The effects of plant standing crop on the foraging of Barnacle Geese

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Summary

Contrary to classical theory, recent studies have suggested that the energy intake of herbivores is maximized in vegetations of intermediate biomass. We tested this hypothesis by comparing the foraging efficiency of captive Barnacle Geese (*Branta leucopsis*) on two natural vegetations (high biomass and intermediate biomass, hereafter referred to as low biomass) and two on which the biomass was manipulated by mowing.

The accessibility of the main food plant, Festuca rubra, was highest on the sites with a lower biomass due to the lesser abundance of standing dead, although total Festuca biomass was lower.

Weight change of the geese did not differ among treatments. Total intake was highest on the low biomass sites, however. Also, more efficient foraging was found at this sites: bite rate was higher and the geese did not look around as often as in the high biomass sites. Bite rate was inversely related to vegetation height. Although larger bites are possible on the high vegetation, it is possible that the geese compensate for this on the low vegetation by taking multiple leaves in one bite.

These differences in foraging efficiency, along with food quality, might give an explanation for the spatial distribution of wild geese that has been observed in our study area.

Introduction

Food availability is a major factor governing the spatial distribution of herbivores (e.g. Drent et al. 1979, Bazely and Jefferies 1986, Olff 1992, Wilmshurst et al. 1995). Several studies have been dedicated to the relation between plant and herbivore density (Holling 1959, Oksanen et al. 1981). Holling (1959) introduced the concept of functional response to describe the relation between plant density and herbivore foraging. In a simple plant-herbivore system (i.e. without any other species such as predators), herbivore foraging would increase as plant biomass increased. He suggested three models in which herbivore foraging eventually reaches an upper limit.

Van de Koppel *et al.* (1995) found a different relation between plant density and herbivore density in their grazing study on the salt marsh of Schiermonnikoog (The Netherlands). For three herbivores, geese, hares and rabbits, an initial increase in herbivore density was found, but a decline as standing crop increased further. They suggested that this was due to a decrease in foraging efficiency of these herbivores in dense vegetations. Several processes may work together in causing this decline of foraging efficiency. High plant biomass is often associated with relatively large percentages of old and died-off leaves and unpalatable plant parts such as stems, which makes these vegetations unsuitable for grazing (e.g. Bakker *et al.* 1983). It has been shown that younger leaves contain more nitrogen and metabolizable energy (Arnold 1963, Boudewijn 1984, Wilmshurst et al. 1995), which would make them preferred by herbivores; grazing on a vegetation rich in young leaves would maximize energy intake (Fryxell 1991). Grazing on these immature vegetations can delay the maturation of the vegetation and thus keep it in a preferred state (Olff 1992, Fryxell 1991). This offers a long-term advantage to the herbivore. Therefore, herbivores would prefer a vegetation of intermediate biomass with younger, more easily digested plants. Similar results were obtained in other studies (e.g. Bazely and Jefferies 1986, Fryxell 1991, Wilmshurst *et al.* 1995).

In this study, we investigated the foraging efficiency of herbivores on different vegetations using captive geese, which were allowed to graze on vegetations of different biomass, but dominated by a single species. Body weight and dung production of the geese were used as the main indicator of foraging efficiency. A number of other parameters that might explain foraging efficiency were measured, and the composition, quantity and quality of the vegetation was also taken into account.

Methods

Study sites

The experiments were performed on the salt-marsh of Schiermonnikoog (The Netherlands), an island in the Wadden Sea. At Schiermonnikoog, various successional stages can be found on the salt marsh, as it has been extending continuously due to sedimentation at the eastern tip of the island. For this experiment, two areas of a different successional age were selected. The first area was located on the young salt marsh (approx. 15 years old), where the numbers of wild geese are highest (Van de Koppel *et al.* 1995), the other was situated on the old salt marsh (approx. 100 years old). Vegetation biomass was intermediate on the young salt marsh and high on the old salt marsh.

The study was performed during spring, when the geese feed on the salt-marsh to fatten up before flying to their breeding grounds. Fat which the geese accumulate during this period is used up during migration and breeding (Ebbinge 1992). Breeding success is directly related to the weight increase during the staging period (Drent et al. 1979, Ebbinge 1992). Efficient foraging and careful selection of food plants thus becomes crucial for a successful reproduction.

Experimental design

The objective of the experiments was to compare vegetations with different total biomass with respect to their effects on herbivore foraging and growth. Two areas were chosen which differed in plant standing crop. At each location, sixteen plots of 4*4 m were selected. In one half of these plots, plant biomass was manipulated by mowing. This way, the effects of biomass alone could be investigated. This resulted in four treatments: low biomass not mown, low biomass mown, high biomass not mown and high biomass mown. To exclude the effects of differences between food species, we selected plots dominated by Festuca rubra, one of the most abundant food plants on the salt marsh. During the experiments, the following parameters were measured: weight of the geese, amount of droppings produced per day, time spent foraging by the geese, bite rates, number of look-ups during foraging, vegetation biomass and composition and energy content and digestibility of the food.

Four pairs of Barnacle Geese were used in the experiment. Three individuals (all unpaired males) were kept in reserve. In four periods, each pair was subjected to each treatment in a repeated measurements format. After two periods, the smallest female in the experimental group had lost so much weight that we decided to retire her from the experiment and replaced her with one of the reserve birds.

Observation experiment

In early April 1995, about two weeks before the start of the experiment, eight of the sixteen plots at each location were mown by hand. Then, all plots were covered with nets to exclude wild herbivores. One week later, a large holding pen (10*10 m) was constructed near the field station on Schiermonnikoog in which the geese were kept. From that moment on, the geese received no more pellets to let them get accustomed to the situation in the experiment, with the vegetation as the only available food source.

The grazing experiments were performed in April and May 1995. There were four experimental periods of four to six days, separated by resting intervals of two to four days. During the intervals the geese received special waterfowl food with a high energy content.

Pairs of geese were allowed to graze every day from about one hour after sunrise (i.e. around 7 am) to about 8 pm. During the day, water was available ad libitum. During the nights, the animals were kept in night cages where they could neither eat nor drink. The geese were weighed every morning before they were released onto the plots; it was assumed that their intestinal system was empty by that time. All droppings produced per pair during the day were collected, weighed, dried at 70 °C for at least two days and then weighed again. Droppings produced during the night were of a negligible amount and therefore ignored.

Every hour, the behaviour of each individual was observed for five minutes by an observer that was invisible to them (inside a small tent some 50 m away). The total time spent foraging was measured using a stopwatch, and the number of look-ups was counted. A look-up was defined as a short interruption of a foraging bout during which the goose raised its head above the body; this behaviour was assumed to be a measure of vigilance. Bite rate was also determined, when possible, by measuring the time required to take 50 bites. This measurement was done just before or just after the five minute observation period.

Each day before the start of the observations, vegetation samples were taken from the plots used on that day. Vegetation composition and biomass was estimated from four samples of 10*10 cm. Sods of this size were cut from the ground and all living above-ground plant parts were sorted to species level. Dead material was put together for all species. All categories were dried at 70 °C for at least two days and weighed. To determine food quality, leaf tips were collected, as these were the only plant parts the geese consumed. With these leaf tips as well as with the droppings, chemical analyses were performed to determine energy content, chromogen content and ADF content.

Food availability was also measured using the 'point-quadrat' method (pq). In this method, a pin is lowered onto the vegetation and the first hit is recorded. This can be a plant species but also dead material or bare soil. This procedure was repeated one hundred times (ten rows of ten points) per plot. It was assumed that this would imitate the way a goose views the vegetation it feeds on.

Determining bite size and intake rate

During one of the resting intervals between the periods of the observation experiment, a special experiment was set up to determine bite sizes of geese at different vegetations. For this purpose, sods of 40*40 cm were taken from each vegetation. On each sod, a large number (50-80) of *Festuca* plants were marked at the base of the stem, while the length of each leaf was measured. The sods were then offered to the geese, placed in holes in the ground to obtain a natural foraging position for the geese. After a grazing period of three hours, the sods were taken away and the marked plants were measured again. Bite size was defined as the decrease in length between the first and the second measurement, plus leaf growth, if any had occurred. Leaf growth was measured on the non-grazed leaves. Average bite size was determined from grazed leaves only. Bite size in grams was calculated by multiplying bite length with specific leaf weight (g/mm). It was assumed that geese take bites from only one leaf at a time.

