

# Spring Feeding Ecology of Brent Geese *Branta bernicla*:

Annual Variation in Salt Marsh Food Supplies  
and Effects of Grazing on Growth of Vegetation

by  
Jesper Madsen

Med et dansk resumé:  
Fødeøkologi hos knortegæs  
*Branta bernicla* om foråret:  
årsvariation i saltmarskens fødemængde  
og gåsegræsningens effekter  
på vegetationens vækst.

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лугах и эффект пастбы гусей на рост ра-  
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## Abstract

Madsen, J. 1989: Spring feeding ecology of Brent Geese *Branta bernicla*: annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. - Dan. Rev. Game Biol. **13** (7).

In the spring seasons 1986-1988 grazing by Brent Geese on salt marsh vegetation was studied in two localities in the Danish Wadden Sea: the island Langli and the foreshore Indvindingen. On Langli, goose grazing pressure in a *Puccinellia* community varied between 31 (1987) and 65 goose droppings per m<sup>2</sup> (1988) cumulated over the spring season, equivalent to a consumption of 47 to 97 g dwt per m<sup>2</sup>. Estimates of net above-ground primary production (NAPP) of grazed *Puccinellia* (from mid March to early June) varied between 54 (1987) and 114 (1988) g dwt per m<sup>2</sup>. Weekly addition of fresh goose droppings (in the same number per area as found in the grazed sward) to exclosed *Puccinellia* plots increased NAPP compared to control plots (87 vs. 28 g dwt per m<sup>2</sup>). In the grazed sward protein content remained high (30%) throughout spring, whereas in control plots it decreased (to 25%). Simulated grazing of *Puccinellia* did not change NAPP significantly compared to control plots.

It is concluded that Brent Geese depleted the *Puccinellia* food supplies, which had bearing on goose numbers. Food supplies varied between seasons as a result of difference in weather conditions. The geese stimulated vegetation growth by defaecation.

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## Introduction

In spring the major part of the world population of Dark-bellied Brent Goose *Branta bernicla bernicla* is concentrated in the Wadden Sea (EBBINGE et al. 1981, PROKOSCH 1984, MADSEN et al. in press), building up bodily nutrient reserves, which are vital for later reproduction on the high-arctic Siberian breeding grounds (EBBINGE et al. 1982, THOMAS 1983). During the staging period, the geese feed on natural and semi-natural salt marshes. When they leave in late May they fly almost non-stop to the breeding grounds. Thus, the acquisition of nutrient reserves is dependent on the amount and quality of the spring forage.

From the 1960s to the 1980s, the population has increased from approximately 40,000 to 150,000-200,000 geese (IWRB GOOSE RESEARCH GROUP, unpubl.). It has been hypothesised, and indirectly indicated by counts, that the habitat capacity (defined as the number of geese an area can support without detrimental effects on the vegetation) of some of the Dutch spring staging areas has been reached (EBBINGE 1979, EBBINGE & BOUDEWIJN 1984). Intensive Dutch studies of exploitation of salt marsh vegetation by the Brent Geese flocks (DRENT & VAN EERDEN 1980, PROP & LOONEN in press) have also shown that the geese heavily graze *Plantago maritima*, one

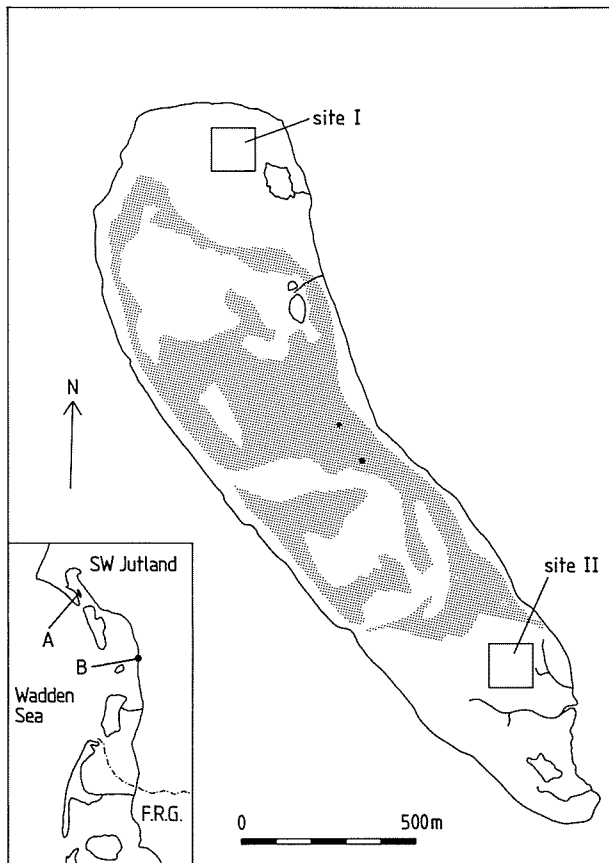


Fig. 1. Langli study area. Shaded areas represent dunes. In site I (northern salt marsh) dropping counts and enclosure experiments were conducted, whereas in site II (southern salt marsh) only dropping counts were performed. Positions of Langli (A) and Indvindingen (B) are indicated on inserted map.

of their primary food plants, so leading to depletion of local food supplies.

