The role of digestibility in the selection of spring feeding sites by Brent Geese

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Introduction

When their numbers were still low the occurrence of Dark-bellied Brent Geese *Branta bernicla bernicla* along the European coasts was restricted to tidal mudlfats and salt-marshes. Following full protection in Denmark in 1972 numbers increased rapidly, and, in the winter of 1973, for the first time large groups of Brent were observed to feed inland in England (Ogilvie & St. Joseph 1976; Owen 1977).

At present Brent Geese wintering in the Dutch part of the Wadden Sea feed predominantly on improved, heavily fertilized grasslands until April. Then they shift their foraging from the grasslands to the newly emerging vegetation on the salt-marsh (Bilt & Helming 1978; Ebbinge *et al.* 1981) and select those plant species which have the highest nutritional value at that time (Ranwell & Downing 1959). Drent *et al.* (1981) suggest they are maximizing their net-energy intake by this shift from improved grassland to salt-marsh.

The intention of this study was to find out whether this shift in preference in the course of the spring can be explained by a simultaneous change in digestibility of the vegetation types, i.e. of the proportion of the food which the geese can extract in the course of digestion.

The use of captive Brent Geese avoids two difficulties inherent in investigating the feeding ecology of their free-ranging wild counterparts. Firstly, captive Brent can be used to measure the digestibility of vegetation types at times when these are ignored by their wild counterparts. Secondly, the place where the Brent have been foraging is exactly known. Because of a gut throughput time of about 1.5 hours, droppings of free-ranging Brent collected at one place may not always originate from there.

Methods

The research was carried out on the island of Schiermonnikoog in the Dutch part of the Wadden Sea in 1978.

Six captive Brent were used. They were all caught as first-winter birds on the island of Terschelling, three in 1976 and three in 1977. The birds were split into two groups. One group was kept permanently on the improved grasslands of the island's polder and the other on the salt-marsh. The higher salt-marsh was rarely flooded by the sea, but the lower marsh was flooded several times a month.

The principal food-plants in the polder are *Poa pratensis* and *Lolium perenne,* while on the higher salt-marsh *Festuca rubra* and on the lower salt-marsh *Puccinellia maritima.*

In the course of the season 18 experiments were carried out, the geese being allowed to graze day and night in a pen measuring 500–600 m². Before and after each experiment, which usually lasted three days, the geese were weighed.

The composition of the vegetation was determined with the point-quadrat method (Mueller-Dombois & Ellenberg 1974). A frame is placed over the vegetation and a wire pin lowered vertically through a hole in the frame. The first plant species hit is recorded. This process was repeated until about 250 hits were scored, evenly spread within the pen. Before and after the experiment the same point location was used for assessing changes in plant cover (Goodall 1952). On one day during each experiment the time spent foraging and the number of bites per minute of foraging were measured. The observations lasted about 10 hours, except for the experiment of 20–24 March in the polder when the pen was illuminated with a 100 Watt lamp during the night. The geese were watched through a telescope and feeding-time was measured during observation bouts of 10 minutes, using a stop-watch.

Twice a day, at dawn and dusk, all the droppings in the pen were collected. After weighing, a sample was taken, weighed and dried at 60°C for further examination. A sample of the principal food species in the pen was also collected and weighed. The

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caloric value and the absolute dry weight of each sample, droppings as well as grass, were determined in the laboratory. The chlorophyll content of droppings and grass was used as a naturally occurring "marker" to measure the digestibility of the food consumed. Chlorophyll is not digested in geese and other herbivores (Kemmink & Dijkstra 1968). Research of Endendijk-Woutersen at the Institute of Poultry Research 'Het Spelderholt' in The Netherlands confirmed that 97–100% of the chlorophyll content of the food is excreted in the droppings. The chlorophyll concentration was determined by measuring the optical density in a spectrophotometer of 1 g dry matter extracted with 100 ml 85% acetone containing 3.78 oxalic acid per litre (Kemmink & Dijkstra 1968).

