INLAND PASTURES ARE AN APPROPRIATE ALTERNATIVE FOR SALT-MARSHES AS A FEEDING AREA FOR SPRING-FATTENING DARK-BELLIED BRENT GEESE *BRANTA BERNICL*A

BERNARD SPAANS1 & PIET POSTMA2


On the Dutch Wadden Sea island Texel, spring-fattening Dark-bellied Brent Geese Branta bernicla fed almost exclusively inland on improved grasslands, whereas the remainder of the flyway population utilised coastal salt-marshes elsewhere in the Wadden Sea. There are indications that inland pastures are ‘second choice habitat’ during this important period. During spring-fattening, salt-marsh food plants just started to grow, offering the geese high quality food, while the growth of grasses on the inland pastures started earlier in the season, so that the nutritional value of inland grasses declined in the course of the spring-fattening period. This paper describes the habitat use of spring-fattening Dark-bellied Brent Geese on Texel and compares the reproductive output of pasture feeding and salt-marsh feeding geese. Dark-bellied Brent Geese on Texel overcame the problem of declining grass quality on inland pastures by tuning their grazing pressure to the plant production in such a manner that they kept the grass in the young, protein rich phase. Observations of individually marked Dark-bellied Brent Geese revealed the site-fidelity of spring-fattening geese on Texel. The annual survival of a sample of Texel geese (89%) was slightly higher than published values for the whole population (86%). Between 1982 and 1993, Dark-bellied Brent Geese successfully bred in six years, while the reproductive success of inland pasture feeders and salt-marsh feeders was similar. The calculated lifetime reproduction of Dark-bellied Brent Geese spring-fattening on Texel amounted to 1.39 offspring per goose, which was in accordance with overall population trends during the period concerned. The results show that an improved grassland reserve can be an appropriate alternative for salt marshes for spring-fattening Brent Geese.

Key-words: Branta bernicla - spring-fattening - breeding success - grazing pressure - pasture grazing - lifetime reproduction - site fidelity.

*Branta bernicla, formerly known as Branta bernicla bernicla (see Ardea 87: 145)

1Netherlands Institute for Sea Research (NIOZ), P.O.Box 59, 1790 AB Den Burg, Texel, The Netherlands; E-mail: spaans@nioz.nl, 2Dutch Forestry Commission-Texel, Abbewaal 2, 1791 WZ Den Burg, Texel, The Netherlands.

INTRODUCTION

The Wadden Sea is used in April and May by almost the entire world population of Dark-bellied Brent Geese Branta bernicla as a spring staging area (Ebbinge et al. 1982; Ebbinge 1989). During their stay, the geese accumulate body stores, needed for their long-distance migration to the Siberian breeding grounds, egg laying and incubation (Ebbinge & Spaans 1995; Spaans et al. 1993). During spring-fattening, Dark-bellied Brent Geese increase their body-mass by 25-35%.
Studies using individually marked geese revealed that female Dark-bellied Brent Geese that returned with offspring to western European wintering quarters were heavier at spring departure from the Wadden Sea than those that returned without (Ebbinge & Spaans 1995). Hence, the deposition of energy stores in spring appeared to be a prerequisite for successful reproduction. For the vast majority of Dark-bellied Brent Geese, salt-marshes provided feeding habitat during spring-fattening, with Red Fescue Festuca rubra, Common Saltmarsh-grass Puccinella maritima, Sea Plantain Plantago maritima and Sea Arrowgrass Trichologin maritimum as their main food plants (Ebbinge & Boudewijn 1984; Prop & Deerenberg 1991). Earlier in spring, Dark-bellied Brent Geese often fed on inland pastures, where the most important food plants were meadow-grasses Poa spp. and ryegrasses Lolium spp. The main reason for their shift towards saltmarshes during spring-fattening is a difference in phenology of the food plants in either habitat. With increasing biomass of the grasses on inland pastures in April, the nutritional value or 'quality' in terms of protein content and digestibility declined. At the same time, the salt-marsh vegetation just started to grow, offering the geese high quality food (Boudewijn 1984; Prop & Deerenberg 1991).

