

## HERBIVORE FUNCTIONAL RESPONSE IN HETEROGENEOUS ENVIRONMENTS: A CONTEST AMONG MODELS

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**Abstract.** Variation in the spatial arrangement of plant tissue modifies the functional response of herbivores. In heterogeneous environments, this variation can occur at multiple spatial scales. We used likelihood-based approaches to examine the strength of evidence in data for models of herbivore functional response to spatial variation in plants. These models represented different hypotheses about plant characteristics controlling intake rate, including biomass, bite mass, plant density, and the composite effects of plant density and bite mass. Models were fit to observations of the food intake rate of elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), prairie dogs (*Cynomys ludovicianus*), domestic rabbits (*Oryctolagus cuniculus*), and lemmings (*Dicrostonyx groenlandicus*) feeding in plant patches where plant density and plant mass ranged over at least two orders of magnitude. The model representing composite effects of bite mass and plant density had more support in the data than any competing models (Akaike weight for the composite model > 0.999). Maximum-likelihood estimates of parameters in the composite model closely resembled independent, direct estimates, giving credence to the mechanisms represented by the model. The composite model portrayed a distance threshold ( $d^*$ , in meters) distinguishing mechanisms regulating functional response. When plant spacing exceeded this threshold, intake rate was regulated by plant density. When the plant spacing was less than the threshold, intake rate was controlled by bite mass. Based on earlier work, we show that the threshold  $d^*$  scales with body mass ( $M$ , in kilograms) as  $7.1M^{0.06}$ . This relationship illustrates that: (1) spatial pattern of plants at patch scales may influence intake rate only when plants occur at very low density; (2) herbivores of very different body mass respond to heterogeneity in a remarkably similar fashion; and (3) variation in leaf-scale characteristics controlling bite mass interact with plant spacing at patch scales to influence herbivore functional response.

**Key words:** bite mass; foraging; functional response; herbivores; heterogeneous environments; intake rate; mammals; model selection; patch; plant spacing.

### INTRODUCTION

The functional response (Solomon 1949, Holling 1959) describes how variability in food resources influences the eating rate of animals. For many years, functional responses of predators and herbivores alike were portrayed in simple models relating food intake to food density or biomass (e.g., Wickstrom et al. 1984, Lundberg 1988, Lundberg and Danell 1990). Recent theoretical work has revealed that mechanisms regulating the functional response of mammalian herbivores differ in important ways from those regulating predator functional response (Laca and Demment 1991, Spalinger and Hobbs 1992). Understanding these mechanisms has provided the basis for the development of several models that are particularly faithful to foraging by herbivores (Illius and Fitzgibbon 1994, Ginnett and

Demment 1995, Farnsworth and Illius 1996, 1998, Pastor et al. 1999, Fortin et al. 2002). Despite these advances, models capable of predicting herbivore functional response in heterogeneous environments remain poorly developed and largely untested (but see Bradbury et al. 1996).

Structural heterogeneity in plant communities arises from variation in the way that plant tissue is arrayed in space. For any given spatial scale, the same biomass of plants can be displayed by large plants rooted sparsely or by small plants rooted close together. Leaves grow in a myriad of shapes, composing canopies with diverse architectures. Presumably, this variation has important consequences for regulation of food intake by mammalian herbivores. Spalinger and Hobbs (1992) proposed that herbivore intake rate is not a function of a single characteristic of plants, but instead responds to the interaction between the geometric arrangement of leaves controlling the mass of tissue that can be

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cropped in a single bite and the geometric arrangement of plants in space controlling encounter rate with bites. This proposition motivated the development of competing mechanistic models of functional response, models that represent alternative hypotheses about the variables and processes controlling herbivore intake rate (Spalinger and Hobbs 1992). Here, we examine the ability of these competing models to predict the short-term intake rate of herbivores feeding in patches containing diverse arrangements of plant tissue. We identify a threshold at which changes in the spacing of plants and the bite mass that they offer causes switching between mechanisms regulating herbivore functional response.

#### METHODS

We evaluated evidence supporting competing models of herbivore functional response when the size and spacing of plants varied among patches. In the following section, we offer a brief theoretical development of four alternative models. In a later section, we describe techniques for evaluating these models based on their information content.

##### *Development of competing models*

Plants eaten by herbivores come in a grand variety of shapes and sizes. One of the ways in which herbivores respond to this variety is by making decisions on how to crop bites from plants. Bites are defined as the mass of plant tissue that can be consumed by a herbivore in a single cropping motion. Bite mass is determined, in part, by morphological characteristics of the animal's mouth (Illius and Gordon 1987, Gordon and Illius 1988) and, in part, by heterogeneity in the plant canopy, i.e., the three-dimensional arrangement of leaves and stems in space (Burlison et al. 1991, Laca et al. 1991, 1992, Jiang and Hudson 1994, Cooper and Ginnett 1998).