It is too early to evaluate possible density dependent impacts of food limitation in spring on reproductive output of the population. One question is whether or not the situation found in the Dutch Wadden Sea is general for the rest of the spring staging range.

The objective of this work has been (1) to assess annual variation in spring standing crop and productivity of salt marsh vegetation in the Danish Wadden Sea and exploitation rates by Brent Geese, and (2) to analyse some mechanisms by which the foraging goose flock affects the growth of vegetation, viz. fertilising effect of faeces and removal of biomass by grazing.

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## Study area

The study was carried out in spring over the years 1986-1988 on the island of Langli (105 ha) in the northern part of the Danish Wadden Sea (Fig. 1). The soil is sandy with a thin layer of clay in low-lying areas. The northern and southern ends of the island are salt marshes, approximately 50 ha in total. The lower parts are dominated by *Puccinellia maritima*, with *Plantago maritima* and *Artemisa maritima*, and the higher

areas by *Festuca rubra* with *Juncus gerardi*. The island is a nature reserve and since 1981 there has been no agricultural practice. Prior to 1981, the island was used for cattle grazing in summer for decades.

In spring 1986, a supplementary study was carried out on Indvindingen, a 130 ha foreshore created by land reclamation, further south in the Danish Wadden Sea (Fig. 1). Here, the salt marsh is dominated by *Puccinellia maritima* with *Plantago maritima*, and is subjected to grazing by cattle from June to October.

## Weather conditions

Weather conditions in spring 1986-1988 differed greatly. Meteorological data were available from Sædden Strand meteorological station, situated six km east of Langli. The date for which the temperature sum t-200 (the daily mean, positive temperatures (°C) summed from 1 January) was reached, was used as an indicator of start of

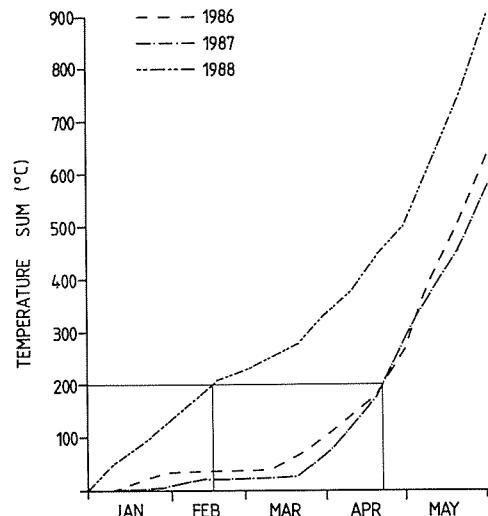


Fig. 2. Development of daily mean, positive temperature sums (°C) from 1 January to 31 May, 1986-1988. Dates for which t-200 was reached are indicated (temperatures registered at Sædden Strand meteorological station six km east of Langli).

the growing season. Fig. 2 shows that in 1986 and 1987 t-200 was reached on 23 April, and in 1988 on 18 February.

The monthly precipitation is presented in Tab. 1. It was about normal in April and May 1986, May 1987 and 1988, whereas precipitation in April 1987 and 1988 was far below normal. In all three years, and especially in 1988, precipitation in March was above normal.

## Methods

Counts of birds, including geese, are routinely made by the staff at Langli field station. In March to May 1986-88, counts were performed on average every second day.

To elucidate food selection, fresh goose droppings were collected from the northern Langli salt marsh in mid April, early May and late May during both 1986 and 1987. Each sample consisted of 20-30 droppings. From a microscopical examination of epidermal plant fragments in the droppings, the frequency of component plant species in the diet was estimated by use of a point quadrat analysis (OWEN 1975).

The timing and intensity of goose grazing in the *Puccinellia* zone in the northern and southern salt marshes (sites I and II, Fig. 1) was measured by counting goose droppings in 10 permanent circles (12.6 m<sup>2</sup>) situated at intervals of 20 m along a transect in each marsh. In both areas the transect was placed in a homogeneous sward, approximately 100 m from the coast. Plots were marked with 10 cm high pegs. Once a week in the spring seasons of 1986-88, droppings were counted and then squeezed, or if dry, removed. In 1987, an additional transect was placed in the *Festuca* zone in the northern marsh.

In spring 1987, an experiment was set up in the *Puccinellia* zone in the northern Langli salt marsh (site I, Fig. 1) to estimate net above-ground primary production

Tab. 1. Monthly precipitation in mm, March to May 1986-1988, compared to normal (average for the period 1931-1960). Average values for Ribe county (based on monthly reports from the National Meteorological Institute).

