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**FORAGING ALONG A SALINITY GRADIENT –
THE EFFECT OF TIDAL INUNDATION ON SITE CHOICE
BY DARK-BELLIED BRENT GEESE *BRANTA BERNICLA*
AND BARNACLE GEESE *B. LEUCOPSIS***

JULIA STAHL¹, DAAN BOS² & MAARTEN J.J.E. LOONEN¹

Stahl J., D. Bos & M.J.J.E. Loonen 2002. Foraging along a salinity gradient – the effect of tidal inundation on site choice by Dark-bellied Brent Geese *Branta bernicla* and Barnacle Geese *B. leucopsis*. *Ardea* 90(2): 201-212.

We report on the effects of salt deposition on food plants on the foraging preferences of Dark-bellied Brent *Branta bernicla* and Barnacle Geese *B. leucopsis* in a coastal staging habitat. Within one salt-marsh plant community, dominated by Red Fescue *Festuca rubra*, grazing pressure by geese increased with elevation (related to mean high tide), although both standing crop and nitrogen content of the forage were highest at plots lower on the salt marsh. Salt deposition on *Festuca* leaves decreased with increasing surface height along the elevational gradient. The matching of census data for three spring seasons and data on soil surface elevation revealed that flocks of Barnacle Geese forage, on average, 0.4 m higher on the salt marsh than sympatric Dark-bellied Brent Geese. 84% of the Barnacle Goose flocks were encountered in areas characterised by an inundation frequency of less than 20 during the period from February through April, whereas this applied to only 44% of the Dark-bellied Brent Goose flocks. Barnacle Geese avoided foraging on salt-marsh vegetation experimentally sprayed with seawater, showing a significant preference for untreated control plots, whereas Dark-bellied Brent Geese did not react to the treatment. Dissection of nasal glands in carcasses of both species revealed that the metabolic mass-specific weight of the nasal glands of Dark-bellied Brent Geese exceeded that of Barnacle Geese by nearly a factor four. Within this species-pair of Dark-bellied Brent and Barnacle Geese, jointly using salt-marsh staging sites in spring, Barnacle Geese appear to be physiologically constrained in their choice of foraging sites within the salinity gradient of their habitat.

Key words: *Branta bernicla* - *Branta leucopsis* - *Festuca rubra* - habitat choice – herbivory - nasal gland - *Puccinellia maritima* - salt marsh - soil elevation

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INTRODUCTION

Salt-marsh sites along the North Sea coasts of Britain, The Netherlands, Germany and Denmark form important staging sites for Dark-bellied Brent *Branta bernicla* and Barnacle Geese *Branta leucopsis* during spring (Madsen *et al.* 1999). In relation to surface elevation, large areas experi-

ence a regular input of sea water or salt spray (Rozema *et al.* 1983), especially with storms during autumn, winter and early spring. As a consequence of their semi-marine habitat choice, *Branta* geese ingest salt with their food and with their often brackish drinking water. Nasal glands, which lie above the orbits on top of the skull (Summers & Smith 1990), remove salt from the



blood and excrete it through the nares (Holmes & Phillips 1985; Goldstein & Skadhauge 2000). In addition, geese perform drinking flights to inland fresh water sources (Ganter 1994; Van Eerden unpubl. data), or might avoid areas with increased salt loads completely, e.g. after extreme inundation.

Although, at present, Dark-bellied Brent and Barnacle Geese both rely on salt-marsh forage during spring fattening, and sometimes even share the same staging sites, as in the case of salt marshes on Schiermonnikoog (Wadden Sea island, The Netherlands), the species differed distinctly in their traditional choice of foraging habitats. Dark-bellied Brent Geese typically foraged on eelgrass *Zostera* sp. and gutweeds *Enteromorpha* sp. on intertidal flats, and only switched to terrestrial salt-marsh plants upon disappearance of sea grass beds within large parts of their winter range during the 1930s (Percival & Evans 1997; Clausen & Percival 1998; Ganter 2000). Today, they still use intertidal flats as night roosts (Madsen *et al.* 1999; pers. observ.). Barnacle Geese are more terrestrial in their habitat choice, alternately using inland pastures, estuarine meadows and salt-marsh sites for foraging (Black *et al.* 1991; Ganter 1994), and they roost in shallow fresh water in dune slacks or behind sea walls (Ydenberg *et al.* 1983). We assume distinct differences in the ability of both species to cope with salt loads encountered during their daily foraging bouts.