Intake rate was used as an indicator of the ability of the geese to exploit a certain vegetation. We calculated intake rate in two different ways. Firstly, we obtained intake rate (g/sec) by multiplying bite rate (bite/sec) with bite size (g/bite). Secondly, we determined intake rate indirectly by dividing total food intake per day (gram) by total foraging time per day (sec). Total foraging time per day was calculated from the observations. Total food intake was calculated from the amount of droppings with the help of digestion:

food intake = droppings / (1 - fraction digestion)

The fraction of the food that was digested by the geese was calculated from the concentration of chromogen and ADF in food and droppings, as both are food components that the goose cannot digest and can therefore be used as markers. The fraction digestion was obtained as follows:

fraction digestion = (C(marker) in droppings - C(marker) in food) / C(marker) in droppings

Chromogen proved to be an unreliable marker, as in some cases a negative digestion was obtained. The use of ADF (Acid Detergent Fibres) yielded more logical results; these were used in further calculations.

Results

Vegetation

Festuca biomass was highest on the unmanipulated high biomass sites (High Not Mown) at 93 g/m^2; the mown plots on this site (High Mown) had a Festuca biomass of 45 g/m^2, which was even lower than on the low biomass plots (Low Not Mown and Low Mown) where biomass was 60 and 56 g/m^2, respectively (see figure 3.1). When the availability of Festuca was estimated using the point-quadrat method, the low biomass sites (Low Not Mown and Low Mown) showed the highest percentage of Festuca: 53% and 52%, respectively. These percentages are relative to the total number of hits including dead material and soil. This was significantly higher than on the high biomass sites: High Mown had 30% Festuca and High Mown had the lowest score, 26% (see fig. 3.2). The amount of dead material in the vegetation was highest on the High Not Mown plot (see fig 3.3). Mowing the high vegetation reduced standing dead to the same level as in the low biomass vegetations. These data are summarized in table 3.1. The high value in the PQ-measurement for 'other', that is, non-Festuca plants, is caused by a rapid length increase of *Juncus gerardii* after mowing.

Table 3.1. Vegetation of the experimental plots. Biomass data are in g/m^2. PQ (point-quadrat) data are in percentages. Numbers in brackets are standard errors. Letters denote significantly different groups at p=0.05. Treatments: High NM = high biomass not mown; High M = high biomass mown; Low NM = low biomass not mown; Low M = low biomass mown.

	High NM	High M	Low NM	Low M
Biomass: Festuca	92.8 (6.9)a	44.5 (3.3)b	59.8 (3.0)b	56.1 (2.6)b
Biomass: standing dead	411.8 (17.8)a	195.5 (14.1)b	172.0 (11.7)b	182.5 (13.1)b
Biomass: other	21.9	16.2	3.9	8.2
PQ: Festuca	30.2 (2.29)a	26.0 (2.19)a	52.9 (2.21)b	51.8 (1.82)b
PQ: standing dead	60.9	46.5	25.5	31.2
PQ: other	8.7	19.4	14.4	11.7

Energy content of the Festuca plants was not significantly different between treatments (table 3.2). ADF-content of Festuca leaves and droppings showed that digestibility also did not differ significantly between treatments. Average digestion of the food was 35%, although this result is based on incomplete data (only one sample for each treatment was available). These figures can also be found in table 3.2.

Table 3.2. Energy content of Festuca leaf tips per treatment, in kJ/g; and digestibility of leaf tips based on ADF content of Festuca leaf tips and goose droppings. Treatments: High NM = high biomass not mown; High M = high biomass mown; Low NM = low biomass not mown; Low M = low biomass mown.

	High NM	High M	Low NM	Low M
Energy content	21.1	21.0	20.8	21.4
% ADF in Festuca	19.3	18.2	19.2	18.9
% ADF in droppings	30.9	26.4	28.9	29.2
Fraction digestion	0.38	0.31	0.34	0.35

Herbivore performance

The body weight of the geese decreased on most of the days on all vegetation types (see appendix II). Average weight change ranged between -26.1 g/day on High Not Mown and -19.5 g/day on Low Mown and did not differ significantly among the four treatments (figure 3.4a). Weight change relative to the daily average also showed no significant differences among treatments (fig. 3.4b).

The amounts of droppings produced by the geese differed significantly among treatments. On the low biomass vegetation, significantly more droppings were collected (ANOVA, $F_{1,71}=12.5$, $p<0.001$, see figure 3.5). The effect of mowing was not significant (ANOVA, $F_{1,71}=3.9$, $p>0.05$). Dropping production per day can be found in appendix III.

The number of look-ups by the geese during foraging, which we used as an indicator for vigilance, was affected by both vegetation height (ANOVA, $F_{1,1421}=16.6$, $p<0.001$) and mowing (ANOVA, $F_{1,1421}=23.8$, $p<0.001$). The geese made the least look-ups on the Low Mown vegetation (see fig. 3.6, table 3.3). Bite rate was highest on the low biomass vegetations. Mowing had a large effect on the high biomass vegetation, but bite rate at Low Not Mown and Low Mown were similar (figure 3.7, table 3.3). Bite rate was inversely related to vegetation height (Pearson correlation coefficient, r^2=0.98, see fig. 3.8). The bite size, measured as length of leaf missing from marked plants after a set period of grazing, was highest on the high vegetations (figure 3.9a and table 3.3). Intake rate based on the bite size experiment was highest on the high biomass plots (table 3.3); this was due to the much higher bite size found here. When intake rate was calculated from dropping weight, digestibility and foraging time, the results are totally different (table 3.3). This calculated intake rate can be divided by bite rate to yield an alternative value for bite size. Calculated bite size is shown in figure 3.9b. Note the differences with figure 3.9a.

Table 3.3. Foraging efficiency. The data shown are averages of all geese per treatment. Treatments: High NM = high biomass not mown; High M = high biomass mown; Low NM = low biomass not mown; Low M = low biomass mown.

	High NM	High M	Low NM	Low M
vigilance (# look-ups/10 sec foraging)	1.66	1.13	1.18	0.94
bite rate (# bites/10 sec foraging)	19.1	23.3	27.4	27.7
bite size (mg dry weight/bite)	1.40	1.38	0.77	0.72
measured intake rate (mg dry weight/sec)	2.67	3.22	2.11	1.99
calculated intake rate (mg dry weight/sec)	2.60	2.19	4.30	3.91

Discussion

No difference in weight change could be found between the treatments. The weight of the animals decreased on all plots. The weight of the control geese also decreased. This was opposite to the natural cycle of the geese, which shows a weight increase during spring. One possible reason for this phenomenon is the fact that the geese used in the experiment were not used to foraging on grass. These animals are used to specially prepared waterfowl food with an energy content that is much higher than the energy content of grass. Wild geese spend most of their days foraging to build up fat reserves for migration and breeding. The geese in the experiment spent much less time foraging. This could be because they are not used to the necessity to forage all day (their usual food is of sufficiently high quality to make long foraging bouts unnecessary). It resulted, however, in a much smaller total energy intake per day leading to weight loss. The stress of being involved in an experiment may also be an important factor. It was clear from the behaviour of the geese that they did not like their confinement to a small space and possibly the presence of observers, although these were at a distance and mostly invisible to the geese. The fact that weight loss was usually highest on the first day of an experimental period suggests that they needed time to get used to their situation. Thus, if the periods had been longer, some differences between treatments might have been found. But even on the later days of a period, they spent a lot of time (and energy!) pacing along the nets that confined them and trying to escape. The question remains why weight loss did not differ among treatments, as intake did. Quite possibly, the differences are too small to be noticed because a lot of other factors play a role, such as stress, weather, disturbances and individual differences among the geese. All these can overrule the effect of differences in total energy intake.