	Normal	1986	1987	1988
March	37	63	49	115
April	41	40	23	23
May	42	50	51	45

(NAPP) in a) grazed, b) ungrazed, and c) ungrazed vegetation with fresh goose droppings added.

NAPP of vegetation ungrazed by geese (i.e. b and c) was estimated by use of exclosures. On 24 March, before the geese started visiting the salt marsh, four 3 m<sup>2</sup> exclosures were established at approximately 30 m intervals along a line in a visually homogeneous *Puccinellia* sward. Exclosures were constructed of stakes (height 40 cm above-ground) connected with strings at two heights. Geese grazed freely immediately outside the exclosures. Two exclosures were used as control plots; in the other two, fresh droppings (produced on the same day) were added once a week in the same number per area as they were counted in the permanent counting plots visited by the geese.

Standing crop was estimated on four occasions between 24 March and 6 June. On 24 March, six turfs, each of 0.06 m<sup>2</sup>, were collected at random in the *Puccinellia* zone; on the other three dates 5-6 turfs were randomly collected outside the exclosures, and 2-3 turfs inside each exclosure. In the laboratory, the vegetation was clipped at the soil surface, washed, separated into live and dead material, and into component species. Samples were dried at 80°C for 24 hours, cooled in an exicator, and then weighed.



NAPP of vegetation ungrazed by geese (b and c) was estimated by adding all increments in biomass over the spring season, excluding the standing crop at the first sample date, which was regarded as production of the previous growing season.

NAPP of vegetation grazed by geese (a) was estimated by the amount of vegetation consumed by the geese:

$$\text{NAPP} = C + x_f - x_i,$$

where C is the forage consumed,  $x_i$  the biomass present at the start of the season, and  $x_f$  the biomass remaining after the departure of the geese (CARGILL & JEFFERIES 1984). C was calculated from the cumulated amount of droppings in the permanent counting plots and the retention rates of the food plants after gut passage. Retention rates were measured using ash content (after removal of silica fraction) and lignin as food components not digested (DRENT et al. 1978). Fresh droppings and samples of live vegetation were collected in mid April and early May.

To achieve an estimate of annual differences in NAPP, dropping counts were repeated in 1988 together with vegetation sampling in the grazed zone before and after the geese had visited the island (16 March and 31 May, respectively).

Live biomass from the vegetation samples were submitted to triplicate analysis of total nitrogen content (Kjeldahl tech-

nique) at the Central Laboratory, Animal Science Institute, Foulum, Denmark. Crude protein content was calculated by multiplying per cent nitrogen content by a factor of 6.25.

In 1986, an experiment similar to that performed at Langli in 1987 was set up in the *Puccinellia* zone at Indvindingen. However, due to displacement of the geese by a Goshawk *Accipiter gentilis* (MADSEN 1988), the salt marsh remained ungrazed during April and May and the experiment had to be abandoned. To achieve an estimate of the effect of pure mechanical removal of biomass on NAPP, NAPP of vegetation in two exclosures ( $3 \times 3 \text{ m}^2$ ), ungrazed by geese, was compared to NAPP of vegetation in six plots of  $0.059 \text{ m}^2$  each, where simulated grazing was performed by clipping. From 24 March to 6 June, samples of standing crop were randomly collected in the exclosures seven times, and the six plots were clipped six times. On each occasion, vegetation was clipped to a height of 1 cm above ground surface. On 6 June, the turfs in the plots were collected. NAPP in the clipped plots was estimated by summation of the biomass clipped and the standing crop on 6 June, subtracting an estimate of biomass at the beginning of the season. Average standing crop in the control plots in March was used as estimate of biomass at the start.

## Results

### Goose numbers

The first Dark-bellied Brent Geese arrived at Langli from early to mid March, and numbers peaked around the end of April (Fig. 3). In 1988 the geese arrived about 10 days earlier than in 1986 and 1987.

As it appears from Fig. 3, the number of geese on the island was not constant over the staging period. Part of the flock some-

times flew to adjacent feeding grounds (Skallingen and northern Fanø, MADSEN et al. in press). From mid May the geese began their migration from the island, and by the turn of the month there were only a few individuals remaining.