Salt-marsh herbivores have to cope with the high salt content of their food plants that is often exacerbated by deposition of salt on the leaf surfaces from tidal inundation. Whereas internal salt contents of plants differ between salt-marsh species in relation to their physiological strategies to cope with salt stress (Adam 1990), we assume that external salt deposition on leaves results directly from the frequency and the duration of tidal inundation, which is related to the position of plants relative to Mean High Tide (MHT). Staging *Bran-ta* geese show distinct foraging preferences for certain plant communities on a salt marsh (Ydenberg & Prins 1981; Prop 1991; Prop & Deerenberg 1991; Van der Wal *et al.* 2000a). Some of these communities cover extensive areas of a marsh

used for staging, such as higher elevation areas of island and mainland salt marshes that provide with Red Fescue *Festuca rubra* up to 90% of the diet of Barnacle Geese in early spring (Ydenberg & Prins 1981; G. van Dinteren unpubl. data). However, little is known about the direct and indirect effects of elevational gradients *within* this preferred plant community on the foraging decisions of geese. Our knowledge on differences in food availability and forage quality along the elevational gradient within a vegetation type is still fragmentary (Olf *et al.* 1997). Whether salt-marsh foragers such as staging geese react to differences in the salt load on vegetation related to inundation is unknown.

We investigated the response of Dark-bellied Brent and Barnacle Geese to elevational gradients and salt deposition on plant forage at a joint staging site on the salt marshes of Schiermonnikoog. We monitored the reaction of geese to an extreme inundation event of swards of Red Fescue. We recorded salt deposition on leaves, the availability of above-ground biomass and forage quality in relation to salt-marsh elevation. We artificially applied salt loads to plots of Red Fescue and recorded the immediate foraging response of both species of geese to treated and untreated swards. An interspecific comparison of the size of nasal glands gave an indication of the physiological ability of both species to cope with salt intake from forage sources and drinking water.

METHODS

This study was conducted at Schiermonnikoog (53°30'N, 06°10'E), a coastal barrier island in the Netherlands. Schiermonnikoog is a joint staging area for Barnacle and Dark-bellied Brent Geese, which mainly forage in intensively managed pastures from October until February (Ebbinge *et al.* 1975). From February until April, both species gradually switch to adjacent cattle-grazed salt marshes or ungrazed salt marshes which are at a younger stage of development (Prins & Ydenberg 1985; Van der Wal *et al.* 2000a). From 1997 to 1999, spring maximum numbers of Barnacle

Geese on Schiermonnikoog ranged between 5845 and 8980 birds, whereas corresponding numbers of Dark-bellied Brent Geese varied between 3024 and 3770 birds. Both species accumulate body reserves during spring staging prior to their migration to Arctic breeding grounds (e.g. Prop & Deerenberg 1991). Barnacle Geese leave the island for their breeding grounds in the Baltic and in Siberia during the last week of April (Van der Jeugd *et al.* 2001), Dark-bellied Brent Geese leave for their journey to Siberia by the end of May (Prop 1991).

Salt deposition on plants following inundation

During the last week of February 1998, we established 56 sampling plots within a grid in a salt-marsh area approximately 35 years of age (Olf *et al.* 1997), ungrazed by cattle and dominated by Red Fescue and Salt-marsh Rush *Juncus gerardi* (nomenclature follows Van der Meijden 1990). The area was demarcated by 2 creeks reaching from the high marsh to the intertidal flat. Water levels rose in the creeks during high tide, but the salt-marsh area was flooded only occasionally with spring tide and storm. Plots had a circular range of 1.13 m and covered an area of 4 m². The centre of each plot was marked by an inconspicuous PVC tube of 20 cm length. Cover of living biomass of Red Fescue was $37 \pm 3\%$ ($n = 56$, visual cover estimates). Dead leaves form a large percentage of the cover within this plant community in early spring. For all plots, soil surface elevation with respect to Mean High Tide (MHT) was measured using a theodolite. Mean tidal amplitude is approximately 230 cm (Oost & De Boer 1994).

Although plots were maintained throughout the staging season, we present data from the first week of March. This period was preceded by an exceptionally high spring tide on 28 February 1998, with a tidal height of 103 cm above MHT which flooded large parts of the salt marsh. We cleared all plots of droppings and drift-line material on 1 March. On the same day, we collected samples of approximately 10 g of fresh plant material from just outside the perimeter of each plot. In the laboratory, the samples were weighed

and rinsed in 100 ml de-ionised water for 60 seconds. We measured the electric conductivity of the solution using a portable conductivity meter (WTW, Weilheim, Germany). The electric conductivity measured (as mS(iemens) cm⁻¹) provided an estimate of the amount of ions present in the solution, and was interpreted here as a measure of salt deposition on the surface of the plant material. Afterwards, each plant sample was dried at 60°C for 48 h and weighed. The measure of electric conductivity was corrected for the weight of the plant sample, assuming that weight and leaf surface area were linearly correlated within the weight range of our grass samples. On 7 March, goose droppings were counted in all plots as a measure of goose visits during the preceding 7-day period. Precipitation was 7.9 mm on the day of the flooding, but less than 3.5 mm during the subsequent 7 days (Meteorological Measuring Site Schiermonnikoog, Vrije Universiteit Amsterdam, H. Vugts unpubl. data).