Daily intake appeared to be highest on the low biomass plots. One possible reason for this is the higher foraging time on these plots, which suggests that grass in the younger stages is preferred by the geese. The main reason, however, seems to be a higher foraging efficiency. The geese feel more at ease (vigilance is lower) and eat faster. There seems to be a trade-off between vegetation height and bite rate. The inverse relation between vegetation height and bite rate was already described by Allden and Whittaker (1970) for sheep. It is uncertain whether the mechanism involved is the similar, however, as sheep can take larger amounts of grass in one bite. The food intake of herbivores foraging on low quality forage is constrained by digestibility (Fryxell 1991), i.e. when the gut is still filled with undigested food the animal cannot consume any more food until the gut has been emptied to some extent. Furthermore, captive birds which do not feed on grass exclusively, have an even shorter gut than wild birds (Owen 1975). There are two reasons why this process is unlikely to play a role in this experiment. First, geese already have relatively short gut systems compared to other herbivores and they never thoroughly digest their food, as can be seen when the droppings are examined under a microscope. Second, the geese on the high biomass treatments had a very low food intake. Since we did not detect any difference in digestibility, it is unlikely that they were more constrained than the birds on the low biomass treatments.

Bite size was both measured and calculated, and the results were different. This means that in at least one of the methods, either the underlying assumptions or the data are incorrect. While bite rate is hard to measure, it is likely that if an error occurs, it will occur on both vegetation types alike. Thus, it is unlikely that errors in bite rate have caused the differences between measured and calculated bite size.

The measured bite size was defined as the amount of leaf taken by the geese. Since the plants on the high biomass were taller, bigger bites were possible. This has also been demonstrated by others (Allden and Whittaker 1970, Gross et al. 1993a). The method used assumes that one bite equals one (piece of) leaf. If the geese can take more leaves at once, it becomes inaccurate because it is uncertain whether the number of leaves per bite is constant. The difference between the measured and calculated bite size is greatest on the low biomass plots, and smaller on the high biomass plots, especially on High Not Mown (fig. 3.9a and 3.9b). If the geese are able to take more than one leaf per bite on the low vegetation, but not on the high vegetation, this can explain the difference. The higher amount of living Festuca plants in the PQ measurements does indicate this is the case. Therefore, it should be easier for the geese to consume more than one leaf in one bite. The lower amount of standing dead would also facilitate this. Gross et al. (1993a) indicated bite size as the major determinant of intake rate, but in their experiment the animals were restricted to a single leaf at a time. Bite size seems to be inversely related to bite rate in several mammalian herbivore species (Spalinger and Hobbs 1992, Gross et al. 1993b, Ginnett and Demment 1995) because a larger bite must be chewed longer before it can be swallowed. This is consistent with the trade-off between vegetation height and bite rate mentioned earlier. However, calculated bite size of the geese in this experiment was highest on the sites where bite rate was also highest. The trade-off between bite size and bite rate might not exist for geese simply because they are unable to chew their food and are thus forced to consume relatively small pieces of leaf.

It seems clear that foraging efficiency is greater on a vegetation of intermediate biomass. This can explain the preference of wild herbivores for these areas on the salt-marsh. The effect of different vegetation densities on weight changes might better be tested in a less intense experiment, where the geese are less subject to stress; furthermore, a longer period for the experiment would be needed. For a better understanding of the processes governing foraging efficiency of geese, more detailed studies are needed for each separate process, such as bite size (including the number of leaves taken), bite rate and digestibility.

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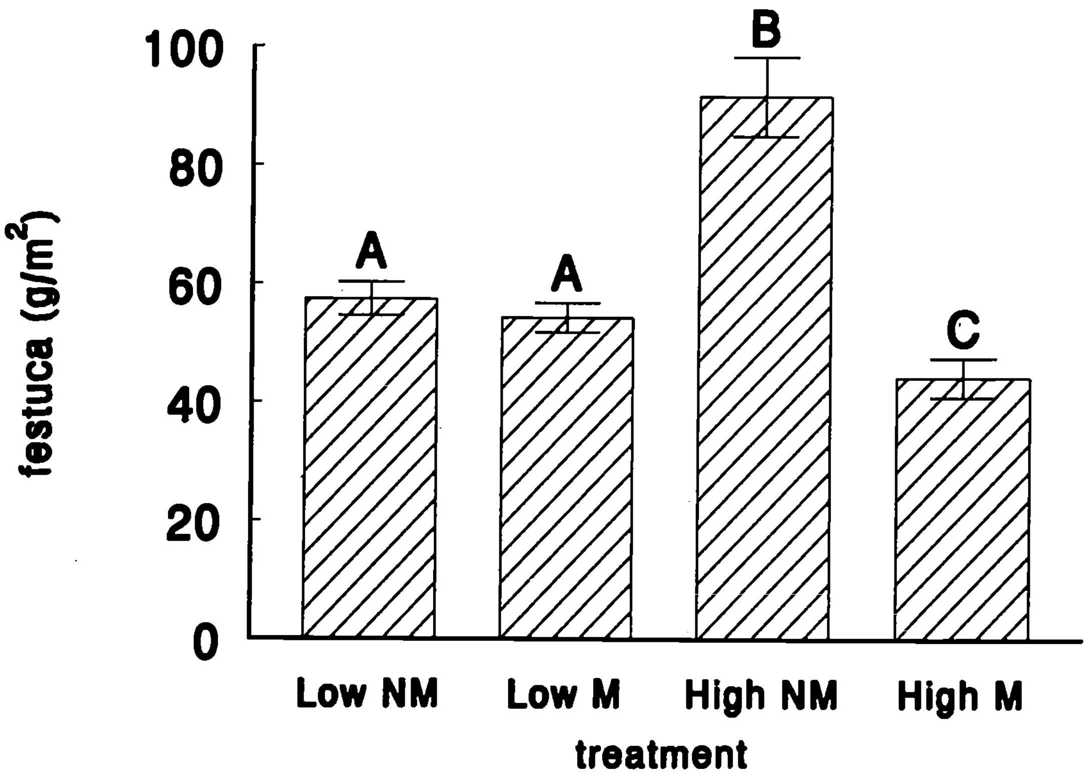

Figure 3.1. Average above-ground Festuca biomass (g/m^2), with standard errors. Letters denote groups significantly different at p=0.05. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

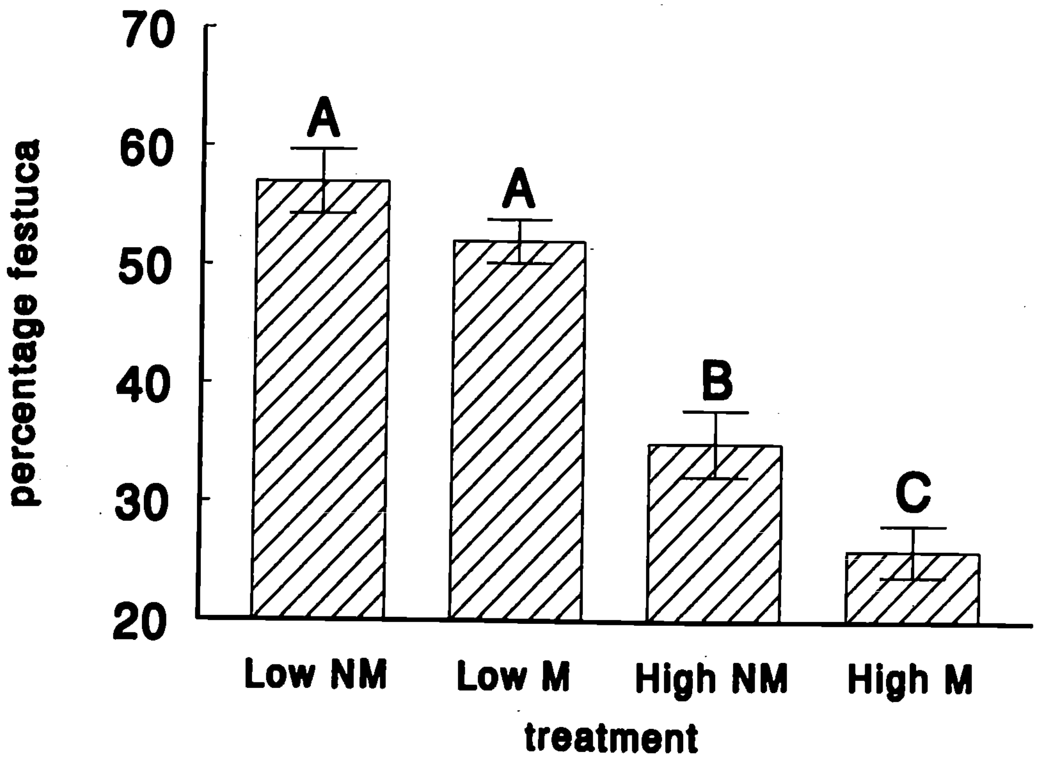

Figure 3.2. Average percentage Festuca in point-quadrat measurement, with standard errors. Letters denote groups significantly different at p=0.05. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

