 012	2946	570	3322	3302	3889	1	1	1	8 Mar	194

Goose numbers in the pasture habitat increased until the beginning of Mar, as new birds arrived from wintering grounds in France and Great Britain (Fig. 2 A). In years with active scaring, Dark-bellied Brent Goose numbers declined after mid-Mar in the pasture habitat (Fig. 2 A), as birds switched to the salt-marsh habitat (Fig. 2 B). While in these years Dark-bellied Brent Geese were almost absent from the agricultural habitat by the beginning of May, Dark-bellied Brent numbers remained high (with on average 2000 birds in May) after the ban of active scaring by farmers. The total population of Dark-bellied Brent Geese on the island in May was thus doubled after scaring was banned in the pasture habitat (Table 2).

Movements of individually marked Dark-bellied Brent Geese

Fig. 3 summarises the staging history of individually marked Dark-bellied 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 one each had previously staged on the island of Texel, Terschelling or Ameland. 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

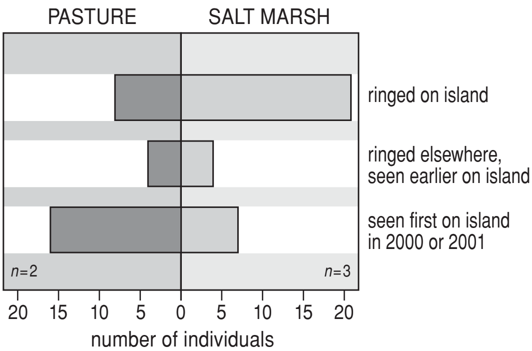

Fig. 3. Spring history of individually marked Dark-bellied Brent Geese recorded on the eastern salt marsh and on the agricultural pastures during May 2000 and 2001, after goose scaring was banned from the island.

year had been recorded at that distinct site the year before. No Dark-bellied 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 Dark-bellied Brent Geese recorded at our focal salt-marsh site has been observed at the pasture site in May, during any of the study years.

Habitat differences concerning food availability

Biomass production of plant species common in the diet of Dark-bellied Brent and Barnacle Geese (Red Fescue, Common salt-marsh grass, pasture grasses) strongly increased during spring (Fig. 4A). On the agricultural pastures, this increase was significantly steeper than on either high (Red Fescue community) or low (Common Salt-marsh Grass community) salt-marsh habitats (GLM: interaction between plant community and day number $F_{2,72}$ = 23.5, P < 0.001, R^2= 0.64). Biomass production on the low salt marsh started only in the second half of Apr and overall production was low (less than 2 g m^{-2} d^{-1}). The high salt marsh was intermediate in terms of primary production when compared to the low marsh and the pasture habitat, but plant growth started early and values exceeded 1 g m^{-2} d^{-1} during the second half of Mar already. Standing biomass followed the same pattern as primary production with lowest amounts of biomass (0-10 g m^{-2}) on the low marsh and highest values (more than 200 g. m^{-2}) in the pasture habitat at the end of spring (Fig. 4B; GLM, interaction between plant community and day number $F_{2,91}$ = 4.74, P = 0.011, R^2 = 0.82). The seasonal development of forage quality, measured as nitrogen content of leaf tissue, followed similar trajectories for all forage species sampled (Fig. 4C). Nitrogen content decreased, as the growing season proceeded. The data are best described by a regression model with day number ($F_{1,99}$=6.36 P<0.05) day number-squared ($F_{1,99}$ = 4.23, P < 0.001) and forage species ($F_{2,99}$ = 38.3, P < 0.001) as independent variables (R^2 = 0.723). Red Fescue showed the lowest nitrogen content compared to pasture grasses and Common Salt-marsh Grass during the entire spring season.