Our first model represents the case in which intake rate is regulated by bite mass ( $S$ , in grams). Spalinger and Hobbs (1992) derived a model of herbivore intake rate that applies when the foraging animal encounters bites of plant tissue more rapidly than it can chew and swallow those bites. To briefly summarize this derivation, we define the time required to crop a bite as  $h$  (in minutes) and the rate of processing of food in the mouth as  $R_{\max}$  (grams per minute). If we assume that time committed to processing and cropping are mutually exclusive (but see Ginnett and Demment 1995), then the time between bites is  $h + S/R_{\max}$  (i.e., handling time, sensu Farnsworth and Illius 1996). It follows that intake rate ( $I$ , in grams per minute) is

$$I = \frac{R_{\max} S}{R_{\max} h + S}. \quad (1)$$

We will refer to Eq. 1 as the bite mass model, which represents the hypothesis that intake rate is controlled solely by bite mass and that the mechanism causing a

Type II functional response is competition between cropping and processing in the mouth.

As an alternative to the bite mass model, Spalinger and Hobbs (1992) considered the case in which plant tissue is dispersed in space. Under these circumstances, the animal encounters plants infrequently and, thus, the time required to process a bite is less than the time required to move between plants. In the simplest case, we assume: (1) that the animal can navigate directly among plants using vision or smell, and moves in straight lines from plant to plant; (2) that the animal consumes a single bite from each plant; and (3) that cropping bites and moving among plants are mutually exclusive. Defining  $V_{\max}$  (meters per minute) as the velocity of travel in the absence of cropping, it follows that the animal's realized foraging velocity,  $V$ , is simply the distance between plants ( $d$ , in meters) divided by the sum of the cropping time and the travel time. Based on these assumptions (Spalinger and Hobbs 1992), intake rate is given by

$$I = \frac{V_{\max} S}{d + V_{\max} h}. \quad (2)$$

We can substitute  $1/a\sqrt{D}$  for  $d$  where  $D$  is the density of plants (number per square meter) and  $a$  is a constant (unitless) that depends on the spatial arrangement of plants ( $a = 2$  when pattern is random,  $a = 1$  when the pattern is uniform; Clark and Evans 1954). After some simplification,

$$I = \frac{V_{\max} a \sqrt{D} S}{1 + ahV_{\max} \sqrt{D}}. \quad (3)$$

We will refer to Eq. 3 as the density model. The density model represents the hypothesis that herbivore intake is regulated by the interplay between plant spacing and characteristics of plant canopies controlling bite mass, and that a decelerating Type II response to plant density results from competition between cropping and travel between plants.

In heterogeneous environments, plants may be concentrated or dispersed within patches. Under these conditions, we require a threshold that describes which mechanism, just now noted, regulates intake rate. We define this threshold as follows. The time required to chew and swallow a bite of plant tissue is simply  $S/R_{\max}$ . The distance that the animal can transverse during that amount of time ( $d^*$ , in meters) is

$$d^* = \frac{V_{\max} S}{R_{\max}}. \quad (4)$$

When the maximum distance between plants in a patch  $< d^*$ , then the animal arrives at a new plant before it processes sufficient mass to allow consumption of a new bite, and the bite mass model (Eq. 1) regulates intake rate. Alternatively, when the minimum distance between plants exceeds  $d^*$ , then the animal fails to

TABLE 1. Species and patch characteristics used in observations of herbivore functional response.

| Species   | $n^\dagger$ | Body mass (kg) | Trials $^\ddagger$ | Plant sizes (g) | Plant densities (no. plants/m <sup>2</sup> ) | Biomasses (g/m <sup>2</sup> ) |
|---|-------------|----------------|--------------------|-----------------|--|-------------------------------|
| Lemming, <i>Discrostonyx groenlandicus</i>            | 11          | 0.05           | 222                | 0.00041–0.021   | 4–4000                                       | 0.002–165.11                  |
| Black-tailed prairie dog, <i>Cynomys ludovicianus</i> | 3/2         | 0.75           | 192                | 0.0027–0.074    | 1–494  | 0.0032–36.7                   |
| Domestic rabbit <i>Oryctolagus cuniculus</i>          | 2/3         | 2.9            | 371                | 0.001–0.40      | 0.20–2500                                    | 0.01–157.5                    |
| White-tailed deer, <i>Odocoileus virginianus</i>      | 2/3         | 25.5           | 195                | 0.048–1.9       | 0.02–31                                      | 0.01–47.8                     |
| Elk, <i>Cervus elaphus</i>                            | 0/3         | 266            | 116                | 0.159–5.5       | 0.07–110                                     | 0.057–598                     |

$^\dagger$  Sample size (no. males/no. females).