On 16 March, biomass samples were collected from 20 randomly selected plots by taking a sod of 10 cm by 10 cm to the laboratory where it was cut to soil level and sorted into living *Festuca*, other living and dead above-ground biomass. Plant material was subsequently washed, dried at 60°C for 48 h, and weighed. We used above-ground living *Festuca* biomass as an indication for food availability in our analyses. On the same day, quality samples were assembled from 12 randomly selected plots, collecting a sample of approximately 4 g (fresh weight) of Red Fescue leaf tips. Samples were washed, dried at 60°C for 48 h, ground and analysed for nitrogen content (automated element analysis, Interscience EA 1110).

Plots that were not visited by geese at all, were excluded from the analysis of goose grazing pressure, as the total absence of goose visitation may well be due to other factors, such as disturbance.

Distribution of geese in relation to soil elevation

From spring 1997 until spring 2000, we performed weekly goose counts on the island of Schiermonnikoog. From fixed observation points

along a standardised route, we assessed the size of each flock of Dark-bellied Brent and Barnacle Geese as well as its position on the salt marsh based on the use of a range finder. This device (Leica Vector 1000 binocular, 7x42) assigned a distance measure (to the nearest meter) and a compass angle (to the nearest degree) to each goose group from the observation point. The data on the distribution of geese, a vegetation map of the island Schiermonnikoog (A.S. Kers, unpubl. report) and a digital elevation model (DEM) of soil elevation (Meetkundige Dienst, Rijkswaterstaat, Delft) were combined in a GIS system. The digital vegetation map was obtained using the Photo Guided Method (Janssen 2001; Zonneveld *et al.* 1979) at a scale of 1:5000 during 1996. The Digital Elevation Model (derived using laser altimetry) contained data based on a grid of 5m by 5m. To obtain an estimate of soil level for each goose flock observed, the grid was converted to a continuous surface using linear interpolation in ARC-INFO (rel. 7.1).

We used census data for the months of February to April from all four years for our analysis. The analysis was limited to flocks of geese within a circular range of 650 m from each observation point to standardise accuracy of the range finder measurements within the data set. Each flock on the salt marsh was treated as one data point irrespective of the size of the flock, as, in social foragers like geese, the choice of foraging sites by individual flock members is guided by decisions within the foraging unit. Mean flock size was 76 ± 4.4 birds for Barnacle Geese ($n = 801$) and 67 ± 5 birds for Dark-bellied Brent Geese ($n = 352$). Separate analyses were conducted for all goose flocks irrespective of foraging site and for flocks foraging on the upper salt marsh (thereby excluding flocks on the intertidal flats and on the plant community dominated by Common Salt-marsh grass *Puccinellia maritima* which characterises the low salt marsh; Dijkema 1983). Inundation frequencies of different surface elevations on the salt marsh were calculated from data on maximum tidal heights for Schiermonnikoog (Meetkundige Dienst, Rijkswaterstaat, Delft).

Testing salt avoidance in the field

In order to test experimentally the response of staging geese to salt deposition on food plants, we artificially applied seawater on short grass swards on a cattle-grazed salt marsh, regularly visited by Barnacle and Dark-bellied Brent Geese during spring staging. During the first week of March 1999, we randomly chose 12 plots (4 m by 5 m) on a salt-marsh site (total size: 10 ha) dominated by homogeneous swards of Red Fescue and visited almost daily by foraging Barnacle Geese. These plots were assigned to the seawater treatment and were matched for homogeneity in vegetation cover with 12 similarly sized control plots. The maximum distance between plots of one pair was 10 m. The spatial proximity guaranteed concurrent detection of paired plots by a visiting flock of geese. In a second experiment in early May, we selected accordingly 8 pairs of plots situated on the lower part of the same cattle-grazed salt marsh, which were dominated by Common Salt-marsh grass and used by Dark-bellied Brent Geese almost daily. We had to select plots on the lower marsh for the Dark-bellied Brent Goose experiment, as the Red Fescue dominated parts of the marsh were visited infrequently during May.

