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Independent Variables for Predicting Intake Rate of Mammalian Herbivores: Biomass
Density, Plant Density, or Bite Size?
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Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size?

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Contemporary models of herbivore functional response are typically driven by one of three potential measures of forage availability: biomass density (g/m^2), prey (plant, tiller, ramet) density (no./m^2), or bite size (g/bite). The choice between these measures is not always obvious, but can have a large influence on the shape of the functional response. Furthermore, under most conditions two or more of these variables are confounded, hampering statistical tests to separate their effects. We designed a set of two, parallel, factorial experiments to separate the effects of plant density, biomass density, and bite size on intake rates of lemmings. Plant density was varied by changing the distance between plants, and biomass density was varied by changing both plant density and plant size. Changes in bite size were imposed on lemmings by offering them plants that varied in height and mass. In our first experiment, we crossed bite size with biomass density, and in the second, we crossed bite size with plant density. Biomass and plant density had no effect on intake rates ($p > 0.2$), but we observed 2–3 fold increases in intake rate in response to increased bite size ($p < 0.0001$). Intake rates we observed corresponded closely with those predicted by a model of functional response driven by bite size alone, indicating that the time needed to process a bite in the mouth exceeded that necessary to travel between plants, even though biomass densities in our feeding trials were much lower than those typical of natural habitats. Our results emphasize that the choice of an independent variable can have a profound influence on the interpretation of studies of herbivore functional response.

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The relationship between an animal's intake rate and food availability, the functional response, is fundamental to many processes in animal ecology. As such, it has been the focus of an intense research effort. For predators, this effort has resulted in the development of widely used mechanistic models that faithfully represent the foraging process (e.g. the disc equation [Holling 1959], randompredator and random-parasitoid models [Rogers 1972]). For herbivores, there are few mechanistic models of functional response (Demment et al. 1987, Illius and Gordon 1987, Lundberg and Åström

1990, Spalinger and Hobbs 1992, Laca and Demment in press), and empirical tests of these models are limited (Lundberg and Danell 1990, Shipley and Spalinger 1992, Gross et al. 1993). Moreover, the emphasis of models for herbivores varies and predicted responses include total biomass consumed, intake rate, and the number of food items "attacked". These differences complicate model comparisons.

Comparisons of models are further hampered by the use of different independent, driving variables. Biomass density is most frequently used to predict herbivore

Plant Size (mg)

	1	8
100	100	12.5
800	800	100

Biomass (mg/m^2)

Plant Size (mg)

	1	8
100	100	800
800	800	6400

Plants/m^2

Fig. 1. Experimental design for lemming foraging trials. In the top chart, the number in the cell is plant density (plants/m^2), and in the bottom chart, the number in the cell is biomass density (mg/m^2). Because biomass density was altered by changing plant density, these factors were confounded.

pendent variables to choose from, and this choice can exert a profound impact on the shape of the functional response (compare Lundberg 1988: Fig. 1 vs Fig. 2). Because changes in plant density, biomass density, and plant size are virtually always confounded, there have been no controlled experiments to distinguish the independent effects of each of these variables.

We undertook this study to determine how three measures of plant availability related to variation in the intake rate of a small mammalian herbivore. Because of their common use and relevance to mechanistic models of herbivore functional response, we were particularly interested in comparing the effect of plant size, plant density, and biomass density on short-term intake rate.

Materials and methods

Animals

We examined intake rates of collared lemmings (*Dicrostonyx groenlandicus*), a small mammalian herbivore. We chose lemmings because they are easy to work with and similar species have been used in studies where intake rates were measured as a function of biomass density (Batzli et al. 1981), plant density (Lundberg 1988), and plant size (Gross et al. 1993), the three indicators of forage availability we wished to examine. Previous studies therefore provided data for comparison.