Since the total weight of all droppings produced is known, the concentration of chlorophyll allows us to calculate the amount of food that had been consumed. Then it is possible to calculate the net energy intake and the percentage utilization of the energy consumed, as follows:

Net-energy intake: $\frac{Md}{Mg} \cdot Eg - Ed$

%-utilization: $\dfrac{\frac{Md}{Mg} \cdot Eg - Ed}{\frac{Md}{Mg} \cdot Eg}$

Md = amount of marker in droppings
Mg = amount of marker in 1 g (dry matter) of food
Ed = total energy (kcal.) of droppings
Eg = energy (kcal.) of 1 g (dry matter) of food

By dealing with each sample of droppings separately it was possible to calculate the average digestibility of the vegetation in each experiment as well as changes in digestibility during the experiment

Since the cellulose of leaves is also not digested, the plant species consumed can be identified by their characteristic epidermal cells when examined microscopically (Owen 1977).

The number of wild Brent on Schiermonnikoog as well as their distribution was assessed by regular counts at high tide.

Results

Spring was late and cold in 1978. In May that year there were no green algae *(Enteromorpha)* available on the mud-flats and as a result the wild Brent did not forage there as reported by Ebbinge *et al.* (1981).

The frequency distribution of the food species in the droppings of the captive animals was largely similar to that of the species in the sward, i.e. there is little selection by the Brent except for *Plantago maritima*, which was clearly preferred (Figs. 1 & 2). Several times the pen with birds on the salt-marsh attracted wild Brent to come and forage next to it, where the vegetation was similar. This provided the opportunity to demonstrate that the food selection of wild and captive Brent did not differ. Both groups had a strong preference for *Plantago maritima*. The digestibility values for the wild Brent were similar to those of the ex-

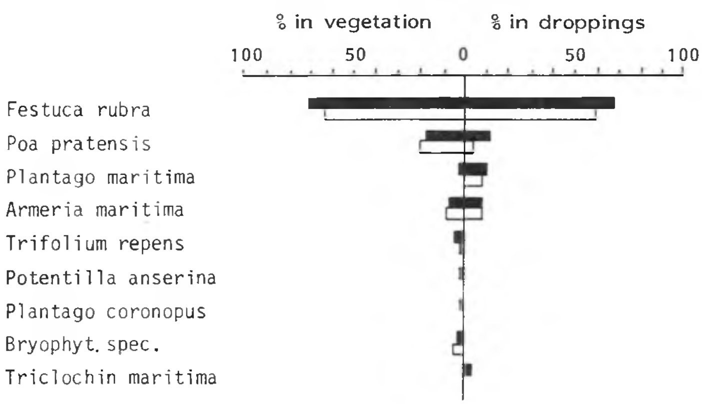

Figure 1. Food selection by Brent Geese on salt-marsh on 5 April. On the left of the figure are shown the proportion of plant species in the sward before (■) and after (□) grazing. On the right, any selection is indicated by the proportion of plant species in the droppings of captive (■) and wild Brent (□).

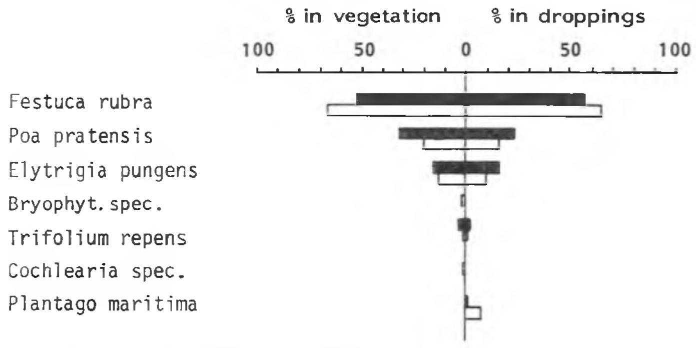

Figure 2. Food selection by Brent Geese on salt-marsh on 20 April. For interpretation see text and Fig. 1.