On the Wadden Sea island Texel in The Netherlands, there are very few salt-marshes and Dark-bellied Brent Geese traditionally utilised inland pastures. In response to local farmers, complaining about the effects of Dark-bellied Brent Geese grazing on their land, an inland pasture was set aside for geese in 1976: 'Zeeburg' reserve. Over the years, the geese have learned that Zeeburg is a safe feeding site, virtually free of disturbance, and up to 10 000 Dark-bellied Brent Geese used the area to build up body reserves in spring (Spaans 1987, P. Postma, unpubl. data). Ebbinge (1992) compared population trends of spring-staging Dark-bellied Brent Geese on a natural salt-marsh 'Boschplaat' on Terschelling (area II in Fig. 1B) with spring-staging geese on Zeeburg. Boschplaat was a traditional staging area for Dark-bellied Brent Geese in spring, with stable numbers for many years, despite a gradually increasing world population. Numbers of geese on Zeeburg, however, fluctuated around an increasing trend, largely in accordance with that of the world population. This phenomenon, in combination with data on immigration and emigration of marked geese brought Ebbinge (1992) to the conclusion that the Boschplaat was a preferred and Zeeburg a second choice habitat. In this study, we measured reproductive success of Dark-bellied Brent Geese feeding on improved grassland in spring and compared with breeding success of geese feeding on salt-marshes elsewhere in the Wadden Sea area. To be able to make this comparison, we had to demonstrate whether geese feeding on the Zeeburg reserve were site-faithful within any one spring period and between years and we collected data on habitat use and food production (grass growth) that could explain how the geese managed to build up sufficient reserves on grassland.

**STUDY AREA AND METHODS**

Zeeburg reserve, 110 ha of grassland, is situated in the north-eastern part of Texel (Fig. 1). Zeeburg is bounded on the east by a sea-dike and extensive intertidal mudflats. The pastures are especially managed for the benefit of geese. In the absence of geese (Jun-Sep), the reserve is grazed by sheep and cattle, resulting in short grassland with a high density of grassleaves. Dominant grasses are Perennial Rye-grass Lolium perenne, Smooth Meadow-grass Poa pratensis and Annual Meadow-grass Poa annua. Fertiliser is applied in early spring (110 kg N ha⁻¹) to advance the first growth and to attract geese. A fresh-water pond was dug in the centre of the southern part of the reserve. The geese use this pond frequently to drink and to rest after disturbance.

Dark-bellied Brent Geese staging at the Zeeburg reserve were counted weekly in April and May over a period of 14 years (1984-97). By counting during high tide, the chance to miss geese that were resting on the intertidal mud-flats was minimised. To indicate the daily feeding pattern,
Fig. 1. Map of the study area on Texel, including the position of the western Wadden Sea Islands in the Netherlands (A), the western Wadden Sea (B) with north-eastern Texel (I) and the natural salt-marsh area 'the Boschplaat' (II), north-eastern Texel (C) with the position of the Dark-bellied Brent Goose reserve Zeeburg (stippled) and a detailed map of Zeeburg (D) on which 5 rows of dropping-plots are indicated by thick lines and the pond by an arrow.

the number of Dark-bellied Brent Geese present at the Zeeburg reserve was counted during a whole day at 16 May 1984. Grazing pressure was recorded by assessing the density of droppings in permanent plots (5 rows of 10 plots of 4 m² each; Fig. 1). From 1984-86, droppings were counted weekly from the beginning of March until the departure of the geese at the end of May. In the
most intensively grazed part of the reserve, near the pond, droppings were counted daily during May. All droppings were removed from the plot during counting.

To measure vegetation growth, grassblades of Poa and Lolium sprouts were marked with small colour-rings in exclosures near the pond (Fig. 1) in April and May 1985. The length of blades was measured every 3 to 7 days and the number and length of new blades (at the same sprout) were recorded. In this way, growth could be expressed as mm blade sprout$^{-1}$ d$^{-1}$. To relate growth to temperature, daily minimum and maximum temperature were recorded during the same period.

Dark-bellied Brent Geese on Texel were captured with cannon-nets in winter 1982/83 ($n = 100$), winter 1983/84 ($n = 78$) and in spring 1984 ($n = 72$), 1985 ($n = 26$) and 1986 ($n = 72$). By deploying colour-rings with inscriptions, the geese could be individually recognised in the field (Ebbinge & St Joseph 1992). To establish presence and site fidelity of individually marked geese on Zeeburg, feeding flocks were frequently scanned for marked individuals during April and May in 1984 (on 46 days), 1985 (47 days) and 1986 (51 days). When calculating return rates for birds marked in the reserve, corrections have been made for birds that have died by using annual survival data from Ebbinge (1992).