The six adult lemmings (average body mass = 69.9 g) in our experiments were raised in captivity and fed a diet of rabbit and horse chow ad lib. Before measurements, they were habituated to the experimental apparatus and the fresh alfalfa (*Medicago sativa* L.) we used for all feeding trials.

functional response. In grasslands, biomass density (g/m^2) is often statistically correlated with intake rate (e.g. Hudson and Watkins 1986, Short 1986, Hudson and Frank 1987), but this relationship fails for animals feeding on forbs or browse (Trudell and White 1981, Wickstrom et al. 1984, Spalinger et al. 1988, but see Lundberg and Danell 1990), and even within grasslands it is frequently subject to a large variation (e.g. Arnold and Dudzinski 1967). Other studies have considered how intake varies in response to changes in the size of bites obtained by the forager (Black and Kenney 1984, Spalinger et al. 1988, Shipley and Spalinger 1992, Gross et al. 1993) or to plant density (Lundberg 1988, Lundberg and Danell 1990). Clearly, there are several inde-

Experimental design and plant patches

We wished to test whether plant size (g dry matter), plant density (plants/m^2), or biomass density (g/m^2) influenced the intake rate of lemmings. However, because biomass density is the product of plant size and plant density, these treatments are confounded (Fig. 1). To separate the independent effects of these variables, we designed two parallel experiments. In Experiment 1, we crossed plant size with biomass density, and in Experiment 2, we crossed plant size with plant density (Fig. 1). In both experiments we used the same sizes of plants and, where possible, the same biomass and plant densities. We designed our treatments to include biomass and plant densities much lower than those normally encountered by lemmings, yet in which lemmings were likely to be limited by food processing (cropping and mastication), rather than movements between plants (Spalinger and Hobbs 1992 discuss switching between processes regulating intake).
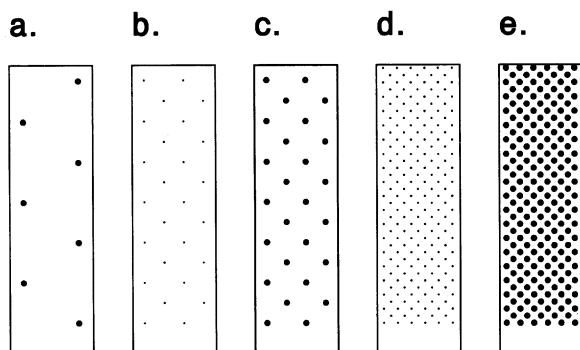
a.   b.   c.   d.   e.

Fig. 2. Diagram of the first 1-m section of the experimental foraging arenas (see Methods for total arena lengths). We varied plant density and the size of plants to create plant patches with different combinations of plant densities, plant sizes, and biomass densities (biomass density = plant density × plant size). The size of dot is proportional to plant size (1 or 8 mg dry matter). Treatments were: (a) 8 mg plants, 12.5 plants/m^2, (b) 1 mg plants, 100 plants/m^2, (c) 8 mg plants, 100 plants/m^2, (d) 1 mg plants, 800 plants/m^2, (e) 8 mg plants, 800 plants/m^2.

We measured intake rates of lemmings in response to variation in plant size, plant density, and biomass density. To do so, we observed lemmings foraging in hand-assembled patches of plants. We assembled plant patches by placing small (1 mg dry matter) or large (8 mg dry matter) leaflets, hereafter referred to as plants, of fresh alfalfa in plastic clips (Gross et al. 1993). The clips were roughly triangular in cross-section, 13 mm high, 5 mm wide at the base, and 280 mm long, and pressure exerted at the apex of the clip held the alfalfa plants. Clips were placed snugly in slots cut into pieces of wood 305 mm wide and approximately 1.2 m long. We placed plants 28.2, 7.1, or 3.5 cm apart to obtain plant densities of 12.5, 100, and 800 plant/m^2, respectively (Fig. 2). The length of low density patches (12.5 plants/m^2) was adjusted to contain 50 plants, medium density patches (100 plant/m^2) either 40 large (8 mg) or 120 small (1 mg) plants, and high density patches (800 plants/m^2) contained 264 plants. Overall patch lengths were 7.3 m, 1.9 m, 4.4 m, or 1.4 m, respectively. Regardless of plant density, we left 10 cm of empty plant patch at each end of the foraging arena (Fig. 2).