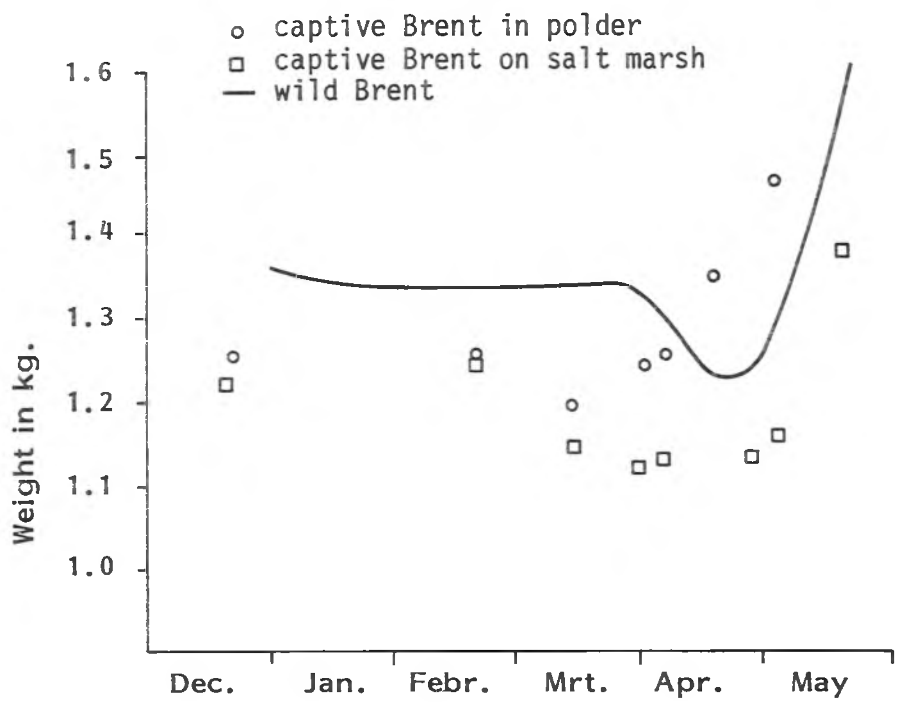

Figure 3. Changes in body-weight of captive (circles and squares) and free-ranging wild Brent (solid line). From Ebbinge *et al.* 1981).

perimental birds, respectively 21% and 22% on 5 April, 28% and 30% on 20 April, but they are not as high as the initial values of each experiment. The changes in body-weight in spring of wild and captive Brent are also comparable. The captive Brent on the salt-marsh remained on a lower level till May, but then body-weight rapidly increased (Fig. 3).

The captive and wild Brent differed in feeding intensity. The captive birds were able to forage during 24 hours per day and spread their food intake over this entire period, alternating feeding and resting bouts (Fig. 4). Wild Brent only visited their feeding grounds during the day (Fig. 5), and then fed twice as intensively (Ebbinge *et al.* 1981).

Table 1 gives the dry matter intake of the captive Brents per day and per hour of foraging. The daily intake on the observation day may show minor deviations from

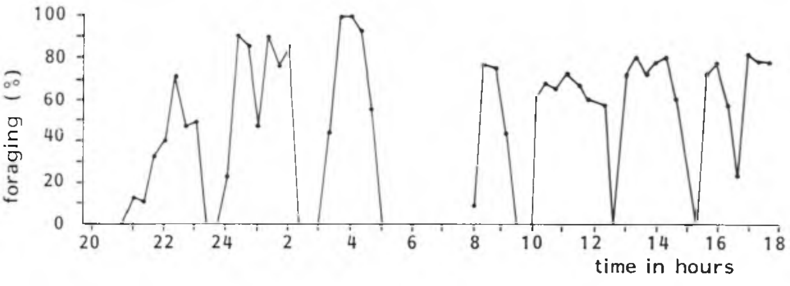

Figure 4. Proportion of time spent foraging by captive Brent at different times through a 24-hour period (22/23 March).