Juvenile geese stay with their parents during part of their first year of life, so that the reproductive success of marked geese could be established on the wintering grounds. For the determination of breeding success, we only used observations from the first three months after arrival of the geese in October, because some juveniles become independent of their parents in the course of winter. These observations were made in autumn 1983-93, mainly on Texel, but also elsewhere in the Dutch Wadden Sea and on staging areas in Germany, England and France. The colour-ringing of Dark-bellied Brent Geese on Texel was part of a larger ringing project (Ebbinge & St Joseph 1992), so that sufficient individually marked geese were available in other spring staging areas in the Wadden Sea to measure reproduction of geese that had been grazing on salt-marshes in spring for comparison.

To calculate proportion of juveniles (%) of a sample of marked geese, the term marked ‘units’ is used rather than marked individuals. A marked unit was defined as either a pair of which both members were ringed or a pair of which one member was ringed (most Dark-bellied Brent Geese have the same partner all their life) or an unpaired ringed goose. Because of the latter category, the number of adults used for the calculation of proportion of juveniles is not automatically two times the number of units. Average breeding success of the whole population was assessed by scanning large flocks of Dark-bellied Brent Geese all over their wintering area in autumn and by determining the ratio of juveniles to the total number of geese in sub-sampled flocks.

To compare breeding success of colour-ringed geese that continued to utilise Texel’s inland pastures in later seasons (‘residents’) with that of geese that were not subsequently observed on Texel (‘emigrants’), all geese that were captured and colour-ringed on Texel were included. For 1982, however, a backward extrapolation had to be made: the marked geese used here were actually caught in December ‘82, while we assumed that individuals of this catch that stayed on Texel in April and May 1983, would also have used the pastures on Texel in spring 1982, while those that were not on Texel in spring 1983 had probably not used Texel in 1982. We decided to include 1982 because that was the most successful breeding year since the recovery of the population (Madsen et al.1999).

RESULTS

Number of Brent Geese at the reserve

Based on weekly counts in spring, numbers of staging Dark-bellied Brent Geese in the Zeeburg reserve varied between 2000 and 10 000 individuals during 1984-97. Regression of these numbers against the world population is highly significant, although the population size explains only 11% of
the variation in the weekly numbers (Fig. 2). The result of the regression of the numbers at Zeeburg against year during the period concerned is not significant ($r^2 = 0.011, P = 0.31$). During the three spring periods with extensive investigations, numbers of Dark-bellied Brent Geese present in the Zeeburg-reserve were relatively high and rather constant in 1984, in 1985 the numbers were lower and in 1986 the number of geese increased in the course of the period (Fig. 3). A low number of geese recorded at Zeeburg during the weekly counts did not necessarily mean that the geese were not present on inland grassland on Texel, because feeding did also occur in some adjacent grassland areas.

As an example of the usual daily feeding pattern on the grasslands, the number of Dark-bellied Brent Geese at Zeeburg on 16 May 1984 is shown (Fig. 4). The first geese arrived a quarter of an hour after sunrise, numbers rapidly increased in the following two hours and remained virtually the same during the rest of the day. A quarter before sunset the geese depart 'en masse' to the adjacent intertidal mud-flats of the Wadden Sea where they spend the night. Brent Geese were never recorded on the inland pastures at night, not even around the period of full moon. Occasionally, the geese abandoned the area and moved to the Wadden Sea after disturbance by, for example, a low flying aeroplane or a bird of prey. Normally, the geese would return within half an hour after such a disturbance.
Habitat use

A significant correlation was found between spring growth of Lolium spp. and Poa spp. and the average daily ambient temperature (°C) in April and May 1985 (linear regression, $r^2 = 0.69$, $P < 0.001$, $n = 13$).