$^\ddagger$  Number of observations of a single animal feeding in a patch. Each patch contained a different combination of plant size and plant density.

encounter a plant before it has processed sufficient mass to allow consumption of a new bite. In this case, the plant density model regulates intake rate because the encounter rate with plant tissue is less than the processing rate.

Deriving this threshold allows us to combine the bite mass and density models, thereby permitting predictions of intake across a diverse set of patches:

$$I = \begin{cases} \frac{R_{\max} S}{R_{\max} h + S} & \text{if } \max(d) \leq \frac{V_{\max} S}{R_{\max}} \\ \frac{V_{\max} a \sqrt{D} S}{1 + ahV_{\max} \sqrt{D}} & \text{if } \min(d) > \frac{V_{\max} S}{R_{\max}} \end{cases} \quad (5)$$

We can simplify Eq. 5 by assuming that plants are uniformly distributed in space within the patch. In this special case of Eq. 5,

$$I = \begin{cases} \frac{R_{\max} S}{R_{\max} h + S} & \text{if } \frac{1}{\sqrt{D}} \leq \frac{V_{\max} S}{R_{\max}} \\ \frac{V_{\max} \sqrt{D} S}{1 + hV_{\max} \sqrt{D}} & \text{if } \frac{1}{\sqrt{D}} > \frac{V_{\max} S}{R_{\max}} \end{cases} \quad (6)$$

We will refer to Eqs. 5 and 6 as the composite model. Similar models applying to the case in which plants are not apparent to the forager were offered by Illius and Fitzgibbon (1994) and Farnsworth and Illius (1996). Our model differs in identifying a distance between apparent plants ( $d^*$ ) that determines the scale of heterogeneity regulating functional response.

The composite model responds to variation in bite mass and plant density. Because plant biomass increases with increasing plant density as well as with increases in the mass of individual plants, it follows that biomass might offer a simple surrogate for the more mechanistic independent variables required by the composite model. Asymptotic relationships between plant biomass and herbivore intake rate have been observed (Wickstrom et al. 1984, Wilmshurst et al. 1995, Bergman et al. 2000). Thus, an empirical alternative to the previous models is given by

$$I = \frac{I_{\max} B}{c + B} \quad (7)$$

where  $I_{\max}$  is the maximum rate of intake (grams per

minute),  $B$  is plant biomass (grams per square meter), and  $c$  is a half saturation constant. We will refer to Eq. 7 as the biomass model, which represents the statistical hypothesis that herbivore intake rate increases as a decelerating, Type II functional response to plant biomass.

#### Experimental tests of model predictions

We confronted competing models with data on herbivore intake rate obtained by observing foraging by five species of mammalian herbivores in  $n = 1096$  individual foraging trials (Table 1). Each trial included observations of animals in a single patch type, characterized by a different arrangement of plant size and plant density. We varied the size of plants offered to animals to control bite mass ( $S$ ), and we varied plant spacing to control density ( $D$ ) within plant patches. The range of plant sizes, densities, and biomasses included in our experiments spanned at least two orders of magnitude for all species (Table 1).

Patches were assembled on plywood boards with holes drilled to accept fresh alfalfa (*Medicago sativa*) plants, which were held firmly in place by a rubber test-tube stopper inserted from the bottom of the board (Gross et al. 1993b). These boards were then attached to wooden frames that allowed us to vary the total length of the patch. Patch length was scaled to animal size. Maximum patch length varied from 200 cm for lemmings to 24 m for elk.

Plant size was modified by changing the height and bulk density of alfalfa in each drilled hole. By changing plant size, we forced differences in the sizes of bites obtained by a foraging herbivore. We offered plants that were smaller than the maximum bite size consumable by an animal. This meant that animals usually removed one bite per plant. We controlled plant density by changing the distance between plants, but each trial included only one density of uniformly distributed plants.

We measured dry matter intake rates of animals feeding in each hand-constructed patch. Measurement techniques were described in detail by Gross et al. (1993b) and are only summarized here. For our tests, we required measurements representing near-maximal intake rates. Consequently, animals were fasted to assure high

interest in feeding (1 h for lemmings, 6–7 h for prairie dogs and rabbits, overnight for deer and elk). For each foraging trial, a single animal was released into a plant patch containing a known amount of alfalfa. As the animal foraged, we counted the number of bites cropped and recorded the elapsed time of active foraging. Upon completion of a trial, we collected all remaining forage and determined intake rate as the difference between forage offered and forage remaining, divided by the elapsed time. All intake rate measurements were corrected to a dry-matter basis.