In 1986-1988, the peak number of Brent Geese recorded was 1,650 (1986), and the

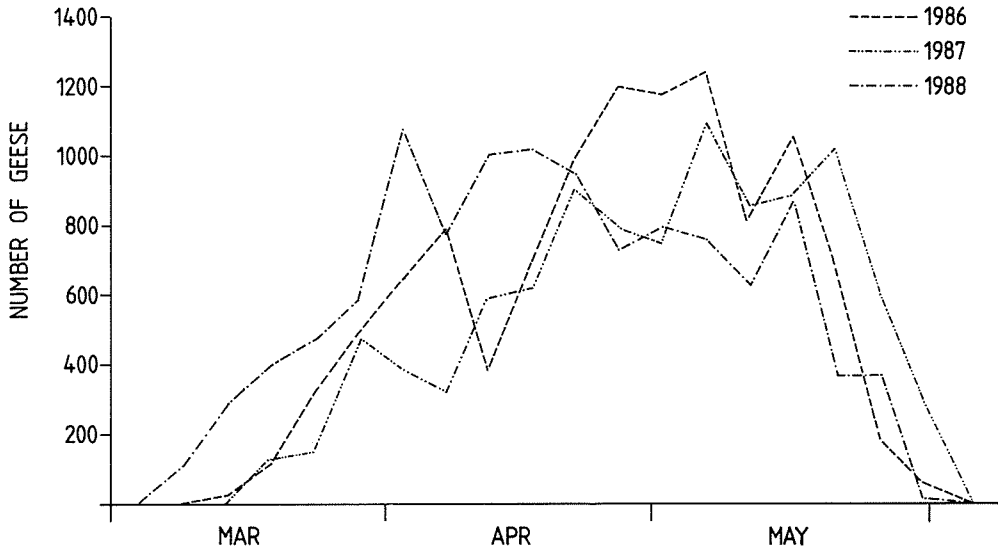


Fig. 3. Number of Dark-bellied Brent Geese on Langli, spring 1986-1988, expressed as mean number in international 5-day periods.

total number of goose-days spent on Langli varied between 39,100 (1987) and 56,000 (1988) (Tab. 2). The variation in number of goose-days was not only related to differences in the peak number of geese, but also to the irregularity in numbers staging at the island. In general, there were fewer geese on the island in 1987 compared to 1986 and 1988.

### Selection of feeding zones and food

Throughout their stay on Langli the Brent Geese foraged in the *Puccinellia* marsh zone (Fig. 4). In 1987, there was a positive correlation between the weekly dropping

deposition in the *Puccinellia* and *Festuca* marsh zones ( $r = 0.923$ ,  $n = 11$ ,  $P < 0.01$ ), indicating that there was no difference in timing of use of the two zones. Grazing pressure, as determined from cumulated dropping density, was highest in the *Puccinellia* zone, viz. 31 droppings per  $m^2$  vs. 17 in the *Festuca* zone.

*Puccinellia* was the staple part of the goose diet from arrival to departure, the frequency varying between 49 and 72% with an average of 65%, and without any apparent seasonal trend. *Festuca* was the second-most frequent component species constituting on average 28% of the diet. *Plantago maritima* made up on average 6% of the diet and did not display any trend.

Tab. 2. Brent Goose numbers in spring 1986-1988 and grazing pressure in *Puccinellia* marsh zones on Langli, expressed as the cumulated number of droppings counted in permanent plots.

Year	Goose-days	Peak number	Cumulative no. of goose droppings per $m^2$	
			N marsh	S marsh
1986	54,200	1,650	57	50
1987	39,100	1,266	31	30
1988	56,000	1,385	65	46

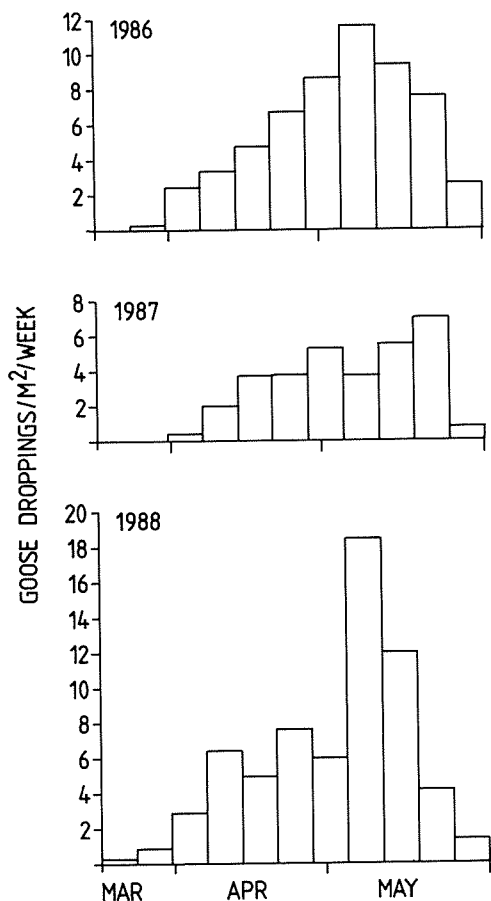


Fig. 4. Grazing pressure exerted by Brent geese in the *Puccinellia* zone of the northern salt marsh on Langli, spring 1986-1988, expressed as dropping densities.