Site fidelity

Usually, at least part of the geese at the Zeeburg reserve were grazing too far away to read the rings and it was therefore impossible to control the presence or absence of all the marked geese each day in the reserve. In April and May 1984, the presence of 154 different individuals was established and on average ($\pm$ SD) each marked bird was observed at 27.1 ± 11.2 days out of a total 46 observation days. In 1985, 183 marked individuals were seen at on average 21.6 ± 10.3 days out of 47 observation days. In 1986, 168
Fig. 7. Intensity of grazing in May at Zeeburg, south-east of the pond, including total number of droppings m$^{-2}$ (total), mean number of droppings m$^{-2}$ d$^{-1}$ ± SD (mean) and number of days on which the dropping density was counted ($n$).

individuals were seen at 20.7 ± 9.2 days out of 51 observation days. Frequency distributions of the number of days on which individual geese were observed feeding on Texel in April and May (Fig. 8), suggest the presence of two groups: birds that stay a prolonged period (16-40 days observed) and birds that pass by (1-15 days observed in the area). Following this subdivision, c. 20% of the marked geese were passing migrants, and 80% were 'residents' for the spring period. Because day to day fluctuations in the number of geese at

Zeeburg were generally rather small, and since most 'residents' were frequently observed between early April and late May, we assume that a large proportion of the residents utilised the inland pastures every day. The passage migrants probably used the reserve at Texel only as a stop-over site during migration to other spring-fattening sites.

The presence of 233 different marked geese on the inland pastures on Texel was established in spring 1984, including the newly caught geese ($n = 79$) in that season. Of these birds, 72% were
subsequently recorded on Texel in spring 1985 and 59% in spring 1986 (Fig. 9). After correction for the birds that died, this would suggest that 82% of the surviving geese returned to Texel in 1985 and in 1986. After elimination of the ‘passage migrants’ among the marked geese, the fraction of surviving geese that returned to Texel in spring was even higher: 86% in 1985 and 91% in 1986 (Fig. 9). In December 1982, 59 juvenile Dark-bellied Brent Geese were captured on Texel. For the following seasons (1982-1993), the surviving number of geese from this sample is shown in Fig. 10. The average survival of these birds after ten seasons amounted to 88.9% y⁻¹. A high proportion of these birds returned every year to Zeeburg for spring-fattening; on average 83.9% y⁻¹ was seen again. This indicates that each year 83.9/88.9 = 94.4% of the surviving geese returned to Texel and, consequently, 5.6% utilised other spring staging areas.

**Breeding success**

Following spring 1984-86, Dark-bellied Brent Geese bred successfully in 1985, but failed in 1984 and 1986 (i.e. juvenile percentage in winter flocks < 3%, no marked individuals accompanied by juveniles observed). In autumn 1985, breeding success was assessed of 75 marked units known to have used Zeeburg and of 279 marked units known to have fed on salt-marshes in spring 1985. There was no difference between these two groups in terms of the percentage of juveniles of

**Table 1.** Breeding success of Dark-bellied Brent Geese known to have been spring-fattening on improved grassland at Texel or on salt-marshes elsewhere in the Wadden Sea area in spring 1985.

<table>
<thead>
<tr>
<th></th>
<th>n marked units</th>
<th>n juveniles</th>
<th>% juveniles</th>
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<tr>
<td>Texel, grassland</td>
<td>75</td>
<td>74</td>
<td>35</td>
</tr>
<tr>
<td>Salt-marshes</td>
<td>279</td>
<td>264</td>
<td>34</td>
</tr>
<tr>
<td>Total population</td>
<td></td>
<td></td>
<td>35</td>
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Fig. 11. Breeding success of 'residents' (on Texel in April/May), the whole population and 'emigrants' (not on Texel in April/May) in 6 years in which Dark-bellied Brent Geese bred successfully (see text). The number of marked units per category is indicated above the bars.

The two marked samples (Table 1). Moreover, the percentage of juveniles of the marked birds corresponded with the overall proportion of juveniles in the entire population in autumn 1985 (Madsen et al. 1999).

Between 1982 and 1993, Dark-bellied Brent Geese bred successfully in six years (Fig. 11), but failed in the other years. Emigrants utilised Texel's pastures at least temporarily, but moved to other areas (salt-marshes) to build up their energy reserves in spring and only individuals of which breeding success could be assessed in the following autumn were used. With goose-families as units of observation, no difference between pasture feeders and salt-marsh feeders was found ($\chi^2 = 4.1$, n.s.; Table 2). Similarly, with years as units of observation, a significant difference between mean number of young per family could not be revealed (paired t-test, $df = 5$, $t = \sqrt{1.52}$, n.s.). In 1982, 1985 and 1988, the percentage of juveniles both in residents

Table 2. Breeding success (number of accompanying juveniles = family-size) of 423 marked pairs spring feeding on pastures (Texel, $n = 136$) or on salt-marshes (elsewhere, $n = 287$) in six successful breeding years.