Behavioral measurement

We were interested in short term, mechanical limitations to intake, exclusive of the effects of animal state (satiety, lactation, etc.) and physiology (digestive constraints, homeostatic regulation). We therefore kept our trials short (approximately 2 min) and offered lemmings a highly palatable forage. This helped ensure that the intake rates we observed were the result of physical limitations such as forage availability, animal travel velocity, cropping rate, and chewing rate, and not a func-

tion of other factors not part of our experimental design. For each trial, a single animal was released from a holding box at the end of a plant patch. We recorded active feeding time while the animal foraged, using a computer to time-stamp behaviors in individual records. Bouts of inactivity or attempts to escape were excluded from calculations of active feeding time.

We used two methods to determine the mass of forage eaten by lemmings during feeding trials. Initially, we calculated the mass consumed as the difference between the mass of forage offered and that remaining, corrected for dry matter (Gross et al. 1993). This protocol required that we replace all plants between foraging trials. As an alternative, we also estimated forage intake by multiplying the number of plants consumed by the average plant mass, allowing us to replace only those plants eaten during a trial. Dry matter corrections for average plant masses were determined daily from subsamples of offered material. For trials with large plants (8 mg), both protocols produced equal measures of forage consumption ($p > 0.5$). For trials with small plants (1 mg), intake rates calculated from the average plant mass exceeded those based on direct measures, but the magnitude of the differences were very small (mean = 0.012 g/min, $p < 0.001$). We considered these differences to be insignificant to the analysis of our experiments and, because of the time and labor saving, adopted the use of an average plant mass to estimate consumption. Intake rates were calculated as the dry mass of plants consumed divided by active foraging time.

Hypotheses and statistical analyses

Based on our previous modeling (Spalinger and Hobbs 1992) and model tests (Gross et al. 1993), we expected a highly significant effect of plant size, but no statistical effect of plant or biomass density. We anticipated no significant interaction between treatments.

Treatment effects were analyzed using a 2-way factorial analysis of variance for a randomized complete blocks design (Sokal and Rohlf 1981). In the first analysis, plant size and biomass density were treatments, and animals were blocks. In the second analysis, plant size and plant density were treatments, and animals were blocks. Analyses were performed using SAS Proc GLM (SAS Institute 1988).

We also compared intake rates we observed to predictions from a mechanistic model of functional response of herbivores foraging in food concentrated patches (Spalinger and Hobbs 1992, Laca and Demment in press). Intake rate (I, g dry matter/min) is the product of cropping rate (B, bites/min) and bite size (S, g/bite). Because cropping and chewing movements cannot occur simultaneously (Ardran et al. 1958, Greaves 1978), B is a function of the average time required to

Table 1. Plant sizes and biomass densities offered to lemmings in hand-assembled plant patches. We fixed plant densities and calculated biomass density as the product of plant density and plant size.

Plant size (mg)		Plant density (plants/m²)	Biomass density (mg/m²)	
Target	Actual		Target	Actual
8	8.8	12.5	100	110
1	1.3	100	100	130
8	9.1	100	800	910
1	1.0	800	800	800
8	7.2	800	6400	5760

Table 2. Results from ANOVA for treatments of plant size and biomass density on intake rates of lemmings feeding on fresh alfalfa.

Source	df	F	P
Plant size	1	163.5	0.0001
Biomass density	1	1.4	0.26
Interaction	1	0.17	0.69
Animal	5	0.68	0.64

crop a single bite (h, min/bite) and the time required to process a bite in the mouth:

$$B = \frac{1}{h} + \frac{R_{max}}{S} = \frac{R_{max}}{R_{max}h + S}, \tag{1}$$

where R_{max} is the maximum rate of processing of plant tissue in the mouth (g/min) that would occur in the absence of cropping (Spalinger and Hobbs 1992). Intake rate can thus be predicted as an asymptotic function of bite size:

$$I = \frac{R_{max}S}{R_{max}h + S}. \tag{2}$$

We parameterized Eq. (2) with values for h and R_{max} obtained from previous foraging trials with lemmings (Gross et al. 1993), accounting for the relationship between the size of alfalfa plant and the size of bite obtained by a lemming. We used linear regression to compare observations to predictions.