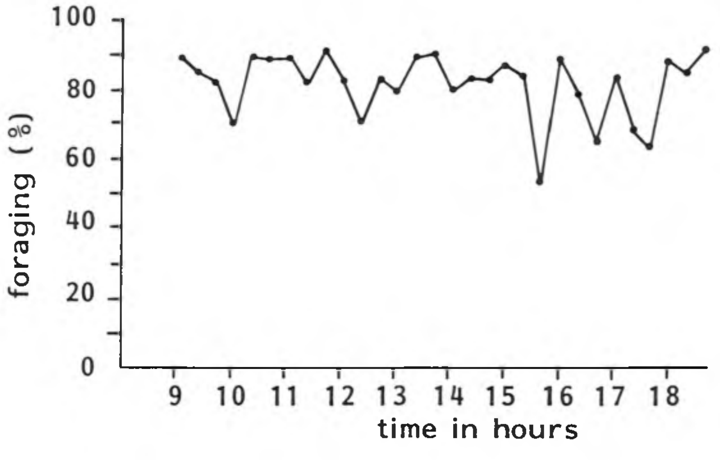

Figure 5. Proportion of wild Brent foraging at different times in daylight (23 March).

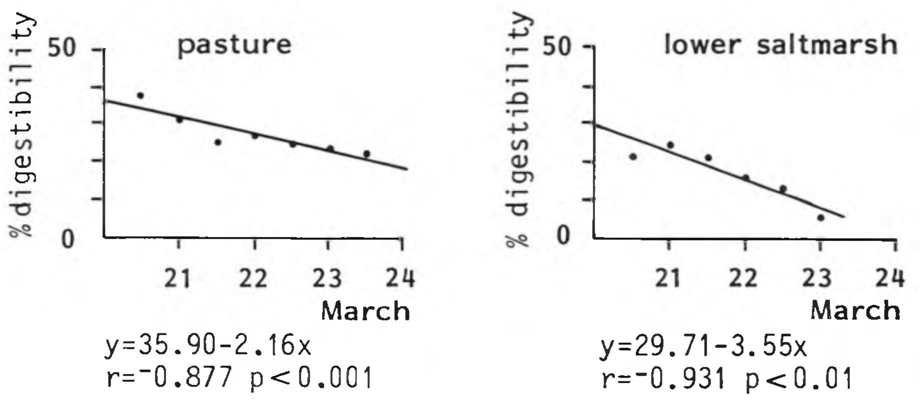

Figure 6. Change in digestibility in the pen vegetation in March.

Table 1. Food intake during the experiments.

Average daily values per whole experiment

	Period	Intake per day per goose dry matter (g)	Intake per day per goose net-energy (kcal)
polder	20/3–24/3	74.4	110.7
	1/4– 4/4	74.4	138.1
	4/4– 7/7	92.0	166.5
	16/4–20/4	109.5	172.9
	4/5– 8/5	106.2	148.7
salt-marsh (high)	24/3–28/3	106.7	151.7
	28/3– 1/4	118.3	196.0
	1/4– 4/4	121.7	216.4
	20/4– 2/5	142.3	206.1
salt-marsh (low)	21/3–24/3	92.1	75.3
	4/4– 7/4	72.5	68.7
	12/4–16/4	92.4	106.8
	16/4–20/4	114.1	143.4
	4/5– 8/5	105.1	158.1
	12/5–21/5	134.8	243.4