<table>
<thead>
<tr>
<th>Family-size</th>
<th>Texel (pairs)</th>
<th></th>
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<th>elsewhere (pairs)</th>
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<tr>
<td></td>
<td>Found</td>
<td>Expected</td>
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<td>Found</td>
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<td>0</td>
<td>78</td>
<td>73.9</td>
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<td></td>
<td>152</td>
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<td>156.1</td>
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<tr>
<td>1</td>
<td>14</td>
<td>14.1</td>
<td></td>
<td></td>
<td>30</td>
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<td>29.9</td>
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<td>2</td>
<td>14</td>
<td>17.4</td>
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<td>40</td>
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<td>36.7</td>
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<td>3</td>
<td>9</td>
<td>11.9</td>
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<td></td>
<td>28</td>
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<td>4</td>
<td>12</td>
<td>10.9</td>
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<td>22</td>
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<td>5</td>
<td>5</td>
<td>4.8</td>
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<td>10</td>
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<td>6 or more</td>
<td>4</td>
<td>2.9</td>
<td></td>
<td></td>
<td>5</td>
<td></td>
<td>6.3</td>
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<tr>
<td>Total</td>
<td>136</td>
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<td></td>
<td></td>
<td>287</td>
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Table 3. Estimation of the lifetime reproductive output of a sample of 59 Dark-bellied Brent Geese born and marked in 1982 and spring-fattening on Zeeburg in four successful breeding years. (A) Number of marked geese of this catch that were spring-fattening on Texel in April and May and of which we were able to determine breeding success in the following autumn. (B) Total number of juveniles which accompanied these marked parents. (C) The average number of juveniles per marked parent: B/A. (D) The fraction of the total sample still alive in the season concerned (Fig. 10). (E) Average number of juveniles per individual of the original sample: C x D. (F) Cumulative number of juveniles per goose.

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<tbody>
<tr>
<td>(A) Number of examined marked geese</td>
<td>20</td>
<td>12</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>(B) Juveniles</td>
<td>13</td>
<td>23</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>(C) Mean juveniles per goose (B/A)</td>
<td>0.65</td>
<td>1.92</td>
<td>1.11</td>
<td>1.38</td>
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<tr>
<td>(D) Survival</td>
<td>0.86</td>
<td>0.59</td>
<td>0.47</td>
<td>0.41</td>
</tr>
<tr>
<td>(E) Mean juveniles per goose (C x D)</td>
<td>0.56</td>
<td>1.13</td>
<td>0.52</td>
<td>0.57</td>
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<tr>
<td>(F) Cumulative number of juveniles</td>
<td>0.56</td>
<td>1.69</td>
<td>2.21</td>
<td>2.78</td>
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</table>

and in emigrants corresponded with the reproduction measured on population level, but from 1990 onward, the marked sample was more successful than the population on average.

**Lifetime reproductive success**

A possible age dependent breeding success flaws the potential of a comparison of the reproductive success of marked geese with that of the total population when the average age of the marked sample is very different from the population average (Fig. 11, 12). Because we have data on the reproductive output of marked geese for a period as long as the average lifetime of a Dark-bellied Brent Goose (8.5 years), it is possible to estimate the lifetime reproductive output of geese of known age that used Zeeburg as a spring-fattening site. 59 geese caught as juvenile on Texel in December 1982, in ten years following their year of birth, bred successfully in 1985, 1988, 1990 and 1991 (Table 3). The total of 2.78 juveniles per marked goose is a minimum estimation of the lifetime reproduction because some geese of the 1982-catch survived the 1991/92 season and were thus able to reproduce in subsequent seasons. Since 2.78 is not the reproduction of a single bird but of a paired individual, the average individual reproduction is 2.78/2 = 1.39 descendants goose⁻¹.