Plant Size (mg)

Biomass (mg/m²)	1	8
100	0.043 (0.0042)	0.119 (0.0083)
800	0.052 (0.0023)	0.123 (0.0054)

Plant Size (mg)

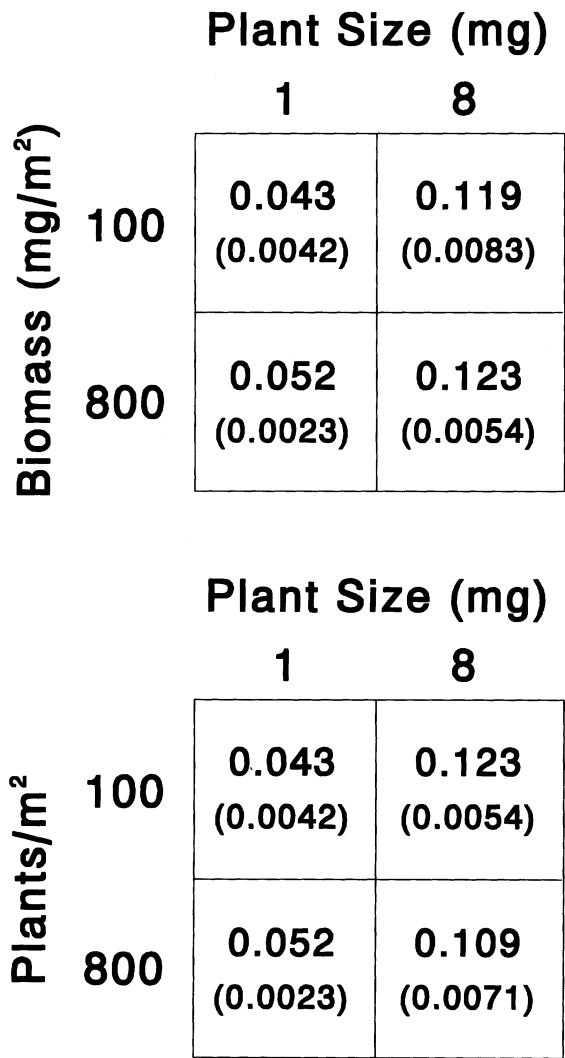| Plants/m²	1	8
100	0.043 (0.0042)	0.123 (0.0054)
800	0.052 (0.0023)	0.109 (0.0071)

Fig. 3. Short-term intake rate (g/min) of lemmings for each treatment. Within each cell, the top number is average intake rate of the six lemmings and the bottom number is the standard error.

Results

Lemmings readily consumed forages from our hand-assembled plant patches, especially those containing dense arrays of large plants (e.g. Figs 2c, e). When plant density was low and plant size small, lemmings occasionally lost interest in feeding and it was necessary to rerun a trial.

The treatments we presented to lemmings were close to those in our design (Table 1). Small plants varied from 1.0 mg to 1.3 mg, and large plants varied from 7.2

Table 3. Results from ANOVA for treatments of plant size and plant density on intake rates of lemmings feeding on fresh alfalfa.