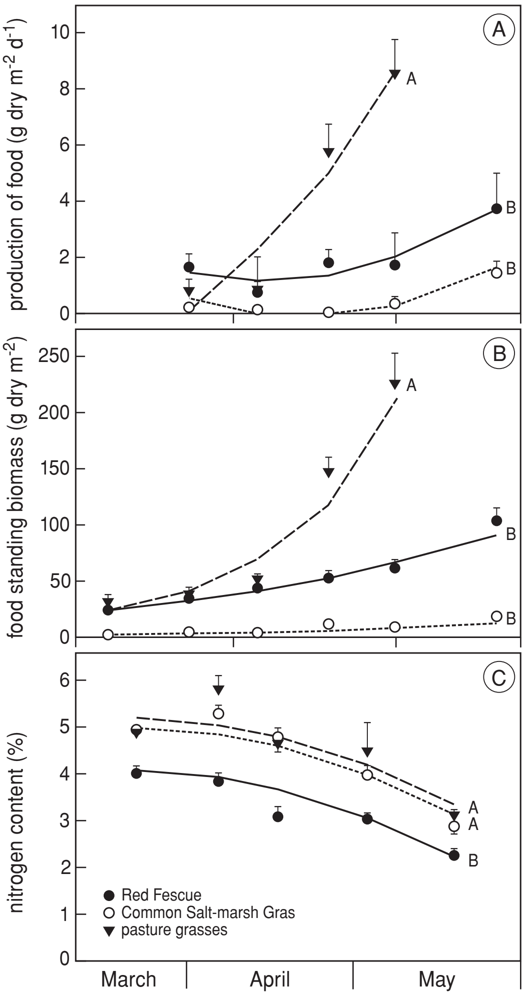

Fig. 4. Spring phenology of forage plants during 1998 (A) Increase in primary production (g dryweight m^{-2} day^{-1}) , (B) Increase in above-ground living biomass of forage plant species (g dryweight m^{-2}) and (C) development of the nitrogen content of grasses in the polder (pasture grasses), on the high (Red Fescue) and the low (Common Salt-marsh grass) salt marsh, calculated as mean + SE. Different letters indicate significant differences between regression lines for the 3 plant species.

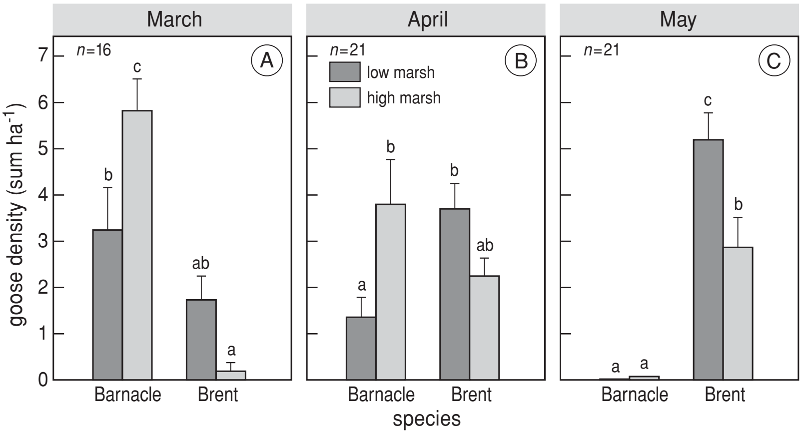

Fig. 5. The average density of Dark-bellied Brent and Barnacle Geese visiting plant communities with a short canopy on the low and the high salt marsh during Mar (A), Apr (B) and May (C). Bars represent mean + SE. Different letters indicate significant differences between mean goose densities. The number of goose counts is indicated as *n*. Data comprise the years 1997 - 2000.

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 Mar and Apr, although the species also frequently used low marsh sites in Mar (Figs. 5A, B). Barnacle Geese leave for their breeding quarters by the last week of Apr (Fig. 5C). Dark-bellied Brent Goose densities tended to be 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 Mar and Apr, 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 Mar: $F_{1,80}$= 15.90, $P <$ 0.001, R^2=0.47, Apr: $F_{1,80}$= 10.01, $P < 0.005$, R^2=0.137, May: $F_{1,80}$= 9.20, $P < 0.005$, R^2=0.67).