Plots were marked with inconspicuous PVC tubes of 20 cm height at a distance of 2 m along the edges of each plot. We recorded goose visits on experimental plots based on counts of fecal pellets within marked areas. It is impossible to discriminate between Dark-bellied Brent and Barnacle Goose droppings in the field. We, therefore, conducted separate experiments to test the response of Dark-bellied Brent and Barnacle Geese.

Prior to the experiments, goose droppings were removed from all plots. The number of droppings removed beforehand did not differ between plots assigned as salt treatment and control plots for both experiments (paired t tests, $t_{\text{Barnacle}} = -0.541$, $P = 0.61$; $t_{\text{Brent}} = 0.341$, $P = 0.76$), demonstrating that all plots were equally preferred by the geese prior to the experiment. During the morning hours, we applied a fine drizzle of sea water (2 liters m^{-2}) on the vegetation of the salt-treatment plots, using a watering-can with a spray nozzle.

Table 1. Body mass, dry weight of nasal glands and body mass-specific dry weight of nasal glands of Brent and Barnacle Geese (mean \pm SE). ^a $t_0 = -5.67$, $P < 0.001$; ^b $t_0 = -8.58$, $P < 0.001$; ^c $t_0 = -7.83$, $P < 0.001$.

	Dark-bellied Brent Goose <i>Branta bernicla</i>	Barnacle Goose <i>Branta leucopsis</i>
$n =$	5	6
body mass (g)	1421 \pm 91	1924 \pm 170
weight of nasal gland (mg) ^a	482.9 \pm 55.4	148.8 \pm 28.1
body mass-specific weight of nasal gland (mg g ⁻¹ body mass) ^b	0.337 \pm 0.027	0.081 \pm 0.016
metabolic mass-specific weight of nasal gland (mg g ⁻¹ metabolic mass) ^c	0.233 \pm 0.044	0.057 \pm 0.026

zle. Control plots were left untreated. We collected a sample of about 5 g of plant material from each plot (salt treatment and control) within the first hour after spraying, which was analysed for an estimate of the surface salt content of leaves in the laboratory (based on measurements of electric conductivity, as described earlier). Goose droppings were counted in all plots after 24 h.

Size of nasal glands in Dark-bellied Brent and Barnacle Geese

We dissected six carcasses of adult Barnacle Geese and five carcasses of adult Dark-bellied Brent Geese to obtain nasal glands. The dead Barnacle Geese were collected on a pasture near the village of Ter Idzard, in Friesland on 17 March 1995, following a heavy thunderstorm. The six Dark-bellied Brent Geese fell victim to a cannon net catch on the island of Terschelling on 16 May 2000. We assumed that the carcasses represent a random sample of healthy adult birds from the spring staging population of both species. The carcasses were kept in a deep-freeze cabinet until dissection in December 2000. Carcass weights were determined to the nearest gram prior to dissection. After removal of the plumage and epidermal tissue on the forehead, we separated the paired nasal gland from the skull of each bird using a scalpel. Gland tissue was dried for 4 h at 103° C in a drying stove (Kelvitron T, Heraeus Instruments), according to ISO standard (ISO 6496-1983(E)), and weighed to the nearest 10⁻¹ milligram.

Data analysis

We applied regression analysis to test the dependence of vegetation parameters and goose grazing pressure on surface elevation. Percentage values were arcsine-square root transformed before analyses. Mann-Whitney U tests were employed on the goose census data. We applied two-sided, paired t-tests to matched pairs of plots treated with sea water and control plots in the salt avoidance experiments, and two-sided, independent samples t-tests to compare weights of salt glands between the two species. Data were analysed using the statistical package SPSS for Windows, rel. 9.0 (SPSS Inc.).

RESULTS

Salt deposition and goose distribution following inundation

Seven days after a tidal flood with a maximum water level of 103 cm above MHT, electric conductivity of liquid solutions, rinsed from plant samples collected along an elevational gradient, decreased with increasing elevation (Fig.1a, regression: $F_{1,55} = 9.12$, $R^2 = 0.15$, $P < 0.01$). The number of droppings collected in the plots increased with increasing soil elevation (Fig.1b, regression: $F_{1,33} = 27.91$, $R^2 = 0.47$, $P < 0.001$ for plots visited by geese). The amount of living biomass of Red Fescue within the plots as well as forage quality, measured as the percentage of nitrogen in leaf tip material, were negatively cor-