### Grazing pressure and NAPP in grazed vegetation

In 1986 and 1987, there was a significant positive correlation between the intensity in use of the *Puccinellia* zone in the northern Langli marsh and the number of goose-

days on the island (Fig. 5). In 1988 there was no such relationship; in March and April the dropping deposition was lower than expected, but in May it was higher. The reason for this remains obscure, but in 1988 there was (unlike the previous two years) an occupied Red Fox *Vulpes vulpes* den close to the marsh, and foxes may have caused disturbance (carcasses of geese taken by foxes were actually found).

Between seasons, the cumulated dropping density varied from 31 (1987) to 65 (1988) per m<sup>2</sup> (Tab. 2). In all three years the highest densities were found in the northern marsh, but the seasonal variation was similar for both marshes.

The retention rate of ingested vegetation increased from April to May (Tab. 3). To calculate the total consumption of vegetation over the spring season, the retention rate found in early April has been used for the period from early March to 20 April, and the retention rate found in mid May for the rest of the staging period. On the basis of data in Tab. 2 and 3, the grazing pressure, expressed as amount of vegetation consumed, can be calculated to vary between 47 (1987) and 97 (1988) g dwt per m<sup>2</sup>.

NAPP in grazed vegetation, estimated as the integral of consumption, showed a high degree of variation between seasons, being highest in 1988 and lowest in 1987 (Tab. 4). Based on this estimate, the geese consumed between 85 and 87% of the NAPP of *Puccinellia*.

### Effect of droppings on vegetation

The experiment in the *Puccinellia* zone in the northern Langli marsh in 1987 revealed

Tab. 3. Estimates of amount of *Puccinellia* leaves ingested per Brent Goose dropping in early April and mid May.

	early April	mid May
Weight of dropping (g dwt)	1.01 (n = 102)	1.05 (n = 82)
Retention rate (%)	25	32
Vegetation ingested per dropping (g dwt)	1.35	1.54

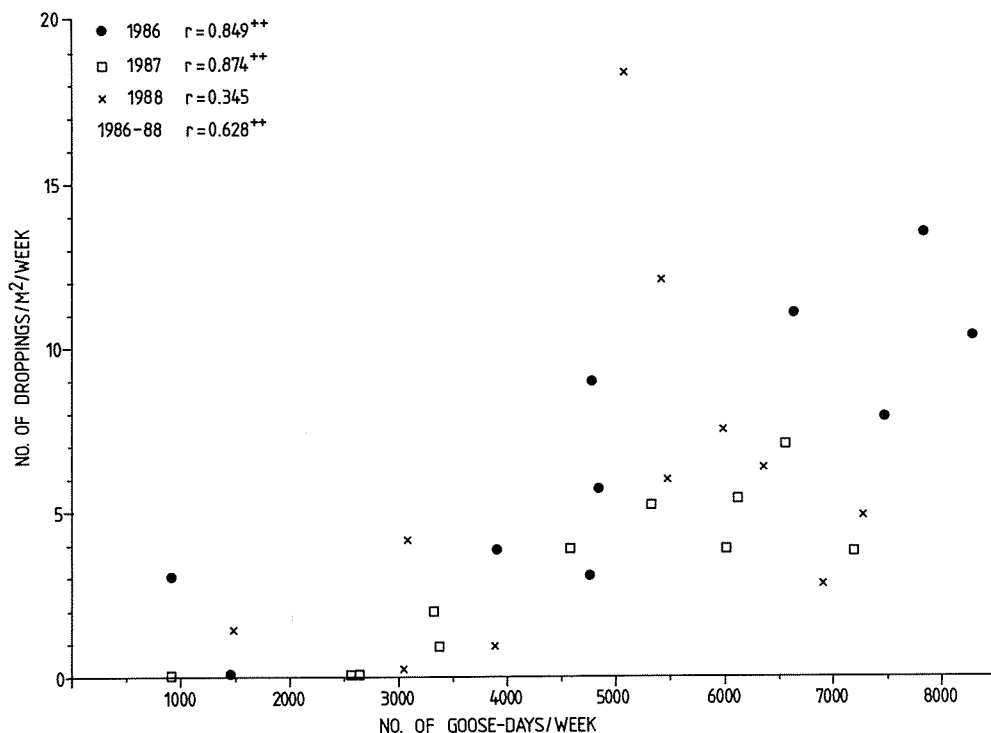


Fig. 5. Correlations between dropping deposition in the Puccinellia zone in the northern salt marsh on Langli and the number of goose-days per week on the island, 1986-1988. ++ indicates a 1% significance level; no signature indicates non-significance.

that fresh goose droppings had a significant stimulating effect on NAPP (Fig. 6A). In late May, there was nearly three times more live standing crop in enclosures with droppings added compared to control enclosures (Student t-test,  $t=4.26$ ,  $P<0.01$ ). In the grazed sward the standing crop re-

mained below 8 g dwt per m<sup>2</sup> throughout spring.