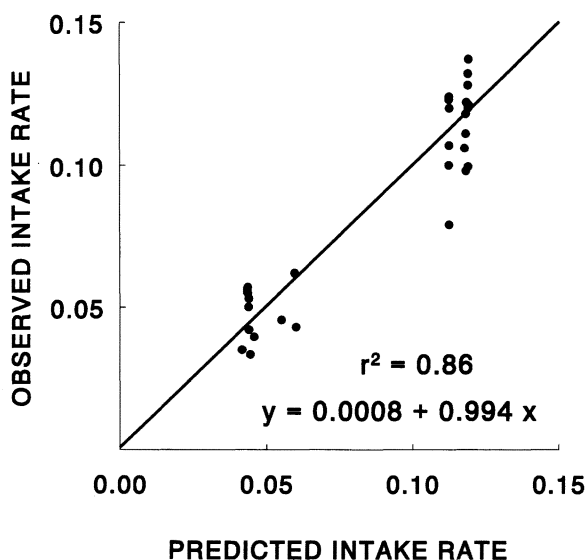| Source	df	F	P
Plant size	1	169.3	0.0001
Plant density	1	0.22	0.64
Interaction	1	4.89	0.04
Animal	5	0.74	0.61

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Fig. 4. Observed and predicted intake rates (g/min) of lemmings feeding on fresh alfalfa. Predicted intake rates were calculated from a model of herbivore functional response (Eq. (2), Spalinger and Hobbs 1992) that used bite size as the independent variable.

to 9.1 mg. Variation in plant size resulted in biomass densities that tended to be slightly higher than those we attempted to produce (Table 1).

We observed a 2–3 fold increase in intake rate in response to a larger plant size (Fig. 3), but no change in intake rate with increases in either biomass density or plant density. Differences in intake rate attributable to plant size were very highly significant ($p \ll 0.001$), whereas the effects of other treatments were not ($p > 0.2$, Tables 2, 3).

Intake rates we observed were very close to those predicted by Eq. (2) (Fig. 4). Predictions from the functional response model accounted for 86% of the variance in observed intake rates ($F_{1,28} = 169$, $p < 0.001$). The intercept from the regression of observations on predictions was not different from 0, and the slope did not differ from 1.

Discussion

In our experiments, plant size accounted for virtually all of the variation in intake rate. We found no evidence that intake rates of lemmings responded to the 8-fold differences in biomass or plant density. We achieved these results, in part, by specifically designing our treatments to uncouple the relationship between plant size, plant density, and biomass density. Because herbivores can chew and walk at the same time, intake is limited only by processing (chewing and swallowing) when it takes longer to process a bite than it takes to travel to

the next one. Thus, in our experiments, plant spacing had no relation to forage availability.

Results from our experiments are clearly explained by the mechanisms regulating herbivore intake rates in food-concentrated patches. Under these conditions intake is a function of the bite size obtained by the animal, primarily because of the need to masticate forages before swallowing them (Spalinger and Hobbs 1992, Gross et al. 1993, Laca and Demment in press). Cropping and chewing jaw movements cannot occur at the same time (Ardran et al. 1958, Greaves 1978, Fortelius 1985), and as bite size is reduced an animal must crop more bites per minute to maintain intake rate. Because there is a limit to the rate of jaw movements, fewer jaw motions are available for mastication as bite size declines, and processing (mastication) rate declines. The rate of input to the mouth cannot exceed output, so competition between cropping and chewing regulates intake and determines the shape of the functional response. A functional response model (Eq. 2) based on this concept successfully accounted for most of the variation in intake rates of a large variety of herbivores in controlled and natural situations (Shipley and Spalinger 1992, Gross et al. 1993). However, in those experiments, the utility of other measures of forage abundance was not evaluated.

We assert that plant size accounted for such a large degree of variation in intake rate because it was an effective surrogate for the size of bites obtained by lemmings. Lemmings generally ingest small plants with one bite that approximates the size of the plant, while very large plants (relative to the animal) are consumed as 2 or more large bites (Gross et al. 1993). When foods are apparent and relatively dense, bite size is an effective predictor of herbivore intake rate in both experimental and natural settings (Black and Kenney 1984, Spalinger et al. 1988, Shipley and Spalinger 1992, Gross et al. 1993). Intake rate is an asymptotic function of plant size, thus an increase in the size of large plants has essentially no impact on intake rate. For lemmings, near-asymptotic intake rates are reached when plant mass is greater than 5–6 mg (Gross et al. 1993). Consequently, the variation in size of our large plants probably had no effect on intake rate.