**DISCUSSION**

The use of a vegetation that runs out of quality

The increasing temperature in spring results in an increasing growth-rate of the food plants (Fig. 5). Grasses are difficult to digest by geese and Dark-bellied Brent Geese in particular have to select young, protein-rich and easy digestible blades (Boudewijn 1984; Prop & Deerenberg 1991). By the intensification of their grazing in preferred parts of the reserve, they appear to be able to keep the vegetation locally very short, resulting in a daily supply of such young protein-rich blades. A similar 'manipulation of food quality' by geese is described for salt-marsh habitats (Prins et al. 1980; Ydenberg & Prins 1981). The concentration of grazing in the area around the pond has consequences for other parts of the reserve. In May 1985 for example, on average 4000 Dark-bellied Brent Geese were grazing at the 110 ha of grassland (Fig. 3) for c. 13 hr d⁻¹ (Fig. 4), resulting in an average grazing pressure of (4000 x 13 x 60)/110 = 28 000 goose-minutes ha⁻¹ d⁻¹. Assuming a dropping interval of 4.5 min (Teunissen et al. 1985), the grazing pressure in the area around the pond, with an average dropping density in May 1985 of 2.2 droppings m⁻² d⁻¹ (Fig. 7), had been 2.2 x 4.5 x 100² = 99 000 goose-minutes ha⁻¹ day⁻¹, or 3.5 times (99 000/28 000) the average.
In some parts of the reserve the geese stopped grazing completely (Fig. 6) and the advanced growth of the grass soon made these areas less attractive for the geese. Apparently, in the course of the spring with rising temperatures and the associated change in growth rate of the vegetation, Dark-bellied Brent Geese were able to keep the vegetation on inland pastures very short, but only by daily grazing (Fig. 7). Because farmers will never allow such intensive utilisation of their pastures by spring-fattening geese, favourable feeding conditions are very sparse in grasslands outside the reserve.

The dropping densities measured on Zeeburg, up to on average 3.1 m$^{-2}$ d$^{-1}$ during May (Fig. 7), are very high compared to dropping densities found on salt-marshes in spring. Here, the highest dropping density varied between 1 and 2 m$^{-2}$ d$^{-1}$ as an average over a period of 10 days on cattle-grazed salt-marshes (Ebbinge & Boudewijn 1984; Ebbinge 1992). Weather conditions in spring may vary considerably between years, and plant production will vary accordingly. Possibly, in cold periods in May, Dark-bellied Brent Geese need the entire reserve area to meet their energetic demands and grazing pressure will be more or less equal in all parts. In such years the area could not accommodate more geese in May than we would normally find, whereas in a productive (warm) spring there would at least in theory be supplies for more geese at the reserve.

**Site fidelity to the spring-fattening area**

To evaluate the importance of the Zeeburg reserve for individual Dark-bellied Brent Geese (hence, pasture grazers rather than salt-marsh foragers), it is important to know if the birds utilise the area for at least the greater part of the spring-fattening period, prior to departure to the Siberian breeding grounds. We assume that the colour-marked birds are a representative fraction of the population of geese frequenting Texel in spring. The weekly counts (Fig. 3), the fixed diurnal rhythm in feeding (exemplified in Fig. 4) and the number of days on which marked individuals were present (Fig. 8), suggest that a large proportion of the Dark-bellied Brent Geese staging on Texel in spring visit the inland pastures daily in April and May. This group of geese, which could be named ‘pasture grazers’, did build up most of their stores needed for a successful journey towards the breeding areas at the Zeeburg reserve.

A large proportion of the geese grazing on Texel in April and May was found to return to Texel in the following spring: 82% for all surviving marked geese, 86-91% for the ‘residents’ (geese that utilised the pastures on Texel in spring for at least 16 days; Fig. 9) and 95% for geese that spent their first winter on Texel (Fig. 10). Prokosch (1984) found for a salt-marsh area on the island of Föhr in the German part of the Wadden Sea, that on average 61% (range 51-73%, annual survival estimated at 0.855; Ebbinge 1992) of the surviving marked geese returned the subsequent spring. However, almost all of the survivors of the geese that returned after one year, also returned in the following springs to the salt-marsh of Föhr. The annual survival of 88.9% of the sample of 59 Dark-bellied Brent Geese which were caught in their first winter on Texel (Fig. 10) is higher than the average annual survival of 85.5% calculated by Ebbinge (1992) for the entire population. Thus, there are no indications for a higher mortality of geese using Texel as a spring-fattening area.