DISCUSSION

In all five years of our study, it was observed that large numbers of Barnacle and Dark-bellied Brent Geese gradually shift the focus of their foraging activities from the agricultural pasture habitat to the salt marsh (Fig. 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-Feb onwards. Dark-bellied Brent Goose numbers started to decline in the same area from mid-Mar, 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 (Figs. 2A & C). It is concluded 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 for both ‘scaring’ and ‘non-scaring’ years, suggesting that this habitat was used to capacity. It should be noted that our study fell within a period when the total flyway population of Barnacle Geese continued to show a slight increase (Ganter *et al.* 1999) while the population of Dark-bellied Brent Geese started to level off and even decrease (Ebbinge *et al.* 2002), the latter trend being strikingly opposed to the increase of our local island population as a reaction to the non-scaring policy described here. Our information from reading coded leg bands gives insights in the movements of individual Dark-bellied Brent Geese. Individuals observed on the eastern salt marsh tended to return each year both with and without scaring, and seem to follow 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 and represent additional immigrants from other staging sites. 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. It is assumed that normally these Dark-bellied 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 Dark-bellied Brent Geese to form a novel staging strategy utilising the pasture habitat during the entire spring period. Systematic goose watching started on the island in 1973, and never before was a concentration of Dark-bellied Brent Geese observed in the 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. In Bos (2002) it is argued that the pasture can only be exploited effectively by Dark-bellied 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 an 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 Dark-bellied 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 Dark-bellied 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.

Finally, the role of tradition and local knowledge must be emphasized. 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. Dark-bellied 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 Pink-footed 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.

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 Dark-bellied Brent, and are recorded in higher numbers on the high marsh. Dark-bellied Brent Geese, on the other hand, concentrate most of their grazing on the low salt marsh (Fig. 5). On the high marsh, Barnacle Geese mainly consume Red Fescue (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 Red Fescue in comparison to all forage species sampled (Fig. 4C). Standing biomass and forage production, by contrast, are higher on the high marsh (Fig. 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 (Red Fescue and Common salt-marsh grass) 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 Sea arrow grass and Sea plantain increases attractiveness of the marsh for Dark-bellied Brent Geese. The nitrogen content of both plant species is prominent as compared to the grass species (May: Sea plantain 3.6 % ± 0.22 SE $n = 7$; Sea arrow grass 4.7 % ± 0.18 SE $n = 6$) 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 Common Salt-marsh grass or Red Fescue swards when compared to pasture grasses, but our first data on Dark-bellied Brent Geese point to higher rates of intake on the marsh (Heuermann 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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SAMENVATTING

In het jaar 2000 is op Schiermonnikoog een gedoogregeling voor ganzen geïmplementeerd. Deze regeling voorzag in een sterke reductie van opzettelijke verstoring door mensen en wordt in deze studie gezien als een experiment waarmee veronderstellingen kunnen worden getoetst over het habitatgebruik van Rot- *Branta bernicla* en Brandganzen *B. leucopsis* in het voorjaar. Gedurende het voorjaar van de experimentele seizoenen (2000 en 2001) hebben de gezamenlijke boeren afgezien van het actief verjagen van ganzen uit de polder (290 ha), waar zich intensief beheerd grasland bevindt. De naburige kwelder (1635 ha) was al rustgebied en functioneert in het late voorjaar, wanneer beide ganzensoorten het zwaartepunt van hun foerageeractiviteiten van de polder naar de kwelder verleggen, als belangrijkste foerageerterrein. Deze overstap valt samen met de toename van de voedselproductie op de kwelder. We suggereren dat de voedselbeschikbaarheid in het vroege voorjaar op de kwelder limiterend is. De benutting van poldergrasland door beide ganzensoorten bleek in de jaren zonder verstoring sterk te zijn toegenomen en langer te duren in vergelijking met de

drie voorafgaande jaren (1997-99), waarin de ganzen actief werden verjaagd. De aantallen ganzen op de kwelder bleken in de jaren met verstoring niet te verschillen van die in jaren zonder actieve verjaging in de polder. Door de vogels niet te verjagen, werden dus randvoorwaarden geschapen voor een aanzienlijke verhoging van het aantal ganzen op het eiland in het late voorjaar. Voor de Rotgans waren de veranderingen het meest drastisch met een verdubbeling van de aantallen op het eiland in de jaren zonder verjaging. Uit ringwaarnemingen bleek dat de dieren die van de nieuwe mogelijkheden gebruikmaakten, in eerdere jaren elders in het Nederlandse Waddengebied waren gezien.

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