Bite mass was determined by dividing the amount of forage consumed by the number of cropping bites observed. Biomass was estimated as the total plant mass divided by the area of a patch. Plant mass was measured as the mass of plant tissue offered at a single point in the patch.

We made direct estimates of model parameters as follows. We estimated processing rates ( $R_{\max}$ ) as the product of chewing effort (number of grams per chew) and chewing frequency (number of chews per minute). We defined a chew to consist of a single up-and-down cycle of the jaw, terminating when the molars occluded. Values for chewing effort were obtained by dividing the total number of chews observed during a feeding trial by the dry mass of alfalfa consumed in the trial. Chewing frequencies were determined by counting at least five consecutive chews and dividing the count by the time elapsed between the first and last chew. Average maximum foraging velocities ( $V_{\max}$ ) were estimated by timing the progress of animals moving between plants in the absence of any cropping activity.

Data on intake in concentrated patches have been analyzed previously by Gross et al. (1993b) using different statistical techniques. The questions that we ask here and the analysis that we use to address those questions differ fundamentally from our earlier work. Data on dispersed patches have not been published.

#### Model selection

We used likelihood-based methods and information theoretics (Akaike's Information Criterion, AIC) to quantify the strength of evidence for alternative models and to estimate their parameters (Edwards 1992, Buckland et al. 1997, Hilborn and Mangel 1997, Royall 1997, Burnham and Anderson 1998, McQuarrie and Tsai 1998, Myung et al. 2000). Because model parameters are estimated based on data, there is some uncertainty that the "best" model would, in fact, emerge as superior if different data were used to compare alternatives. We quantified this uncertainty with Akaike weights,  $w_r$  (Burnham and Anderson 1998). Akaike weights are based on the likelihood of a candidate model ( $g_r$ ) given the data,  $\mathcal{L}(g_r|\text{data}) = \exp(-1/2\Delta_r)$  where the  $\Delta_r$  is the difference between the AIC value of model  $r$  and the AIC value of the best approximating model.

We can normalize these model likelihoods so that they are relative weights that sum to 1:

$$w_r = \frac{\exp\left(-\frac{1}{2}\Delta_r\right)}{\sum_{i=1}^R \exp\left(-\frac{1}{2}\Delta_i\right)}. \quad (8)$$

The relative likelihood of model  $r$  vs. model  $j$  is  $w_r/w_j$ . Alternatively, these  $w_r$  may be thought of as "probabilities" that the estimated model  $r$  is the best Kullback-Leibler model for the data at hand, given the set of models considered (Burnham and Anderson 1998). This interpretation comes from Monte Carlo simulation, using data approximated from known models. In these simulations, the best approximating model is chosen in  $w_r$  proportion of simulations as the number of simulations becomes large.

There is evidence that models selected with AIC may be overfit relative to those chosen with other criteria, notably Bayesian Information Criterion, BIC (Chen et al. 1993, Chatfield 1996). However, Burnham and Anderson (1998:166) make the case that BIC often leads to underfitting. The problem of overfitting is minimal in the work presented here because the number of parameters in candidate models is small and similar (one vs. three), and because the number of parameters in the most detailed model is far fewer than the number of observations (3 vs. >100) (Burnham and Anderson 1998:294).

Maximum-likelihood estimates of model parameters, confidence intervals on model parameters, and AIC values were obtained by nonlinear fitting of model predictions with observations using the Gauss-Hermite quadrature method with adaptive scaling implemented in PROC NLMIXED (SAS Institute 2000). We assumed normally distributed errors and verified this assumption by examining histograms of residuals after model fitting.

#### RESULTS

The composite model (Eq. 6) had greater support in the data than any alternative (Table 2, Figs. 1–3). There was virtually no uncertainty ( $w_r > 0.999$ , Figs. 1–3) that the composite model offered the best approximation of the data for all five species of herbivores feeding in structurally diverse patches. For all species, likelihood ratios based on the  $w_r$ 's show that the composite model had at least three orders of magnitude more support in the data than any of the competing models. Predictions of the composite model accounted for  $\geq 69\%$  of the variation in observations for all species, and in the case of elk, accounted for  $> 90\%$  (Figs. 1–3). The bite mass model had the next most support in the data for all species. Support for the density and biomass models was consistently the weakest of all alternatives.