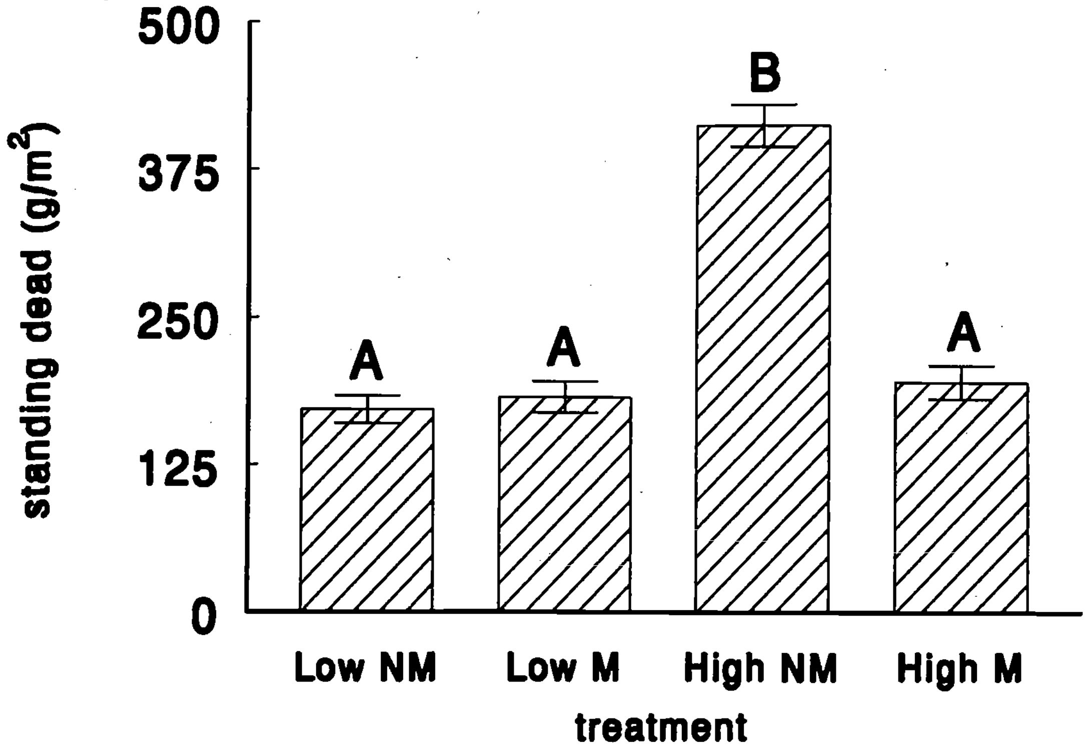

Figure 3.3. Average weight of above-ground dead plant material (g/m^2), with standard errors. Letters denote groups significantly different at p=0.05. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

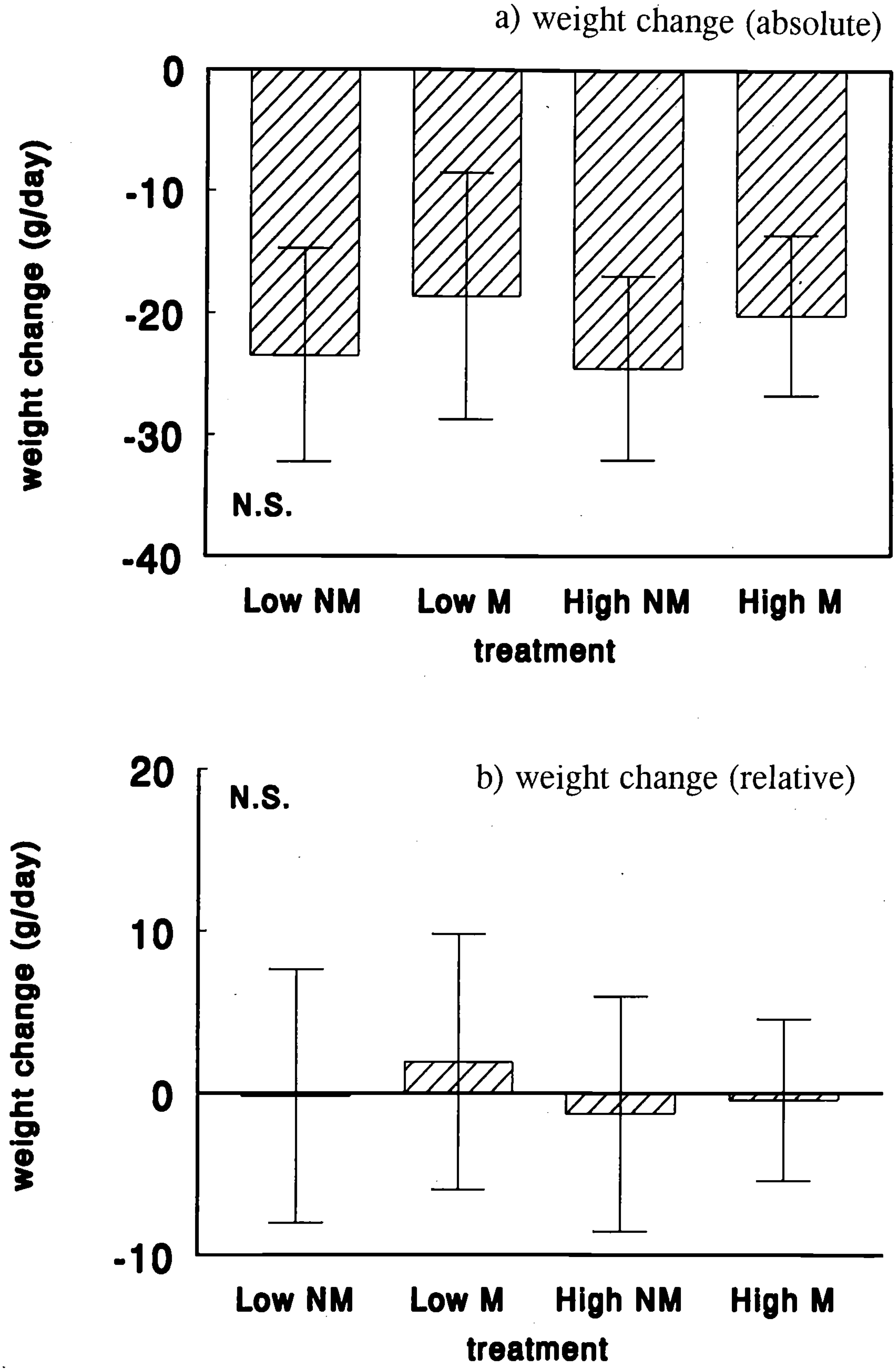

Figure 3.4. a) Average daily weight change of individual geese, with standard errors. b) Average differences between daily weight change of the geese on one treatement, and the average weight change of the geese on all treatments, with standard errors. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