Average hourly values obtained during the one day the birds' behaviour was observed

	min/hour spent foraging	bites/hour of foraging	Intake per hour of foraging dry matter (g)	Intake per hour of foraging net-energy (kcal)
polder	26.5	9000	10.8	16.9
	–	–	–	–
	25.7	9480	15.6	27.0
	25.7	7980	13.8	22.6
	–	–	–	–
salt-marsh (high)		no observations		
salt-marsh (low)	21.5	10560	7.2	7.6
	29.2	10560	10.8	11.5
	28.3	10080	12.6	13.1
	25.9	9300	12.6	18.0
	–	–	–	–
	24.7	–	15.0	23.4

the overall mean of the experiment. The dry matter intake per day in the polder was smaller than that on the lower parts of the salt-marsh. Until the end of May the dry matter intake per minute of foraging was greater in the polder than on the salt-marsh. The number of bites per minute of foraging was significantly smaller on the improved grassland than on the salt-marsh (Mann-Whitney test, $p < 0.001$). The dry matter intake of the wild Brent differed from the intake of the captive ones, for the amount of food consumed is far greater; in winter 175 g of dry matter and in April–May 270 g (Drent *et al.* 1981). But there was no difference in the total number of droppings. During daylight wild Brents produced about 16 droppings per hour in spring (Drent *et al.* 1981). The captive animals produced about 200 droppings over the entire 24 hours in April–May. However, droppings of wild geese were twice as heavy as those of the captive ones.

Figures 6 and 7 show the digestibility on

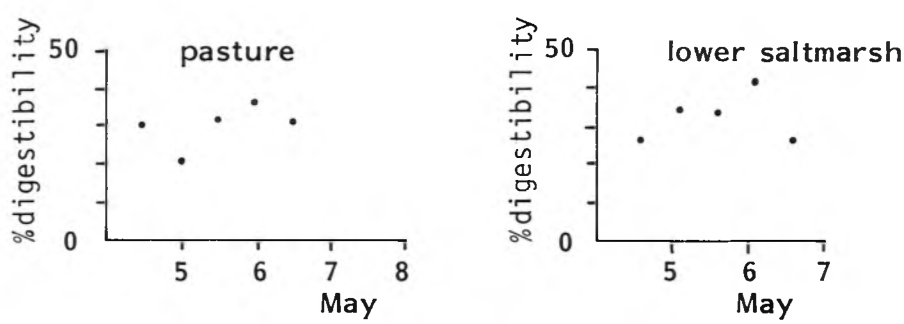

Figure 7. Change in digestibility in the pen vegetation in the first week of May.

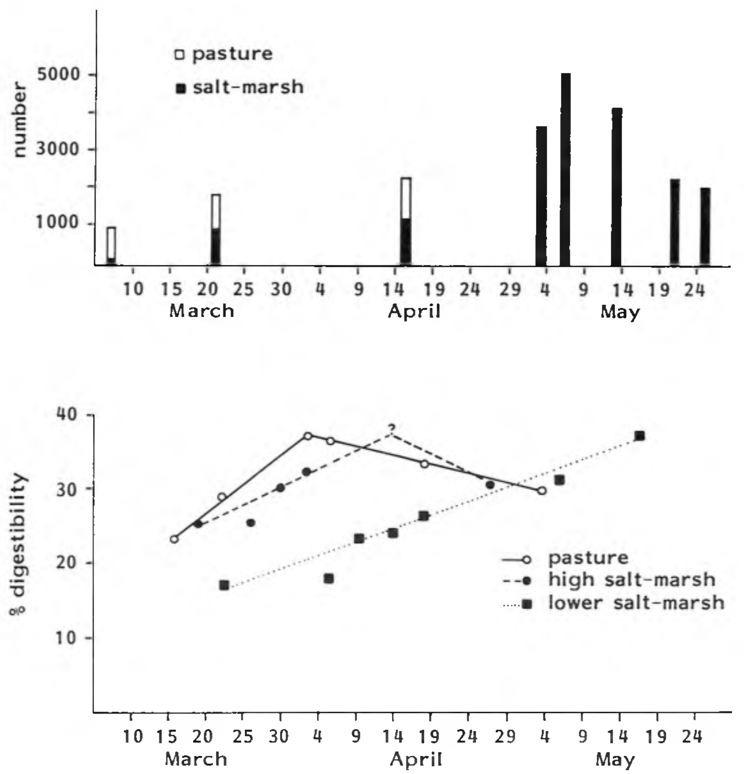

Figure 8. Numbers and distribution of wild Brent Geese on the island of Schiermonnikoog (upper panel) and changes in the digestibility of the three types of vegetation in the course of spring (lower panel).

the improved grasslands and on the lower salt-marsh in the months of March and May. At the end of March the digestibility of grass in the polder was greater than that of salt-marsh plants. Early in May the food quality had become similar on both situations.