**Breeding success**

We found no indications for a difference in reproductive output between geese fattening up on inland pastures and those grazing on salt-marshes. Also, there was no difference between residents and emigrants utilising Texel at least temporarily (Table 2, Fig. 11). Breeding success, expressed as the percentage of juveniles, in 1982, 1985 and 1988 in residents and in emigrants corresponded with the reproduction measured on population level. However, from 1990 onward, the marked sample was apparently more successful than the population on as a whole. This could be explained by a different age composition of either sample. After 1986, geese catching on Texel was discontinued, resulting in an increasing difference between the average age of the marked.
geese (relatively old, experienced birds) and that of the total population. Data on the reproduction of marked geese of known age (captured as juveniles) suggested an age dependent breeding success. To illustrate this, the breeding success of 59 geese caught as juveniles in December 1982 was evaluated and expressed as an index: percentage of juveniles of this sample divided by the percentage of juveniles in the whole population (Fig. 12). At an age of three years, the subset of geese of known age reproduced not as good as the population as a whole (index < 1). At between six and eight yr of age, breeding success of both groups was similar (index = 1), but older geese (> 8 years of age) reproduced better than the entire population on average. This might explain why the sample of residents and emigrants is more successful than the population-average from 1990 onwards (Fig. 11).

The average lifetime reproduction amounted to at least 1.39 descendants per goose, born and marked in 1982 and feeding on inland pastures in the spring periods previous to the successful breeding summers. The world population of Dark-bellied Brent Geese has increased on average with a factor 1.044 yr\(^{-1}\) between 1980 and 1995 (Madsen et al. 1999). Following Seber (1982), the mean life span of geese (yr) can be calculated from the annual survival (S): mean life span = -1/ln(S). Based on 0.889 as a survival rate for Dark-bellied Brent Geese spring-fattening at Texel, the expected mean life span would be 8.5 yr. On average, the geese have to produce 1.044\(^{8.5}\) = 1.44 descendants during its 8.5 yr of life. In fact, geese utilising Texel’s inland pastures produced 1.39 descendants per goose, which is very close to expectation. As mentioned earlier, 1.39 descend- dants per individual is a minimum estimation: some geese of our sample survived the 1991/92 season and were consequently able to reproduce in the following summers. In conclusion, calculations of the lifetime reproduction calculations confirm that there is no difference in reproductive output between Dark-bellied Brent Geese feeding on inland pastures in spring and the rest of the population, mainly feeding on salt-marsh habitats.

**Is Zeeburg a second choice habitat?**

The ‘buffer-mechanism’ (Kluyver & Tinbergen 1953) could explain the distribution of Dark-bellied Brent Geese over a preferred (salt-marsh) and a second choice (Texel) habitats (Ebbinge 1992). The principle of this mechanism is now known as ‘the ideal free distribution’ (reviewed in Van der Meer & Ens 1997): a rich (food) habitat will be occupied first, but with increasing density the intra-specific competition will increase resulting in a decline of the attractiveness of the rich habitat and the subsequent occupation of less preferred areas, thus leading to an equilibrium with the same intake rate in both habitats. These models usually consider intake rate as the central currency, to be interpreted as an approximation of fitness. Our data indicate that geese using Texel as a spring-fattening area are site-faithful within a year and between years. Survival and reproductive success equals that of geese elsewhere in the Wadden Sea area, which is in accordance with predictions from the ideal free distribution theory. However, the improved grasslands are more intensively grazed than the salt-marshes, so that the density (carrying capacity per unit area) is even higher. The question is now whether this habitat must indeed be considered as less preferred. It is obvious that, under pressure of the increasing population size in the 1970s (Madsen et al. 1999), salt marsh feeding geese under pressure from increasing densities were forced to look for alternative feeding areas. One could argue that, by discovering the recently well-fertilised grasslands on Texel, the geese did not emigrate to a poorer food area, as the theory predicts, but even to a richer area. On the other hand, the fact that the size of the world population had some effect on the numbers of geese visiting Zeeburg in spring (Fig. 2) suggests that some geese have abandoned Zeeburg in years when the population was lower, apparently to utilise the more traditional habitats. This would suggest that Texel’s grasslands were indeed a less preferred habitat.