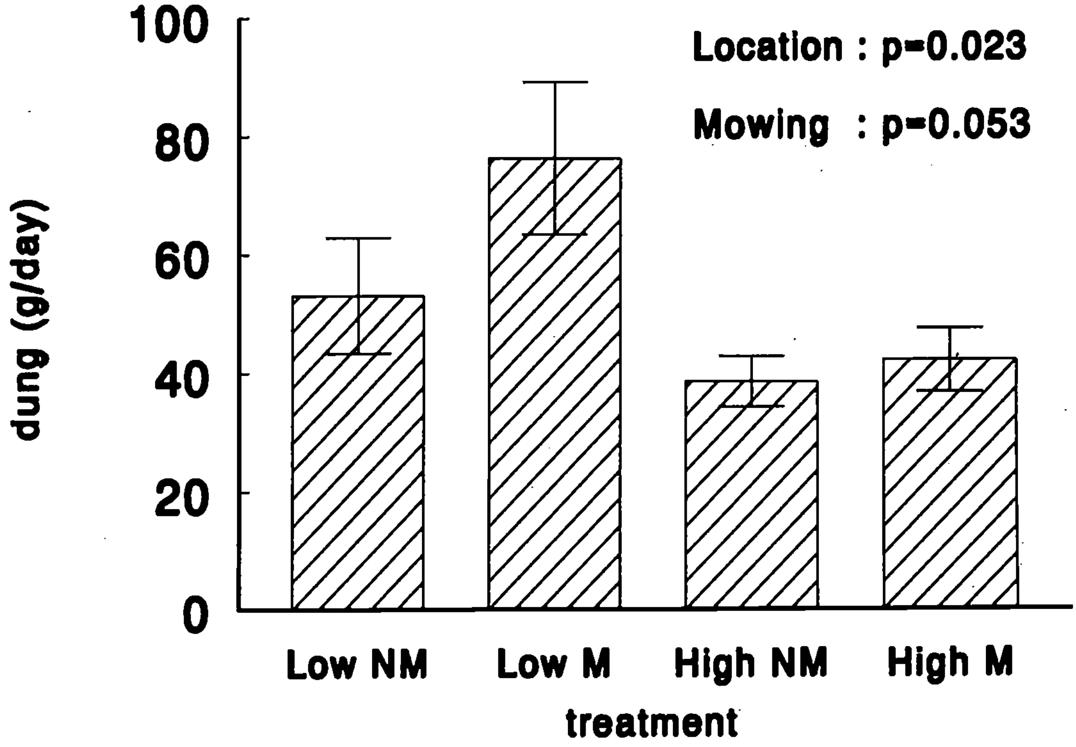

Figure 3.5. Average dropping weight per pair per day (g dry weight), with standard errors. The significance of the effects of site and mowing is indicated by the p-values from an ANOVA-test. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

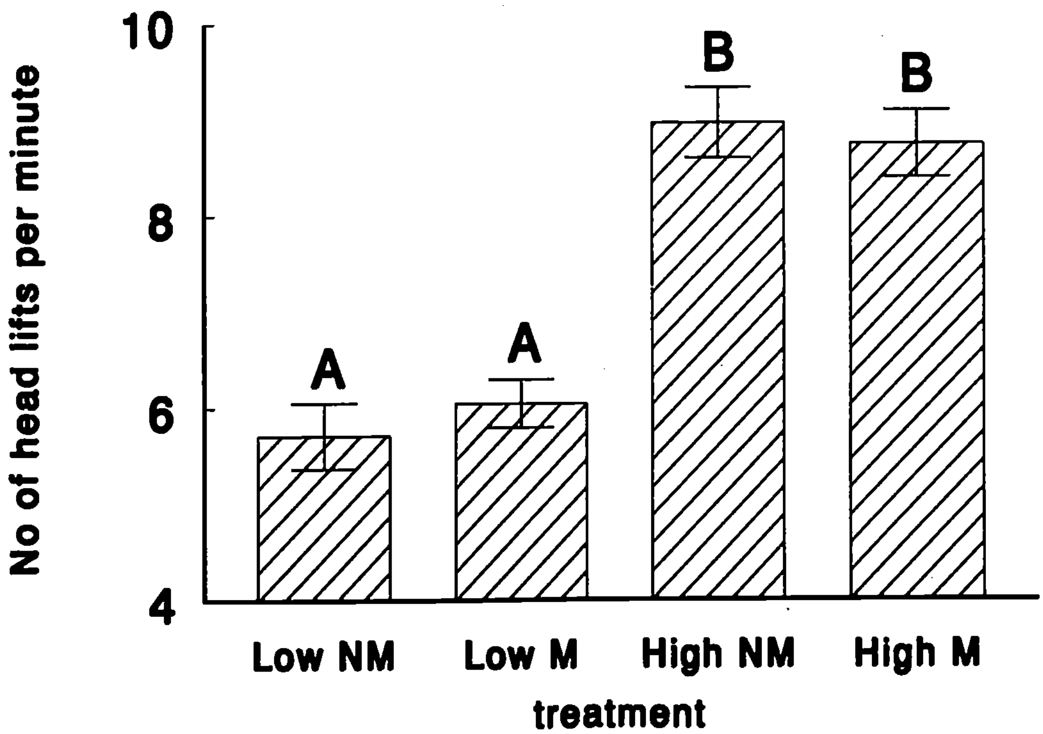

Figure 3.6. Number of look-ups during foraging bouts (# look-ups/10 seconds of foraging), with standard errors. Letters indicate groups significantly different at p = 0.05. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

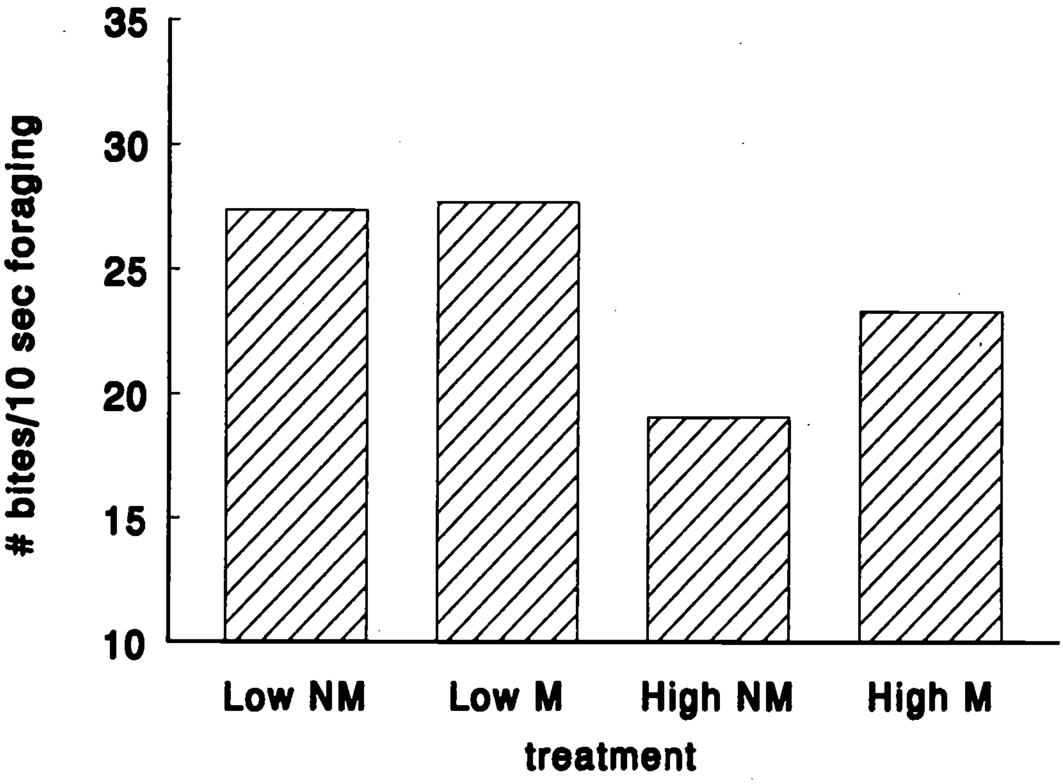

Figure 3.7. Bite rate (# bites/10 seconds of foraging). Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