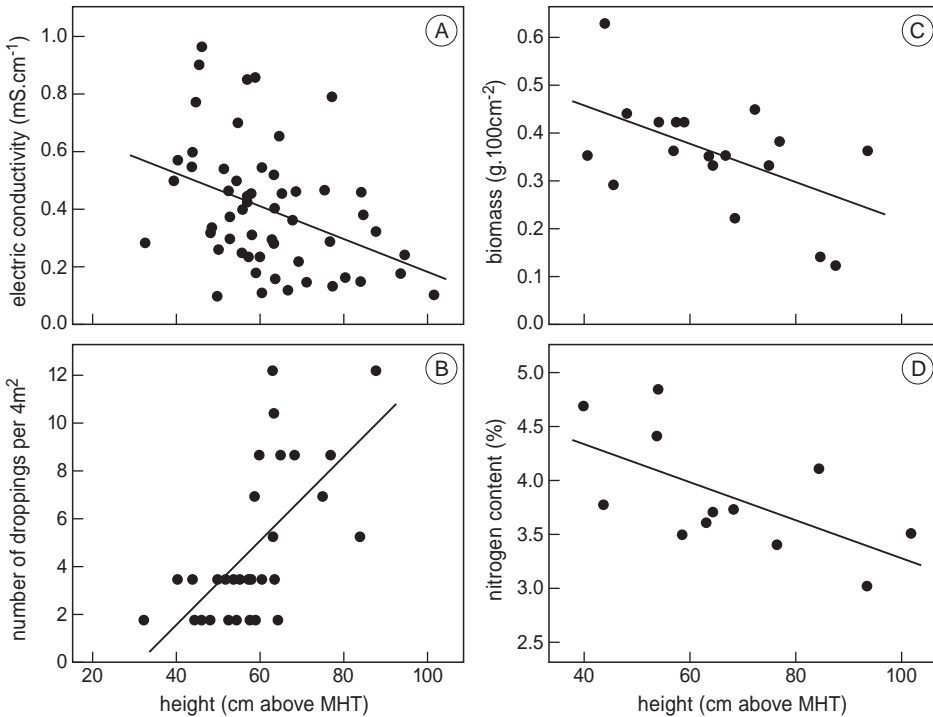


Fig. 1. Effect of complete inundation of Red Fescue *Festuca rubra* meadows during an extreme spring tide on 28 February 1998: (a) Electric conductivity of solutions obtained by rinsing fixed quantities of plant material with de-ionised water in relation to elevation of sampling plots; (b) goose visits within 7 days of inundation in relation to elevation of the sampling plots (for plots visited by geese only); (c) available aboveground biomass of Red Fescue (dry weight); (d) nitrogen content of leaf tips of Red Fescue. Surface elevation is given as height above Mean High Tide (MHT).

related with soil elevation of the sampling plots. Thus, *Festuca*-plots situated lowest within the elevational gradient offered the highest amount of edible biomass and the highest nitrogen content of the forage to geese (regression for biomass: $F_{1,19} = 7.18$, $R^2 = 0.29$, $P < 0.05$, Fig. 1c; regression for quality: $F_{1,11} = 6.22$, $R^2 = 0.38$, $P < 0.05$, Fig. 1d).

Distribution of geese in relation to soil elevation

From February to April, when both goose species use salt-marsh sites to forage, mean elevation of foraging sites used by Barnacle Geese is distinctly higher than that of Dark-bellied Brent Geese (for Barnacle Goose flocks: elevation = 0.92 ± 0.02 m, $n = 801$; for Dark-bellied Brent Goose flocks: elevation = 0.51 ± 0.02 m, $n = 352$;

mean \pm SE, Mann-Whitney *U*-test, $Z = -14.418$, $P < 0.001$). Figure 2 shows the inundation frequency for different soil heights for the period from 1 February until 30 April 1998 for Schiermonnikoog and the frequency distribution of both Barnacle and Dark-bellied Brent Goose flocks along the elevational gradient. 84% of the Barnacle Goose flocks were encountered at sites with an inundation frequency of less than 20. The same was true for only 44% of the Dark-bellied Brent Goose flocks. Even within the higher salt-marsh sites (excluding flocks on the intertidal flats and on *Puccinellia*-dominated communities of the low marsh), Barnacle Goose flocks forage at distinctly higher sites compared to Dark-bellied Brent Geese (for Barnacle Goose flocks:

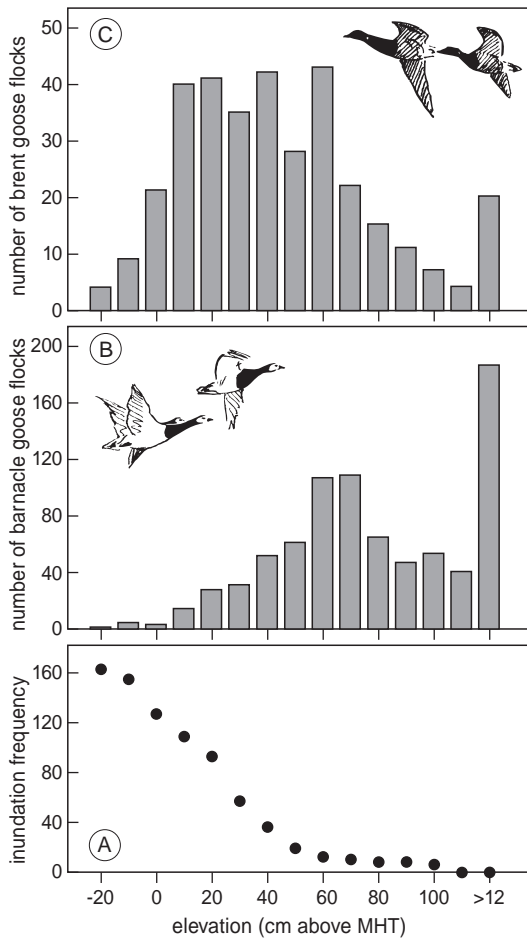


Fig. 2. Frequency distribution of (a) inundation events, (b) Barnacle Goose flocks and (c) Brent Goose flocks along the elevational gradient from 1 February to 30 April 1998.

elevation_{high marsh} = 0.99 ± 0.02 m, $n = 679$; for Dark-bellied Brent Goose flocks: elevation_{high marsh} = 0.74 ± 0.03 m, $n = 175$; mean \pm SE, Mann-Whitney U test, $Z = -7.743$, $P < 0.001$).

Testing salt avoidance in the field

The experimental application of sea water resulted in more than 3 times higher measurement of electric conductivity for water adhering to the plant samples from the salt treatment plots com-

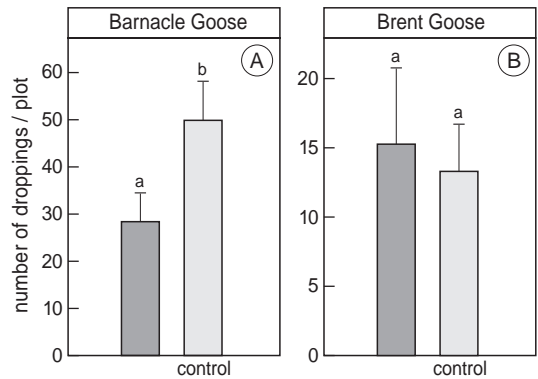


Fig. 3. Response of (a) Barnacle and (b) Brent Geese to plots experimentally sprayed with sea water compared to untreated control plots ($N = 12$ for the Barnacle Goose plots, $N = 8$ for the Brent Goose plots, separate experiments for each species). Goose visits were measured as the number of droppings counted in each plot within 24 h. Plot size was 20 m^2 . Bars represent means \pm SE. Different letters indicate significant differences between treatments ($P < 0.001$).

pared to the control plots during both experiments in March and in May (in March: $EC_{\text{salt plots}} = 0.65 \pm 0.07 \text{ mS cm}^{-1}$, $EC_{\text{control plots}} = 0.17 \pm 0.05 \text{ mS cm}^{-1}$, mean \pm SE, paired t -test $t_{12} = -7.34$, $P < 0.001$; in May: $EC_{\text{salt plots}} = 0.26 \pm 0.07 \text{ mS cm}^{-1}$, $EC_{\text{control plots}} = 0.07 \pm 0.02 \text{ mS cm}^{-1}$, mean \pm SE, paired t -test $t_{12} = -3.61$, $P < 0.01$). In the Barnacle Goose experiment, the number of droppings in the salt-treated plots was significantly lower than that in control plots (paired t -test, $t_{11} = -5.01$, $P < 0.001$) and amounted to only 57% of the total number of droppings counted in untreated control plots (Fig.3a). The number of droppings of Dark-bellied Brent Geese counted did not differ between salt-treated plots and untreated controls (paired t -test, $t_7 = 0.535$, NS, Fig.3b).

Size of nasal glands in Dark-bellied Brent and Barnacle Geese

Dissection of the nasal glands of five Dark-bellied Brent Geese and six Barnacle Geese revealed large differences in gland mass between the two species (Table 1, Fig. 4). The nasal gland



Fig. 4. Nasal glands of a Dark-bellied Brent Goose (left) and a Barnacle Goose (right) after removal of the skin. Note that the nasal glands of the Brent Goose cover the whole skull region between the eyes whereas nasal glands of the Barnacle Goose are restricted to a small region above the orbits.

of a Dark-bellied Brent Goose was on average 3.3 times heavier compared to that of a Barnacle Goose. Total body weight differed significantly between the two species (independent samples t -test $t_9 = 2.45$, $P < 0.05$). Therefore, we corrected the dry weights of the nasal glands for body mass. The mass-specific weight of the nasal gland of a Dark-bellied Brent Goose was 4.2 times larger compared to a Barnacle Goose (independent samples t -test, $t_9 = -8.59$, $P < 0.001$). For a more physiologically relevant comparison between the two species we corrected the weight of the nasal glands for metabolic mass, calculating metabolic body mass according to the equation $m_{\text{metab.}} = m^{0.74}$ (King & Farner 1961). Metabolic mass-specific weight of the nasal gland of a Dark-bellied Brent Goose exceeded the gland weight of a Barnacle Goose by a factor 3.9 (independent samples t -test, $t_9 = -7.83$, $P < 0.001$).