**The pros and cons of alternative feeding areas**

A final question, mainly of conservation con-
cern, is whether the creation of alternative feeding sites like Zeeburg is advisable. One might argue that by creating such areas, geese become accustomed to feeding on improved grassland, perhaps causing even more problems with farmers in other areas. Moreover, it is very likely that the total area of salt-marshes in the Wadden Sea available for geese in spring is a limiting factor for the population size, since the amount of body reserves accumulated by the geese in these areas will determine their reproductive success (Ebbinge & Spaans 1995). If so, the creation of alternative feeding areas in the Wadden Sea area could artificially increase the population, again potentially leading to further problems with farmers. The construction of the Zeeburg reserve on Texel led to the establishment of a large spring population of Dark-bellied Brent Geese, but the spring-fattening geese cause fewer problems on the farmland at the same time. The flocks of many thousands of Dark-bellied Brent Geese that are easy to observe for naturalists and tourists now represent a considerable economic value for the island. Independent from the question whether it is desirable to create alternative feeding areas like Zeeburg, this study shows that the principle works: 5-10 000 Dark-bellied Brent Geese are able to build up sufficient body stores in spring on only 110 hectares of improved grassland.

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SAMENVATTING

Rotganzen Branta bernicla foerageren in de opvetperiode voorafgaand aan de trek naar het broedgebied (april en mei) vrijwel overal in het Waddengebied op kwelders. Op Texel echter foerageren de ganzen vrijwel uitsluitend op binnendijks cultuurgrasland, voornamelijk in het speciaal daarvoor ingestelde reservaat Zeeburg. Er zijn aanwijzingen dat kwelders de voorkeur genieten gedurende deze voor de ganzen zo belangrijke periode en dat cultuurgrasland een tweede keus is. Om te weten te komen of cultuurgrasland wel een volwaardig alternatief voor kwelders is, wordt in dit artikel, met behulp van individueel gemerkte Rotganzen, het broedresultaat vergeleken van ganzen die op het Texelse cultuurgrasland opvetten en ganzen die dit elders op kweldevegetatie doen. Daarnaast wordt aandacht geschonken aan de manier waarop het cultuurgrasland benut wordt in de voorjaarsperiode.

De reden waarom de meeste ganzen in april en mei op kwelders foerageren, is dat de voedselplanten daar dan net beginnen te groeien en daardoor van optimale kwaliteit (makkelijk verteerbaar, hoog eiwitgehalte) voor de ganzen zijn. Op cultuurgrasland begint de groei al veel eerder in het seizoen en daalt de kwaliteit voor ganzen in de loop van het voorjaar. Op het cultuurgrasland van Zeeburg bleek dat de ganzen, door lokaal de begrazingsdruk af te stemmen op de groei, in staat waren om tot hun vertrek eind mei het gras kort en daarmee van hoge kwaliteit te houden. In mei, bij hoge plantproductie, betekende dit dat de ganzen dezelfde stukken vrijwel dagelijks zeer intensief begraasden. Waarnemingen van gemerkte Rotganzen op Texel laten zien dat er een hoge mate van plaatstrouw bestaat binnen een voorjaarsperiode. Er is dus sprake van een vaat-geen ganzen die opvetten op het cultuurgrasland. Ook was er een hoge mate van plaatstrouw van jaar op jaar en bleek de jaarlijkse overleving van ganzen op Texel minstens even hoog als het populatiegemiddelde. Tussen 1982 en 1993 kwamen de rotganzen 6 keer vergezeld van jongen uit het broedgebied terug en in deze jaren bleek er geen verschil in broedresultaat te zijn tussen cultuurgraslandganzen en kwelderganzen. Van een groep Rotganzen die als jong gemerkt waren op Texel en die daarna het ciland bleven gebruiken als opvetgebied kon het totaal aantal nakomelingen gedurende hun gehele levensduur bepaald worden. Het resultaat hiervan, gemiddeld 1,39 nakomelingen per gans, komt goed overeen met de toename van de totale populatie gedurende de betreffende periode. Ook hieruit blijkt dat ganzen op cultuurgraslanden zich evengoed voorplanten als vogels van kwelders. Uit deze resultaten blijkt dat een cultuurgraslandreservaat voor opvetende rotganzen een volwaardig alternatief kan zijn voor kwelders.

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