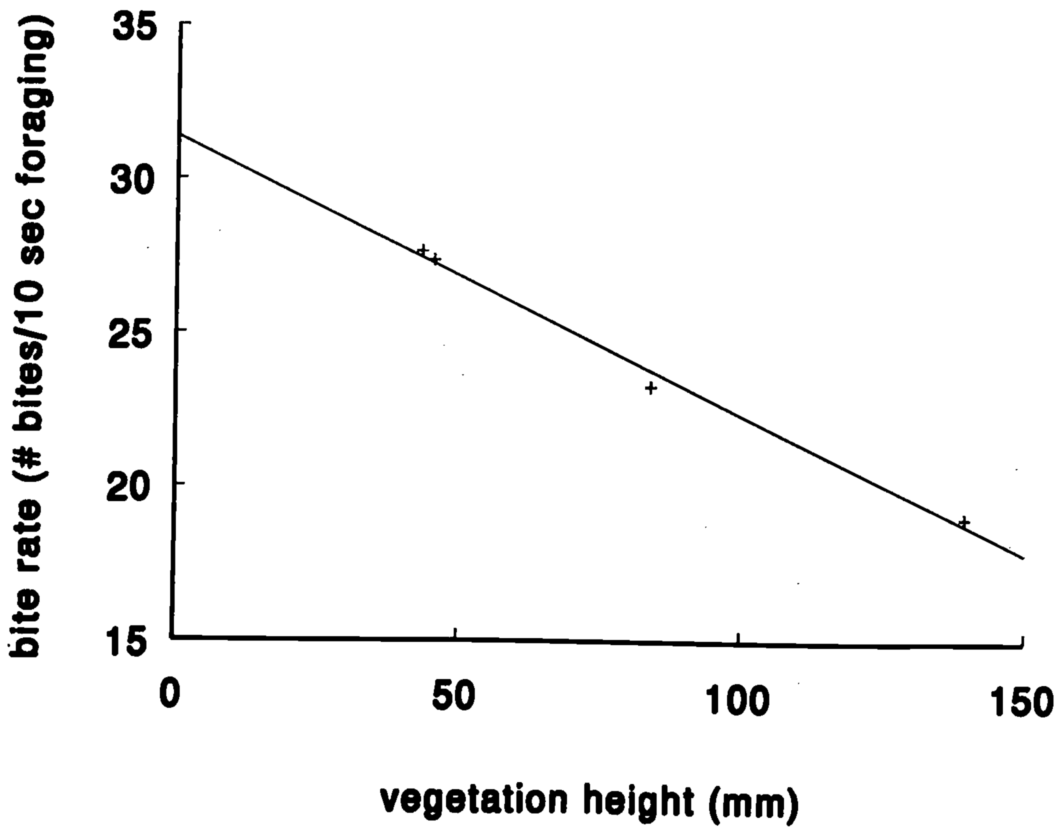

Figure 3.8. Bite rate (# bites/10 seconds of foraging) in relation to vegetation height (mm). The line is the regression line: bite rate = -0.09*height + 31.4, $r^2=0.98$.

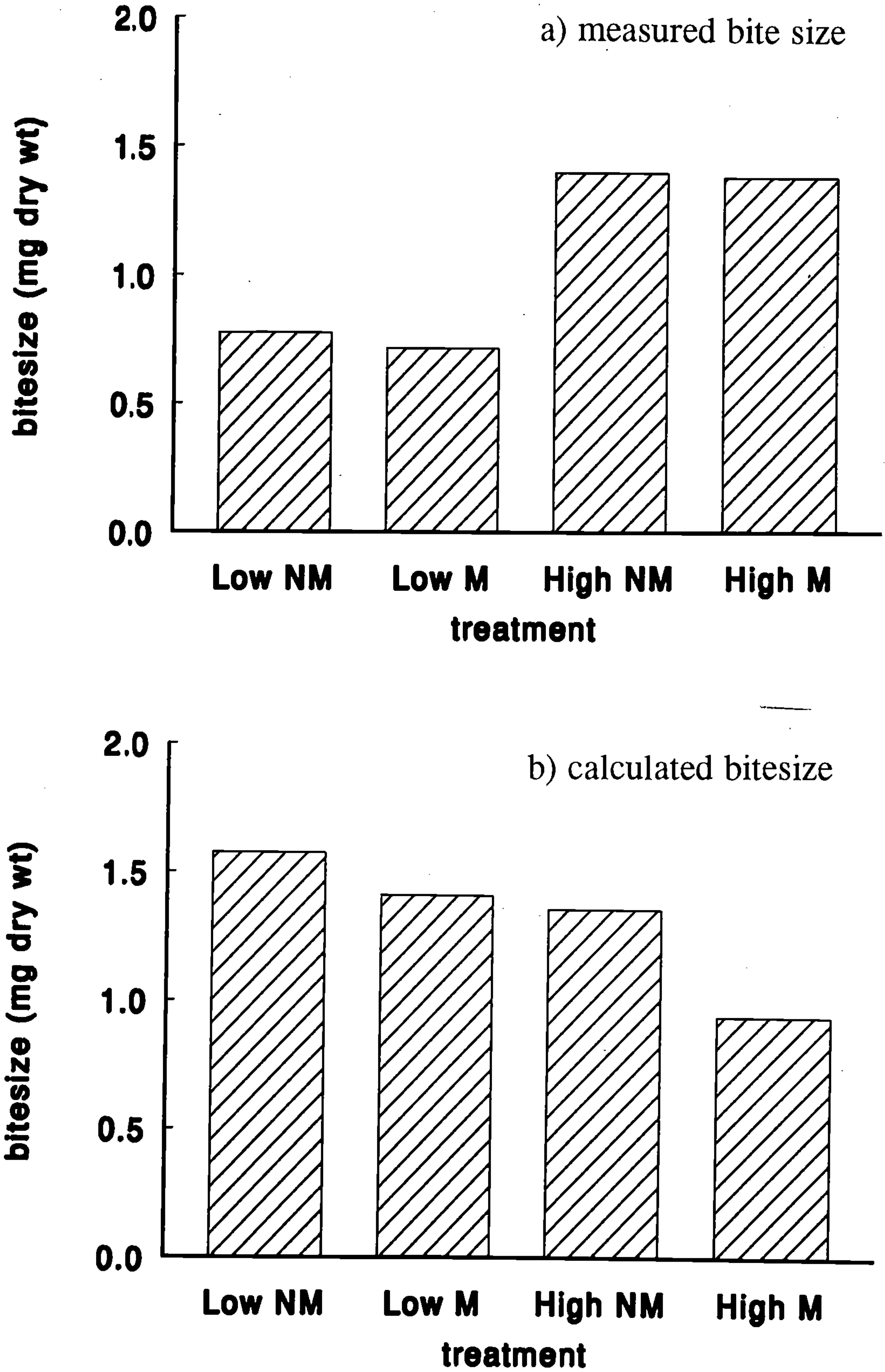

Figure 3.9. a) Bite size (mg dry weight/bite) obtained in the experiment with marked leaves. b) Bite size (mg dry weight/bite) calculated from daily food intake and behavioural observation data. Treatments: Low NM = low biomass not mown; Low M = low biomass mown; High NM = high biomass not mown; High M = high biomass mown.

Appendix I. Vegetation characteristics per treatment per day. Plant biomass and standing dead are given as the total amount in four samples of 10*10 cm (grams dry weight). PQ-numbers are percentages of total hits (including dead material and soil). Groups: B-dead = standing dead; B-Fest = Festuca biomass; B-other = biomass of other species; PQ-Fest = percentage Festuca in PQ-measurement; PQ-other = percentage of hits that were neither Festuca nor dead material (includes bare soil); PQ-dead = percentage of dead material in PQ-measurement. Treatments: HNM = high biomass not mown; HM = high biomass mown; LNM = low biomass not mown; LM = low biomass mown.