DISCUSSION

Dark-bellied Brent and Barnacle Geese, both migratory herbivores, jointly using spring staging sites in a coastal habitat, distribute themselves species-specifically along the elevational gradient of the salt-marsh habitat (Fig. 2). Along the entire elevational gradient of an island salt marsh, as well as within grass-dominated communities of the upper marsh, Barnacle Goose flocks were encountered on sites significantly higher in elevation compared to Dark-bellied Brent Goose flocks.

Whereas Dark-bellied Brent Geese showed no preference for vegetation either experimentally sprayed with salt water or left untreated, Barnacle Geese avoided vegetation with a high salt load on leaves (Fig. 3). This is in line with findings on the size of nasal glands in both species, which are responsible for a large part of salt excretion in birds of marine environments (Schmidt-Nielsen *et al.* 1958; Peaker & Linzell 1975). Mass-specific weights of nasal glands were nearly 4 times higher in Dark-bellied Brent Geese compared to Barnacle Geese (Table 1), suggesting a difference in the physiological ability of these species to cope with salt loads in their environment. Although Barnacle Geese make drinking flights on mainland salt marshes where inland fresh water areas is nearby (Van Eerden, unpubl. data), birds in the eastern part of the island salt marsh rely on shallow puddles of rain water. Flights to fresh water sources (at a minimum distance of 4-5 km) are rarely observed, although they regularly occur within a radius of 2 km (own observations).

Within the *Festuca* community, grazing pressure by geese was higher on plots on the upper salt marsh, where at the same time salt deposits on the leaves of food plants were lowest compared to plots situated lower on the salt marsh (Fig. 1). In the same data set, biomass and nitrogen availability were highest in plots low on the salt marsh. Our data on nitrogen content of Red Fescue along an elevational gradient are well in line with earlier findings by Olf *et al.* (1997). Various studies suggest that salt-stressed plants are more benefi-

cial to herbivores as organic solutes produced by the plant in response to osmoregulation (Jefferies *et al.* 1979) increase the nutritional quality of the forage from a herbivore's perspective (Bink 1986; Brodbeck & Strong 1987; Crawley 1997; Bowdish & Stiling 1998). The well-documented restriction of Dark-bellied Brent Geese to sites on the low marsh at the end of their staging period in April and May (Prop & Deerenberg 1991; Olff *et al.* 1997; Van der Wal *et al.* 2000a) was attributed to both the distribution of food species and the increasing quality of these foraging plants at lower elevations (Olff *et al.* 1997). Facing extreme inundations during early spring staging, however, geese might prefer sites providing them with a lowered intake of salt along with their forage, thereby accepting lower forage quality and availability.

To the best of our knowledge, this is the first study to compare the influence of a salinity gradient on two bird species jointly using a coastal habitat, but originating from an either more terrestrial (Barnacle Goose) or more marine (Dark-bellied Brent Goose) environment. Future detailed studies on the energetic costs of salt excretion, potentially along the lines of ecophysiological trials with Common Eider *Somateria mollissima* by Nehls (1996), are needed to fully understand the implications of exposure to saline habitats for both species of *Branta* geese. As size (Holmes & Stewart 1968) and secretion of salt glands (Hughes 1989) as well as glomerular filtration rates (Hughes 1980) were reported to be flexible in their reaction to changing environments for different duck and goose species, we point to the need of experiments with either wild or well-acclimated captive birds. This is particularly important as evidence has accumulated recently that long-distance migrating birds are capable of considerable reductions in organ size as an adjunct of their migratory life-style (Piersma & Gill 1998; Piersma *et al.* 1999). Summers & Smith (1990) investigated the size of nasal glands in subadult and adult Dark-bellied Brent Geese, but found only minor evidence for either age or habitat-related modification. Their mean value for

adult Dark-bellied Brent (0.60 mg per gram body weight, based on a sample of 39) is slightly higher than the value reported here.