In March, there was 0.16 g dwt dead biomass per m<sup>2</sup> in the sward. In the grazed sward and in control enclosures, the dead biomass varied between 0.44 and 0.83 g dwt per m<sup>2</sup> in April and May (no significant de-

Tab. 4. Estimates of net above-ground primary production (NAPP) of Puccinellia in the northern Langli salt marsh 1986-1988, on basis of goose consumption of vegetation, biomass before arrival ( $x_i$ ) and biomass after departure ( $x_f$ ) of the geese. For 1986, biomass values have been calculated as a mean of 1987 and 1988. Standard deviation of the mean is given in brackets.

Year	Live biomass (g/m <sup>2</sup> )		Dead biomass		$x_f-x_i$ (live + dead)	Consumption (g/m <sup>2</sup> )	NAPP (g/m <sup>2</sup> )
	$x_i$	$x_f$	$x_i$	$x_f$			
1986	-	-	-	-	(12.57)	85.9	(98.5)
1987	3.38 (3.13)	10.36 (6.80)	0.16 (0.11)	0.74 (0.54)	7.56	46.6	54.2
1988	9.08 (3.12)	26.12 (9.12)	0.09 (0.04)	0.63 (0.28)	17.58	96.6	114.3

velopment); in exclosures with droppings added the dead biomass increased from 0.66 g dwt per m<sup>2</sup> in April to 3.70 g in late May ( $t=3.24$ ,  $P<0.05$ ).

NAPP calculated as the positive increment in biomass from late March to late May was 27.7 g dwt per m<sup>2</sup> in control exclosures, and 87.2 g dwt per m<sup>2</sup> in exclosures with droppings added (3.2 × control).

Protein levels in grazed *Puccinellia* were constant throughout spring (Fig. 6B). In ungrazed vegetation, the protein content peaked in mid April and then decreased. The rate of decrease was highest in the vegetation where droppings had been added.

### Effect of simulated grazing

The results of the clipping experiment on Indvindingen in 1986 are summarised in Tab. 5. The estimate of NAPP is based on data from seven sampling dates. Although there was a tendency for higher biomass and NAPP in control plots compared to clipped plots in June, the difference in standing crop was not significant ( $t=1.847$ ,  $P>0.05$ ). The NAPP estimates from Indvindingen are about double that for the grazed marsh on Langli (compare Tab. 4).

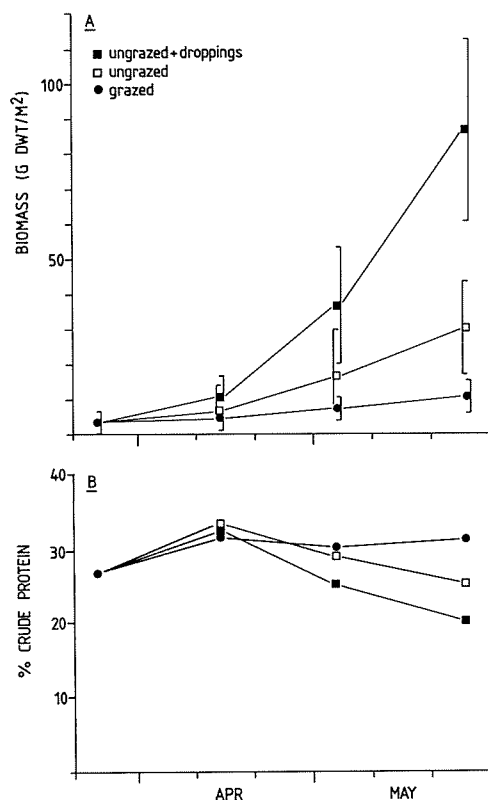


Fig. 6. Development in live standing crop (A) and protein content (B) of *Puccinellia* in the northern salt marsh on Langli, spring 1987, shown for grazed sward, control exclosures, and exclosures with fresh goose droppings added, respectively. Bars indicate standard deviation.

Tab. 5. Effects of simulated grazing by clipping on biomass and net above-ground primary production (NAPP) of *Puccinellia*, Indvindingen 1986. Standard deviation of the mean is given in brackets.

	24 March		6 June		March-June
	Biomass (g/m <sup>2</sup> ) live	Biomass (g/m <sup>2</sup> ) dead	Biomass (g/m <sup>2</sup> ) live	Biomass (g/m <sup>2</sup> ) dead	NAPP (g/m <sup>2</sup> )
Control plots	7.58 (2.62)	0.53 (0.17)	221.76 (47.03)	9.56 (2.58)	223.4
Clipped plots <sup>1</sup>	-	-	188.20 (18.41)	3.83 (1.66)	184.6

Note 1: including material clipped off during the period.

## Discussion

The results of this study show that Brent Geese removed a substantial proportion of the spring net above-ground primary production of the *Puccinellia* sward on Langli. Furthermore, the results indicate that there was a large seasonal variation in food supplies caused by differences in spring weather conditions. Thus in the early spring of 1988, geese arrived earlier, and the number of goose-days, the grazing pressure and NAPP were higher than in 1986 and 1987. The data suggest that variation in available food supplies was responsible for seasonal variation in grazing intensity and number of geese on Langli.