Date	Period	Day	Trtm	B-dead	B-Fest	B-other	PQ-Fest	PQ-other	PQ-dead
27-Apr-95	1	1	LNM	6.84	1.64	0.05	N/A	N/A	N/A
27-Apr-95	1	1	LM	5.46	1.28	0.34	N/A	N/A	N/A
27-Apr-95	1	1	HNM	19.76	3.91	3.16	43	3	54
27-Apr-95	1	1	HM	14.9	3.54	1.39	31	20	49
28-Apr-95	1	2	LNM	9.31	2.42	0.45	35	30	35
28-Apr-95	1	2	LM	14.2	3.39	0.59	44	10	46
28-Apr-95	1	2	HNM	18.55	1.62	2.32	41	1	58
28-Apr-95	1	2	HM	N/A	N/A	N/A	35	10	55
29-Apr-95	1	3	LNM	13.51	2.07	0.13	69	24	7
29-Apr-95	1	3	LM	5.39	N/A	0.23	74	20	6
29-Apr-95	1	3	HNM	20.81	4.69	3.46	29	1	70
29-Apr-95	1	3	HM	15.36	1.78	1.3	40	11	49
30-Apr-95	1	4	LNM	N/A	1.39	0.52	55	15	30
30-Apr-95	1	4	LM	8.24	1.74	0.62	42	20	38
30-Apr-95	1	4	HNM	11.92	1.22	1.27	34	3	63
30-Apr-95	1	4	HM	7.28	1.53	1.36	30	17	53
01-Mei-95	1	5	LNM	6.4	2.28	0.39	52	25	23
01-Mei-95	1	5	LM	8.14	1.17	0.35	43	17	40
01-Mei-95	1	5	HNM	19.2	4.26	3.06	27	4	69
01-Mei-95	1	5	HM	8.46	1.25	1.16	13	29	58
02-Mei-95	1	6	LNM	5.79	2.57	0.26	36	32	32
02-Mei-95	1	6	LM	17.67	2.91	1.76	N/A	N/A	N/A
02-Mei-95	1	6	HNM	N/A	N/A	N/A	20	7	73
02-Mei-95	1	6	HM	8.23	2.05	0.86	25	33	42
05-Mei-95	2	1	LNM	9.51	2.29	0.62	47	24	29
05-Mei-95	2	1	LM	7.21	1.81	0.09	50	14	36
05-Mei-95	2	1	HNM	19.35	2.61	2.2	26	1	73
05-Mei-95	2	1	HM	6.61	1.12	1.89	8	35	57
06-Mei-95	2	2	LNM	8.16	2.09	0.16	59	6	35
06-Mei-95	2	2	LM	4.74	1.5	0.46	53	15	32
06-Mei-95	2	2	HNM	15.24	2.87	3.39	18	4	78
06-Mei-95	2	2	HM	4.28	0.79	2.58	16	26	58
07-Mei-95	2	3	LNM	2.9	1.1	0.59	52	17	31
07-Mei-95	2	3	LM	2.92	1.2	0.57	57	6	37
07-Mei-95	2	3	HNM	16.19	2.19	1.42	16	3	81
07-Mei-95	2	3	HM	16.09	1.23	0.69	25	15	60
08-Mei-95	2	4	LNM	3.88	2.55	0.73	55	18	27
08-Mei-95	2	4	LM	5.55	2.16	1.32	53	19	28
08-Mei-95	2	4	HNM	16.43	3.14	4.32	7	16	77
08-Mei-95	2	4	HM	6.42	0.92	0.84	17	21	62
13-Mei-95	3	1	LNM	3.77	2.89	0.38	52	28	20
13-Mei-95	3	1	LM	N/A	N/A	N/A	47	27	26
13-Mei-95	3	1	HNM	18.65	2.17	0.6	31	6	63
13-Mei-95	3	1	HM	8.48	3.09	1.66	38	11	51
14-Mei-95	3	2	LNM	6.73	3.16	1.77	56	22	22
14-Mei-95	3	2	LM	7.93	2.52	1.3	57	17	26
14-Mei-95	3	2	HNM	13.93	4.78	2.76	28	7	65
14-Mei-95	3	2	HM	3.21	1.3	1.05	24	27	49
15-Mei-95	3	3	LNM	5.51	2.74	0.24	48	19	33
15-Mei-95	3	3	LM	5.422	3.04	0.33	44	17	39

15-Mei-95	3	3	HNM	25.36	5.84	2.69	25	11	64
15-Mei-95	3	3	HM	8.07	2.31	1.98	21	32	47
16-Mei-95	3	4	LNM	9.93	3.04	0.07	70	4	26
16-Mei-95	3	4	LM	8.37	2.52	0.12	49	10	41
16-Mei-95	3	4	HNM	14.78	4.45	3.2	36	15	49
16-Mei-95	3	4	HM	6.41	1.76	2.74	25	38	37
17-Mei-95	3	5	LNM	6.96	1.83	0.7	57	20	23
17-Mei-95	3	5	LM	7.08	2.32	0.3	56	9	35
17-Mei-95	3	5	HNM	13.96	3.34	0.65	26	16	58
17-Mei-95	3	5	HM	8.44	0.68	1.68	28	27	45
22-Mei-95	4	1	LNM	7.33	3.24	1.24	47	35	18
22-Mei-95	4	1	LM	3.85	2.53	1.63	51	18	31
22-Mei-95	4	1	HNM	15.42	4.71	4.62	42	12	46
22-Mei-95	4	1	HM	3.22	0.86	3.61	14	51	35
23-Mei-95	4	2	LNM	4.48	2.72	0.49	55	17	28
23-Mei-95	4	2	LM	10.4	2.92	1.31	52	30	18
23-Mei-95	4	2	HNM	12.28	5.23	1.03	29	27	44
23-Mei-95	4	2	HM	3.92	2.39	2.2	29	26	45
24-Mei-95	4	3	LNM	5.59	2.59	0.43	59	21	20
24-Mei-95	4	3	LM	8.27	3.01	0.6	59	11	30
24-Mei-95	4	3	HNM	15.7	2.48	2.51	39	14	47
24-Mei-95	4	3	HM	7.71	2.43	1.88	48	38	14
25-Mei-95	4	4	LNM	2.81	2.33	0.88	39	44	17
25-Mei-95	4	4	LM	3.19	1.98	1.49	45	33	22
25-Mei-95	4	4	HNM	19.95	5.95	3.62	40	8	52
25-Mei-95	4	4	HM	5.7	1.99	1.49	28	42	30
26-Mei-95	4	5	LNM	8.37	3.17	0.29	63	8	29
26-Mei-95	4	5	LM	6.99	3.01	0.92	56	13	31
26-Mei-95	4	5	HNM	10.24	6.52	2.88	47	19	34
26-Mei-95	4	5	HM	5.82	2.78	1.73	24	42	34

Appendix II. Body weights of the geese; the geese were weighed in the morning before they were allowed to eat or drink. Geese are indicated by their ring codes and are arranged per pair. After each pair the treatment they were in during that period is given. The last three individuals are the reserve birds. In periods 3 and 4, one of these (Y7) replaced DHH in the experiment. Treatments: HNM = high biomass not mown; HM = high biomass mown; LNM = low biomass not mown; LM = low biomass mown.