Our results do not show that plant or biomass density cannot influence herbivore intake rate. To the contrary, we have presented models and data which demonstrate the regulating effects of plant density and bite size under conditions where foods are dispersed in space (Spalinger and Hobbs 1992, Gross et al. unpubl.). In this experiment we presented lemmings with plants that consisted of a single bite and that were of uniform quality. Predicting bite size or intake rate under conditions where bite size, bite quality, and the number of bites at a feeding station may be under volitional control is far more complicated than in our experimental patches (Ungar and Noy-Meir 1988, Lundberg and Åström 1990, Laca and Demment in press). We do,

however, show that when foods are readily visible and relatively concentrated, plant size (a surrogate for bite size) can exert an overwhelming control on intake. This occurred even at the extremely low biomass densities (0.1 g/m^2 to 6.4 g/m^2) we offered lemmings. In natural habitats, biomass densities are usually between 20 and $1\,000 \text{ g/m}^2$ (reviewed by Schwartz and Hobbs 1985), yet we observed near-maximum intake rates even at the lowest biomass density offered.

Our failure to detect an effect of plant density on intake rates of lemmings is relevant to interpreting Lundberg's (1988) study of bank voles (Clethrionomys glareolus) feeding on patches of willow shoots. Voles are nearly the same size as lemmings (about 50 g) and presumably have similar foraging abilities (Gross et al. 1993). Lundberg observed that essentially all willow shoots were "attacked" (i.e. foraged on) regardless of shoot density, but that biomass consumption during a 3-h trial increased with plant density. He suggested, based on the greater per shoot consumption in low density patches, that mortality rates of plants would be lower in high density stands. Our results suggest an alternative interpretation. Lemmings in our trials were presented with larger foraging arenas than the 1 m^2 areas Lundberg used, and were clearly able to exploit individual forage items at rates much greater than allowed by Lundberg's experimental design (a maximum of 36 shoots per 3-h trial). Thus, we suggest Lundberg's observation that consumption varied with shoot density was more likely due to the decline in food quality with shoot consumption, rather than the dynamics of short-term intake rate. In addition, we found that active feeding time by hungry lemmings decreased exponentially after about 4 min when animals consumed alfalfa (unpubl.), suggesting that in Lundberg's experiments the effects of forage quality, digestive constraints or satiety, and plant density were confounded. These observations indicate that in response to diminishing shoot density, bank voles are capable of increasing their foraging area to maintain intake rate, and therefore vole density is probably more important than shoot density alone in determining plant mortality.

For over 20 years bite size has been recognized as an important regulator of herbivore intake rate (Allden and Whittaker 1970, Chacon and Stobbs 1976). Yet, empirical and modeling studies continue to emphasize the use of biomass density to represent forage availability (Hudson and Watkins 1986, Short 1986, McCorquodale 1991). Biomass density and bite size are often highly correlated in grasslands, and biomass density may therefore function as an effective predictor of intake rate in these habitats. However, statistical descriptions of herbivore functional response based on biomass density have eluded generalization, and provide little insight into the mechanisms responsible for the observed patterns. Therefore, we advocate the development of better techniques for estimating the size and availability of bites for herbivores. These will likely include metrics such as bulk density (Stobbs 1973, 1975, Burlison et al. 1991, Laca et al. 1992), leaf size (Wickstrom et al. 1984, Reid and Jinchu 1991), and bite density (Spalinger and Hobbs 1992). Unfortunately, these efforts will certainly be complicated by a need to simultaneously define the relationship between bite size and bite quality (e.g. Ungar and Noy-Meir 1988, Laca and Demment in press). To understand and model foraging by herbivores, we must be able to describe forage availability as perceived by the animal.

Despite 8-fold differences in plant density and biomass density, we observed no change in intake rates of lemmings. These results emphasize that the choice of independent variable is critical to the interpretation of field and laboratory studies of herbivore functional response, and to understanding the processes that control intake rate.

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