In a study by Bowdish & Stiling (1998) on herbivory of the planthopper *Prokelesia marginata* on Salt-marsh Cordgrass *Spartina alterniflora* direct effects of salinity and plant nitrogen on herbivore abundance outweighed indirect effects of plants on parasitoids of planthopper eggs. Following suggestions by Schoener (1993), Bowdish & Stiling (1998) conclude that in stressful habitats, like salt marshes, the influence of abiotic parameters on certain species will affect the whole community. We reason that salinity can play a substantial role in the competitive interplay of small vertebrate herbivores in a salt-marsh ecosystem. Our data suggest that Barnacle Geese reach limits of their physiological capacity to cope with salt stress within the salinity gradient of their salt-marsh habitat and are, as a result, constrained in their choice of foraging sites. As a consequence of their preference for foraging sites on the upper marsh, Barnacle Geese potentially encounter substantial resource competition with both Rabbits *Oryctolagus cuniculus* on their part confined to high and dry parts of the marsh by their burrows (van der Wal *et al.* 2000b), and Brown Hares *Lepus europaeus*. In particular, resident Brown Hares overlap with Barnacle as well as Dark-bellied Brent Geese in their use of certain successional stages of the salt marsh (Van de Koppel *et al.* 1996), and actively compete with Dark-bellied Brent Geese for Red Fescue late in spring (Van der Wal *et al.* 1998; Stahl *et al.* 2001) During early spring staging, overlap of use of *Festuca*-meadows on the upper marsh is presumably even more profound between hares and Barnacle Geese as the diet of both species largely depends on *Festuca* (for hares see Van der Wal *et al.* 2000b; for Barnacle Geese see Ydenberg & Prins 1981), but the first experimental evidence of competitive interactions between these two salt-marsh herbivores has only recently been provided (Stahl *et al.* 2001).

As shown elsewhere (Van der Graaf *et al.* 2001), increased costs for thermoregulation,

encountered by small herbivores in their exposed coastal staging sites, can be mitigated by selecting for sheltered types of microhabitat, i.e. higher parts of the salt marsh close to the dune ridges. As these potential savings increase with severity of weather conditions and in turn, strong winds often facilitate higher tidal amplitudes in the Wadden Sea region, it is impossible to assign foraging preferences of geese for upper parts of the salt marsh to either wind shelter effects or salinity avoidance alone. We suppose that Barnacle Geese balance the deficit in nutrient intake at higher salt-marsh sites, resulting from lower biomass and nutrient availability, with energetic savings incurred by decreased rates of salt excretion and advantages of wind shelter. Explicit experiments should reveal whether interference and resource competition between herbivores at sites on the upper salt marsh withhold alternative foraging sites from Dark-bellied Brent Geese during the early spring staging period.

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SAMENVATTING

We berichten over de effecten van zoutdepositie op voedselplanten op de foerageerkeuzes van Rotganzen *Branta bernicla* en Brandganzen *B. leucopsis* in een kusthabitat, de kwelders van het eiland Schiermonnikoog. Binnen een plantengemeenschap op de kwelder, gedomineerd door Rood Zwenkgras *Festuca rubra*, steeg de begrazingsdruk door ganzen met toenemende hoogteligging van het terrein, alhoewel de bovengrondse biomassa en het stikstofgehalte van de voedselplanten op de lage kwelder het hoogst waren. De depositie van zout op bladeren van *Festuca rubra* nam met toenemende hoogteligging langs de hoogtegradiënt op de kwelder af. Een vergelijking van ganzenellingen uit drie voorjaren en gegevens over bodemhoogtes lieten zien dat brandgansgroepen gemiddeld 0.4 m hoger op de kwelder foerageerden dan in dezelfde gebieden

voorkomende rotganzen. 84% van de brandgansgroepen werden in gebieden aangetroffen, die door een overstromingsfrequentie van minder dan 20 in de periode van februari-april gekarakteriseerd zijn. Dit geldt echter alleen voor 44% van de rotgansgroepen. Brandganzen meden kweldervegetatie die experimenteel met zout water besproeid was, en lieten een significante voorkeur voor onbehandelde controleplots zien. Rotganzen reageerden niet op de behandeling. Een dissectie van zoutklieren uit karkassen van beide ganzensoorten liet zien dat het (voor het metabolische lichaamsgewicht gecorrigeerde) gewicht van de zoutklier van een Rotgans bijna vier keer hoger is dan het zoutkliergewicht van een Brandgans. Van de twee ganzensoorten die gebruikmaken van gezamenlijke pleisterplaatsen op kwelders in het voorjaar, blijken Brandganzen fysiologisch beperkt in hun keuzes van foerageergebieden binnen de natuurlijke zoutgradiënt van hun habitat.

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