date	period	day	DIV	DIU	trtm	Y9	YP	trtm	DHH	7J	trtm	BTG	Wit	trtm	BTH	Y7	YY
			male	female		male	female		fema.	male		male	female		male	male	male
19-Apr-95	0	0	2450	2090	LNM	2477	1910	LM	1599	1732	HNM	1930	1472	HM	1735	2034	2121
27-Apr-95	1	1	2330	2088	LNM	2440	1796	LM	1489	1734	HNM	1879	1496	HM	1657	2010	2096
28-Apr-95	1	2	N/A	N/A	LNM	N/A	N/A	LM	1460	1665	HNM	1850	1440	HM	1626	1979	2091
29-Apr-95	1	3	2260	1964	LNM	2353	1719	LM	1438	1673	HNM	1873	1408	HM	1782	2096	2186
30-Apr-95	1	4	2224	1955	LNM	2351	1699	LM	1415	1662	HNM	1848	1421	HM	1607	1977	2082
01-May-95	1	5	2205	1970	LNM	2190	1680	LM	1267	1636	HNM	1912	1391	HM	1626	1956	2071
02-May-95	1	6	2190	1930	LNM	2295	1670	LM	1298	1624	HNM	1819	1384	HM	1586	1937	2052
03-May-95	1	7	2188	1956	LNM	2297	1683	LM	1292	1637	HNM	1829	1390	HM	N/A	2004	2144
05-May-95	2	1	2155	1950	HM	2265	1730	HNM	1242	1682	LNM	1806	1441	LM	1613	1988	2103
06-May-95	2	2	2140	1931	HM	2217	1675	HNM	1207	1632	LNM	1828	1382	LM	N/A	N/A	N/A
07-May-95	2	3	2129	1919	HM	2214	1669	HNM	1190	1662	LNM	1762	1268	LM	1591	1990	2072
08-May-95	2	4	2114	1931	HM	2218	1666	HNM	1206	1621	LNM	1816	1376	LM	1592	1972	2067
09-May-95	2	5	2114	1911	HM	2224	1652	HNM	1249	1653	LNM	1820	1396	LM	1628	1998	2099
13-May-95	3	1	2255	2014	HNM	2325	1878	HM	1431	1797	LM	1925	1546	LNM	1655	2084	2126
14-May-95	3	2	2175	1948	HNM	2210	1777	HM	1389	1730	LM	1879	1497	LNM	1605	2065	2079
15-May-95	3	3	2150	1910	HNM	2210	1770	HM	1367	1714	LM	1879	1454	LNM	1585	2039	2070
16-May-95	3	4	2086	1906	HNM	2204	1749	HM	1337	1695	LM	1862	1426	LNM	1562	1990	2037
17-May-95	3	5	2070	2027	HNM	2164	1749	HM	N/A	1670	LM	1855	1265	LNM	N/A	1985	N/A
18-May-95	3	6	2085	1875	HNM	2165	1714	HM	1297	1648	LM	1832	1402	LNM	1604	1958	2015
22-May-95	4	1	2268	2015	LM	2303	1972	LNM	1505	1809	HM	1932	1564	HNM	1701	2125	2121
23-May-95	4	2	2159	1915	LM	2208	1862	LNM	N/A	1715	HM	1915	1485	HNM	N/A	2085	N/A
24-May-95	4	3	2164	1919	LM	2206	1806	LNM	1420	1708	HM	1884	1464	HNM	1605	2043	2055
25-May-95	4	4	2133	1923	LM	2175	1740	LNM	1401	1697	HM	1867	1432	HNM	1604	2012	2035
26-May-95	4	5	2110	1880	LM	2151	1731	LNM	1379	1675	HM	1822	1430	HNM	1606	1986	2013
27-May-95	4	6	2105	1873	LM	2150	1720	LNM	1366	1649	HM	1789	1386	HNM	1584	1955	1987

Appendix III. Dung production and number of bites per pair per day. Dung fresh and dry weight are given; number of bites were calculated from foraging time and bite rate. Geese are indicated by their ring codes (see app. II for sex of the birds). Treatments: HNM = high biomass not mown; HM = high biomass mown; LNM = low biomass not mown; LM = low biomass mown.

Date	Period	Day	Geese	Trtmname	Dung fresh	Dung dry	# bites
27-Apr-95	1	1	DIV+DIU	LNM	154	23	N/A
28-Apr-95	1	2	DIV+DIU	LNM	137	46	N/A
29-Apr-95	1	3	DIV+DIU	LNM	229	53	70122
30-Apr-95	1	4	DIV+DIU	LNM	178	53	42604
01-May-95	1	5	DIV+DIU	LNM	200	57	37937
02-May-95	1	6	DIV+DIU	LNM	217	69	66112
05-May-95	2	1	DIV+DIU	HM	172	41	44091
06-May-95	2	2	DIV+DIU	HM	222	64	67706
07-May-95	2	3	DIV+DIU	HM	174	55	89287
08-May-95	2	4	DIV+DIU	HM	333	87	119305
13-May-95	3	1	DIV+DIU	HNM	195	53	32949
14-May-95	3	2	DIV+DIU	HNM	175	52	52703
15-May-95	3	3	DIV+DIU	HNM	205	41	41843
16-May-95	3	4	DIV+DIU	HNM	148	47	68455
17-May-95	3	5	DIV+DIU	HNM	470	60	96726
22-May-95	4	1	DIV+DIU	LM	342	112	79480
23-May-95	4	2	DIV+DIU	LM	392	119	115148
24-May-95	4	3	DIV+DIU	LM	370	126	85843
25-May-95	4	4	DIV+DIU	LM	452	117	106417
26-May-95	4	5	DIV+DIU	LM	482	145	137015
27-Apr-95	1	1	YP+Y9	LM	113	33	N/A
28-Apr-95	1	2	YP+Y9	LM	83	27	N/A
29-Apr-95	1	3	YP+Y9	LM	50	29	30780
30-Apr-95	1	4	YP+Y9	LM	87	21	25694
01-May-95	1	5	YP+Y9	LM	58	17	53678
02-May-95	1	6	YP+Y9	LM	98	25	38391
05-May-95	2	1	YP+Y9	HNM	57	12	20020
06-May-95	2	2	YP+Y9	HNM	83	21	21336
07-May-95	2	3	YP+Y9	HNM	95	22	42568
08-May-95	2	4	YP+Y9	HNM	103	21	35216
13-May-95	3	1	YP+Y9	HM	127	29	33380
14-May-95	3	2	YP+Y9	HM	135	31	36919
15-May-95	3	3	YP+Y9	HM	168	32	55269
16-May-95	3	4	YP+Y9	HM	194	48	46090
17-May-95	3	5	YP+Y9	HM	336	40	82666
22-May-95	4	1	YP+Y9	LNM	136	38	59117
23-May-95	4	2	YP+Y9	LNM	49	10	10079
24-May-95	4	3	YP+Y9	LNM	70	16	27195
25-May-95	4	4	YP+Y9	LNM	49	9	10355
26-May-95	4	5	YP+Y9	LNM	87	20	29653
27-Apr-95	1	1	DHH+7J	HNM	N/A	N/A	N/A
28-Apr-95	1	2	DHH+7J	HNM	27	N/A	N/A
29-Apr-95	1	3	DHH+7J	HNM	38	7	5721
30-Apr-95	1	4	DHH+7J	HNM	47	8	10499
01-May-95	1	5	DHH+7J	HNM	67	17	29142
02-May-95	1	6	DHH+7J	HNM	65	13	5809
05-May-95	2	1	DHH+7J	LNM	223	44	28223
06-May-95	2	2	DHH+7J	LNM	271	54	30485
07-May-95	2	3	DHH+7J	LNM	N/A	N/A	49119
08-May-95	2	4	DHH+7J	LNM	390	42	30141
13-May-95	3	1	Y7+7J	LM	209	43	52959
14-May-95	3	2	Y7+7J	LM	235	49	26122
15-May-95	3	3	Y7+7J	LM	218	56	82717
16-May-95	3	4	Y7+7J	LM	234	69	81394

17-May-95	3	5	Y7+7J	LM	566	91	119693
22-May-95	4	1	Y7+7J	HM	109	28	39018
23-May-95	4	2	Y7+7J	HM	77	N/A	27653
24-May-95	4	3	Y7+7J	HM	84	24	65068
25-May-95	4	4	Y7+7J	HM	179	40	73373
26-May-95	4	5	Y7+7J	HM	159	41	102867
27-Apr-95	1	1	Wit+BTG	HM	N/A	N/A	N/A
28-Apr-95	1	2	Wit+BTG	HM	N/A	10	N/A
29-Apr-95	1	3	Wit+BTG	HM	53	13	62875
30-Apr-95	1	4	Wit+BTG	HM	187	51	125457
01-May-95	1	5	Wit+BTG	HM	104	39	127965
02-May-95	1	6	Wit+BTG	HM	80	53	130838
05-May-95	2	1	Wit+BTG	LM	208	35	85699
06-May-95	2	2	Wit+BTG	LM	374	97	99778
07-May-95	2	3	Wit+BTG	LM	320	102	172125
08-May-95	2	4	Wit+BTG	LM	511	140	176827
13-May-95	3	1	Wit+BTG	LNM	138	40	52500
14-May-95	3	2	Wit+BTG	LNM	274	78	70717
15-May-95	3	3	Wit+BTG	LNM	323	87	116489
16-May-95	3	4	Wit+BTG	LNM	276	87	103186
17-May-95	3	5	Wit+BTG	LNM	754	163	180041
22-May-95	4	1	Wit+BTG	HNM	100	29	36155
23-May-95	4	2	Wit+BTG	HNM	86	30	66001
24-May-95	4	3	Wit+BTG	HNM	180	49	51520
25-May-95	4	4	Wit+BTG	HNM	246	58	86316
26-May-95	4	5	Wit+BTG	HNM	211	47	82513