According to EBBINGE (1979), Brent Geese start putting on weight from early to mid April and maintain a weight increase rate of approximately 10 g per day until departure at the end of May. In mid April 1987, growth of *Puccinellia* on Langli had hardly started, and so food may have been in short supply. This suggests that in late spring seasons such as in 1987 the amount of food in the natural habitat can be critical for acquisition of adequate nutrient reserves for the subsequent nesting season.

In the present study, goose droppings significantly enhanced NAPP of *Puccinellia* (by 215%), and the effect was so immediate that the geese benefitted from the increased growth within the same spring season.

Stimulation of vegetation productivity by grazing herbivores has been reported from other studies (MCNAUGHTON 1976, CARGILL & JEFFERIES 1984), and in some recent studies the underlying mechanisms have been analysed.

Two studies have demonstrated a fertilising effect of goose droppings on vegetation growth. BALKENKOL et al. (1984) reported that addition of goose droppings to meadow vegetation in early spring en-

hanced standing crop at harvest in summer. The most comprehensive study has been done by BAZELY & JEFFERIES (1985) who demonstrated that growth of salt marsh vegetation in sub-arctic Canada was highly stimulated by droppings from grazing Snow Geese *Anser caerulescens*. In a previous study, CARGILL & JEFFERIES (1984) had found that in swards of *Carex subspathacea* and *Puccinellia phryganodes* goose grazing resulted in a 35-77% increase in NAPP compared to ungrazed vegetation. BAZELY & JEFFERIES (1985) found that much of the nitrogen in goose faeces was soluble (mainly ammonia), and within a few days following defaecation the soluble nitrogen content of the droppings declined considerably. Transport of nitrogen to the sediment was not quantified but was believed to be considerable. The authors suggested that the geese were agents for acceleration of transfer of mobile nitrogen, leading to higher productivity of the food plants.

The salt marsh under study in Canada was nitrogen-deficient, which accounted for the pronounced effect of droppings on NAPP. The same situation probably applies to the *Puccinellia* zone on Langli. JENSEN et al. (1987) found that addition of 150 kg N per ha to *Puccinellia maritima* communities in Danish salt marshes resulted in a 42-67% increase in yield compared to control plots.

Estimates of NAPP in enclosures with addition of goose droppings, and of NAPP in grazed *Puccinellia* sward should be expected to be alike, provided defaecation was the only mechanism increasing NAPP. The former estimate was, however, higher than the latter (87 vs. 54 g dwt per m<sup>2</sup>). The difference may have arisen from methodological bias or variation, but the lower productivity in the grazed sward may also

be interpreted as a negative effect of heavy grazing. The clipping experiment performed on Indvindingen revealed a tendency, although not significant, for decreased standing crop and NAPP in clipped plots compared to control plots. In other studies it has been shown that increased cutting frequency decreases yield (CHESTNUTT et al. 1977, DETLING et al. 1979), and the same may apply to the *Puccinellia* marsh which is grazed by the geese at frequent intervals and kept extremely short (vegetation height less than 0.5 cm).

Turnover of plant material has not been taken into account in the calculation of NAPP. Decay of *Puccinellia* can be considerable as a direct effect of goose trampling of vegetation and grazing of leaves (J. PROP pers. comm.). Considering this, the NAPP of the grazed sward in particular is

probably under-estimated, and the consumption rates over-estimated. However, this does not affect the general conclusion that the geese depleted the food supplies. Removal of biomass by grazing may, on the other hand, have a positive effect on NAPP. For example, KOTANEN & JEFFERIES (1987) found that shoots of *Carex subspathacea* grazed by Snow Geese produced more leaves than ungrazed shoots.

From various studies it is well-known that geese flocks grazing on the spring growth of vegetation can keep the forage plants in a state with high nitrogen content and low content of structural cell wall components (HARWOOD 1977, PRINS et al. 1980, YDENBERG & PRINS 1981, CARGILL & JEFFERIES 1984, MADSEN & MORTENSEN 1987). The results of the present study are consistent with these reports.

## Dansk resumé

Fødeøkologi hos knortegæs *Branta bernicla* om foråret: årsvariation i saltmarskens fødemængde og gåsegræsningens effekter på vegetationens vækst.

I forårssæsonerne 1986-1988 blev knortegæs-senes græsning på saltmarsken i Vadehavet studeret på øen Langli, suppleret med undersøgelser på forlandet Indvindingen (Fig. 1). Fra midten af marts til slutningen af maj opholder der sig op til 1.650 Mørkbugede Knortegæs *B. b. bernicla* på Langli (Tab. 2, Fig. 2). Antallet af gåsedage tilbragt på øen i løbet af foråret var højest i 1988 og lavest i 1987 (Tab. 2).