Until the beginning of May the average digestibility proved to be greater on improved grasslands than on the lower salt-marsh (Fig. 8). During May, however, the digestibility of the vegetation on the lower salt-marsh became greater. In this period wild Brent visited only the lower salt-marsh, their numbers peaking after the first week of May (Fig. 8, upper panel). The higher *(Festuca)* part of the salt-marsh was intermediate between the two extremes. Marken Lichtenbelt and van Dijk (1984) show that

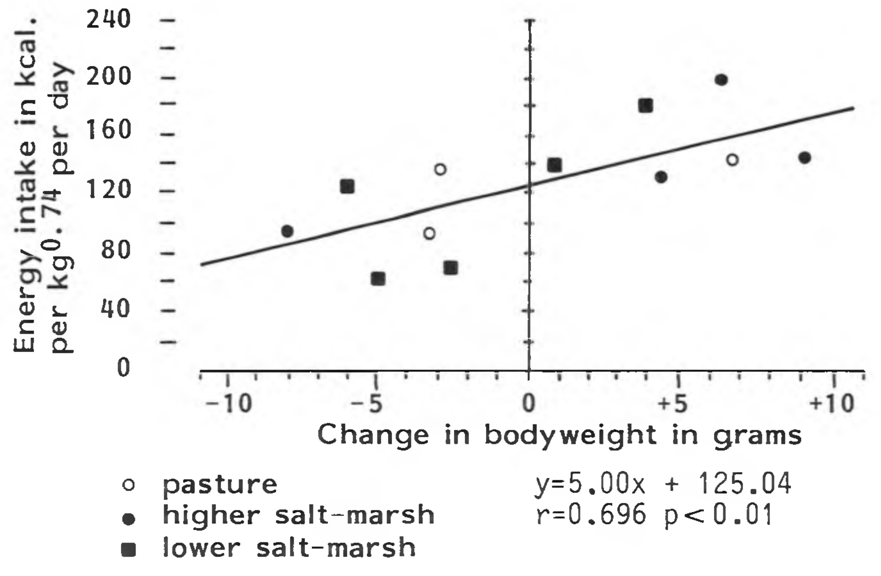

Figure 9. Relation between changes in body-weight and the net-energy intake per day by captive Brent.

the maximum digestibility of *Festuca* for Barnacle Geese was 36% in April. If this value would also hold for Brent it would coincide precisely with the question mark in Figure 8.

The net-energy intake is a function of both the quality and the amount of food consumed. Table 1 shows that until May the net-energy intake on the lower salt-marsh was less than in the polder. On the higher parts of the salt-marsh the net-energy intake was greatest, but wild Brent seldom foraged there (Drent *et al.* 1981). The net-energy intake per hour of foraging was less on the lower salt-marsh than in the polder.

Knowing the net-energy intake and the changes in body-weight during the experiments, it was possible to calculate the energy involved in losing or gaining one gram of body-weight. The net-energy intake varies with respect to body-weight by an exponential function proportional to the .74 power of body-weight (King & Farner 1961). After correcting with this factor, the net-energy requirement to maintain body-weight can be calculated (Fig. 9). Captive Brent are shown to need 123 kcal per day per kg $^{.74}$ to maintain their body-weight and 5 kcal more or less per day means a positive or a negative change of one gram of body-weight.

Discussion

There are neither marked differences in food selection nor in digestive capacity between wild Brent Geese and the captive birds (Figs. 1 and 2). At the start of an experiment higher values were obtained for the digestibility of the food, but during the experiment these values dropped, demonstrating how selective these birds are (Fig. 5). The best parts are taken first, and being confined to a small pen our experimental birds had to take lower-quality food later in the experiment.