Udtrykt ved den samlede tæthed af gåseekskrementer igennem en forårssæson i udvalgte felter i et plantesamfund domineret af annelgræs *Puccinellia maritima*, varierede gæssenes græsningstryk mellem 31 (1987) og 65 gåseekskrementer pr. m<sup>2</sup> (1988) (Tab. 2).

Det er omregnet til, at gæssene konsumerede 47-97 g tørvægt pr. m<sup>2</sup> (Tab. 3 og 4). Gæssene holdt vegetationen kortgræsset gennem hele foråret. Nettoprimærproduktionen i det gåsegræssede annelgræssamfund blev fra midten af marts til begyndelsen af juni beregnet til

at variere mellem 54 (1987) og 114 (1988) g tørvægt pr. m<sup>2</sup> (Tab. 4).

Indhegnede felter, hvor gæssene ikke kunne græsse, blev i foråret 1987 ugentligt tilført friske gåseekskrementer med samme tæthed som fundet i felter inden for afgræssede områder. I forhold til indhegninger, der ikke fik tilført ekskrementer, blev nettoprimærproduktionen af annelgræs næsten tredoblet i felter med tilførsel af ekskrementer (Fig. 6A). Proteinindholdet forblev højt gennem hele foråret i annelgræs, der blev afgræsset af gæssene, mens det faldt i ugræsset annelgræs (Fig. 6B).

Simuleret afgræsning ved gentagen afklipping af friske skud af annelgræs, ændrede ikke nettoprimærproduktionen i forhold til ikke-afklippet annelgræs (Tab. 5).

Bæreevnen af saltmarsken på Langli var i alle tre forår næsten nået, og antallet af gæs blev sandsynligvis reguleret af fødemængden. Årsvariationen i vegetationens produktion syntes

forårsaget af vejrforholdene, som var meget forskellige i forårene 1986-1988 (Tab. 1, Fig. 2). Gæssene kan få problemer med at nå at opbygge tilstrækkelige fedt- og proteindepoter på krop-

pen i sene og tørre forår, som i 1987. Depoterne er af afgørende betydning for, om gæssene kan gennemføre ynglesæsonen på de nordsibiriske ynglepladser med succes.

Резюме на русском языке:

Пищевая экология черной казарки Branta bernicla весной: Годовые изменения количества пищи на солончаковых приморских лугах и эффект пастьбы гусей на рост растительности.

В весенних сезонах 1986-1988 г. изучалась пастьба черных казарок на приморских лугах ниже уровня моря у датских морских отмелей на острове Лангли, с дополнительными исследованиями на приморской полосе Индвиндингей (Фиг. 1). С середины марта по конец мая на Лангли находятся до 1650 темнобрюхих черных казарок B. b. Bernicla (Табл. 2, Фиг. 2). Число гусей/дней, проведенных на острове в течение весны, было высшим в 1988 г. и низшим в 1987 г. (Табл. 2).

Выражено общей плотностью гусиных испражнений в течение весеннего сезона в избранных участках растительности, в которой преобладает трава Puccinellia maritima, интенсивность пастьбы гусей колебалась между 31 (в 1987 г.) и 65 гусиных испражнений (в 1988 г.) (Табл. 2). В пересчете из этого следует, что гуси поедали 47-97 г сухого веса за м<sup>2</sup> (Табл. 3 и 4). В течение всей весны гуси содержат траву короткой. Первичная продукция нетто в участке пастьбы гусей на траве Puccinellia по расчету с середины марта до начала июня колеблется между 54 (в 1987 г.) и 114 г сухого веса за м<sup>2</sup> (Табл. 4).

В огороженные участки, на которых гуси не могли пастись, весной 1987 г. ежедневно вводились свежие гусиные испраж-

нения той-же плотностью, которая была определена на участках пастьбы. По сравнению с огороженными участками, в которые гусиные испражнения не вводились, продукция нетто травы Puccinellia на участках с введенными испражнениями повышалась почти втрое (Фиг. 6A). Содержание протеина в течение всей весны оставалось высоким в траве, на которой паслись гуси, а снижалось в траве, на которой они не паслись (Фиг. 6B).

Пастьба, симулированная неоднократным срезыванием свежих побегов травы Puccinellia, не изменяла продукцию нетто по сравнению с несрезанной травой (Табл. 5).

Предел способности питания на солончаковых лугах острова Лангли во все три весны был почти достигнут, и численность гусей вероятно регулировалась количеством пищи. Казалось, что годовые изменения продукции растительности были вызваны погодой, которая в веснах 1986-1988 г. была очень неодинаковой (Табл. 1, Фиг. 2). У гусей могут возникнуть проблемы, так как они должны успеть создать на теле достаточные запасы протеина такой поздней и сухой весной, как в 1987 г. Эти запасы имеют решающее значение для способности гусей успешно провести сезон их размножения в северно-сибирских районах гнездования.



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