Ebbinge and Ebbinge-Dallmeijer (1975) and Prop *et al.* (1981) found that, like our captive Brent, Barnacle Geese *Branta leucopsis* on Spitsbergen during the arctic summer foraged in bouts spread over the entire 24-hour period, thus slowing down their throughput time considerably. It has been suggested by these authors that increasing the retention time enhances the digestion. This agrees with the greater digestibility of similar food obtained with our experimental birds (compared with that for wild Brent) at the start of an experiment.

The 123 kcal per day per kg $^{.74}$ needed by captive Brents to maintain body-weight agrees with the values of wild Brent found by Drent *et al.* (1981). Compiling data on the relation between body-weight and the energy expenditure for free-living, non-breeding birds they found a Daily Energy Expenditure (DEE) 2.6 times the Basic Metabolic Rate (BMR), while existence in our pens cost 2 times BMR.

Using the data of Drent *et al.* (1981) on Brent in winter (weight 1.35 kg and DEE 201 kcal) the calculated BMR per kg $^{.74}$ is 61.9 kcal. This is almost equal to the BMR of 62.5 kcal per kg $^{.74}$ of the captive animals, as can be calculated from Fig. 9. This indicates that the value of 5 kcal for gaining or losing one gram of body-weight reliable and probably holds for free-living Brent as well.

Using the weights of female Brent in April and May (Ebbinge *et al.* 1982; and unpublished data of Ebbinge and Prokosch) it is possible to calculate the increase of the daily net-energy intake in that period. Correcting for increasing body-weight the net-energy intake can vary considerably between good breeding years and unsuccessful ones. In May the difference may be 95 kcal per day. Assuming a digestibility of 36% in this period, this means a net-energy intake of 1.8 kcal per gram dry matter. In the spring of 1982 the dry matter intake per day was 52 g, about 40% more than in the spring of 1977. The daily net-energy intake in May shows a high correlation with the breeding success that summer ($r = 0.981$, $p = 0.02$).

The average values of all experiments yield a pattern of changing digestibility in the course of the season (Fig. 8), which will also apply to wild Brent. The latter, however, can shift to other sites within an area, having consumed only the best parts of the available food. The captive Brent were confined to the pen. The geese, kept in the polder, could profit from a favourable feeding site and were in a position to increase their body-weight like the wild Brent in spring, while the weights of the captive Brent on the salt-marsh did not increase in March and April. In May, however, the feeding sites of the captive birds on the salt-marsh were much improved (Fig. 8) and their body-weights then increased rapidly. As demonstrated by Prins *et al.* (1980) wild Brent show a cycle of visitations to particular sites, thus manipulating the growth of their food-plants to their own benefit. Feeding sites chosen are those which have the highest digestibility at that moment (Figs. 8 & 9). At the end of April and in May the choice of the feeding area is especially critical, for Brent build up their energy reserves, important for the breeding success in this period (Table 2; Newton & Kerbes 1974; Newton 1977; Drent & Daan 1981; Ebbinge *et al.* 1982). This emphasises the value of the lower salt-marsh for the Brent in May. Maximum digestibility occurs there when demands by the Brent are highest.

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Summary

In spring, staging Dark-bellied Brent Geese *Branta bernicla bernicla* show a marked shift in feeding site preference from improved grassland before mid-April to salt-marsh in May. Using two groups of three captive Brent Geese each, the changes in digestibility were studied from March until the end of May in both vegetation types. There was no difference in selectivity and digestive capacity between the captive birds and their wild counterparts.

The earlier growth of improved grassland as opposed to salt-marsh resulted in a higher digestibility of the former until mid-April, but later the digestibility dropped as the grass started to flower. Spring growth of the salt-marsh vegetation lagged behind, resulting in a higher digestibility in May. In this way the highest quality food is available on the lower salt-marshes exactly when the Brent are building up their body reserves to migrate to, and breed on, the high-arctic tundras of Siberia.

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