Plots of observations vs. predictions revealed that the density model consistently underestimated intake rates that were high and overestimated those that were



TABLE 2. Maximum-likelihood estimates and 95% confidence intervals for model parameters for different species.

| Species and model | $R_{\max}$ |             | $h$      |               | $V_{\max}$ |            | $I_{\max}$ |               | $c$      |               |
|-------------------|------------|-------------|----------|---------------|------------|------------|------------|---------------|----------|---------------|
|                   | Estimate   | 95% CI      | Estimate | 95% CI        | Estimate   | 95% CI     | Estimate   | 95% CI        | Estimate | 95% CI        |
| Elk               |            |             |          |               |            |            |            |               |          |               |
| Composite         | 53.3       | 48.1–58.5   | 0.014    | 0.012–0.016   | 27.1       | 22.9–31.3  |            |               |          |               |
| Bite mass         | 53.0       | 41.2–64.8   | 0.018    | 0.014–0.022   |            |            |            |               |          |               |
| Density           |            |             | 0.035    | 0.032–0.038   | 64.8       | 33.7–96.0  | 28.2       | 24.2–32.0     | 4.4      | 0.4–8.4       |
| Biomass           |            |             |          |               |            |            |            |               |          |               |
| White-tailed deer |            |             |          |               |            |            |            |               |          |               |
| Composite         | 8.9        | 8.4–9.3     | 0.010    | 0.008–0.012   | 28.3       | 26.4–30.1  |            |               |          |               |
| Bite mass         | 8.9        | 8.0–9.7     | 0.021    | 0.016–0.025   |            |            |            |               |          |               |
| Density           |            |             | 0.070    | 0.062–0.077   | 42.3       | 30.6–54.0  | 6.7        | 6.3–7.1       | 0.040    | 0.027–0.045   |
| Biomass           |            |             |          |               |            |            |            |               |          |               |
| Prairie dogs      |            |             |          |               |            |            |            |               |          |               |
| Composite         | 0.71       | 0.65–0.77   | 0.01     | 0.01–0.01     | 30.0       | 27.0–33.0  |            |               |          |               |
| Bite mass         | 0.85       | 0.73–0.96   | 0.014    | 0.012–0.016   |            |            |            |               |          |               |
| Density           |            |             | 0.032    | 0.030–0.034   | 114.5      | 55.0–173.9 | 0.45       | 0.42–0.47     | 0.007    | 0.004–0.009   |
| Biomass           |            |             |          |               |            |            |            |               |          |               |
| Rabbits           |            |             |          |               |            |            |            |               |          |               |
| Composite         | 0.95       | 0.90–0.99   | 0.014    | 0.011–0.017   | 19.9       | 17.7–22.1  |            |               |          |               |
| Bite mass         | 1.0        | 0.9–1.1     | 0.024    | 0.020–0.027   |            |            |            |               |          |               |
| Density           |            |             | 0.12     | 0.11–0.13     | 41.0       | 19.4–62.7  | 0.72       | 0.68–0.75     | 0.011    | 0.007–0.015   |
| Biomass           |            |             |          |               |            |            |            |               |          |               |
| Lemmings          |            |             |          |               |            |            |            |               |          |               |
| Composite         | 0.155      | 0.143–0.168 | 0.0139   | 0.0116–0.0163 | 12.6       | 10.8–14.5  |            |               |          |               |
| Bite mass         | 0.174      | 0.157–0.191 | 0.0191   | 0.0166–0.0216 |            |            |            |               |          |               |
| Density           |            |             | 0.0483   | 0.0452–0.0514 | 31.5       | 17.7–45.2  | 0.0900     | 0.0841–0.0960 | 0.0117   | 0.0638–0.0171 |
| Biomass           |            |             |          |               |            |            |            |               |          |               |

low (Figs. 1–3). Other models showed a consistent 1:1 relationship between observations and predictions with little bias (Figs. 1–3). Although some of the slopes of these regressions differed significantly from 1.0, all were  $>0.92$ . Thus, we surmise that significant departures from unity can be attributed to our very large sample size rather than to large bias in model predictions.

However, when observations were grouped into functional categories based on plant density and bite mass, we expected consistent biases for all models except the composite. We accomplished that grouping as follows. Eq. 4 provides a hypothesized threshold ( $d^*$ ) for switching between two mechanisms regulating functional response. When plants are spatially concentrated (spacing  $\leq d^*$ ), then competition between cropping and processing regulates intake rate. When plants are spatially dispersed (spacing  $> d^*$ ), then competition between cropping and traveling regulates intake rate. If this switch operates as hypothesized, then we would expect the residuals for the density and bite mass models to depart from zero on either side of the threshold portrayed in Eq. 4. This is because the alternatives to

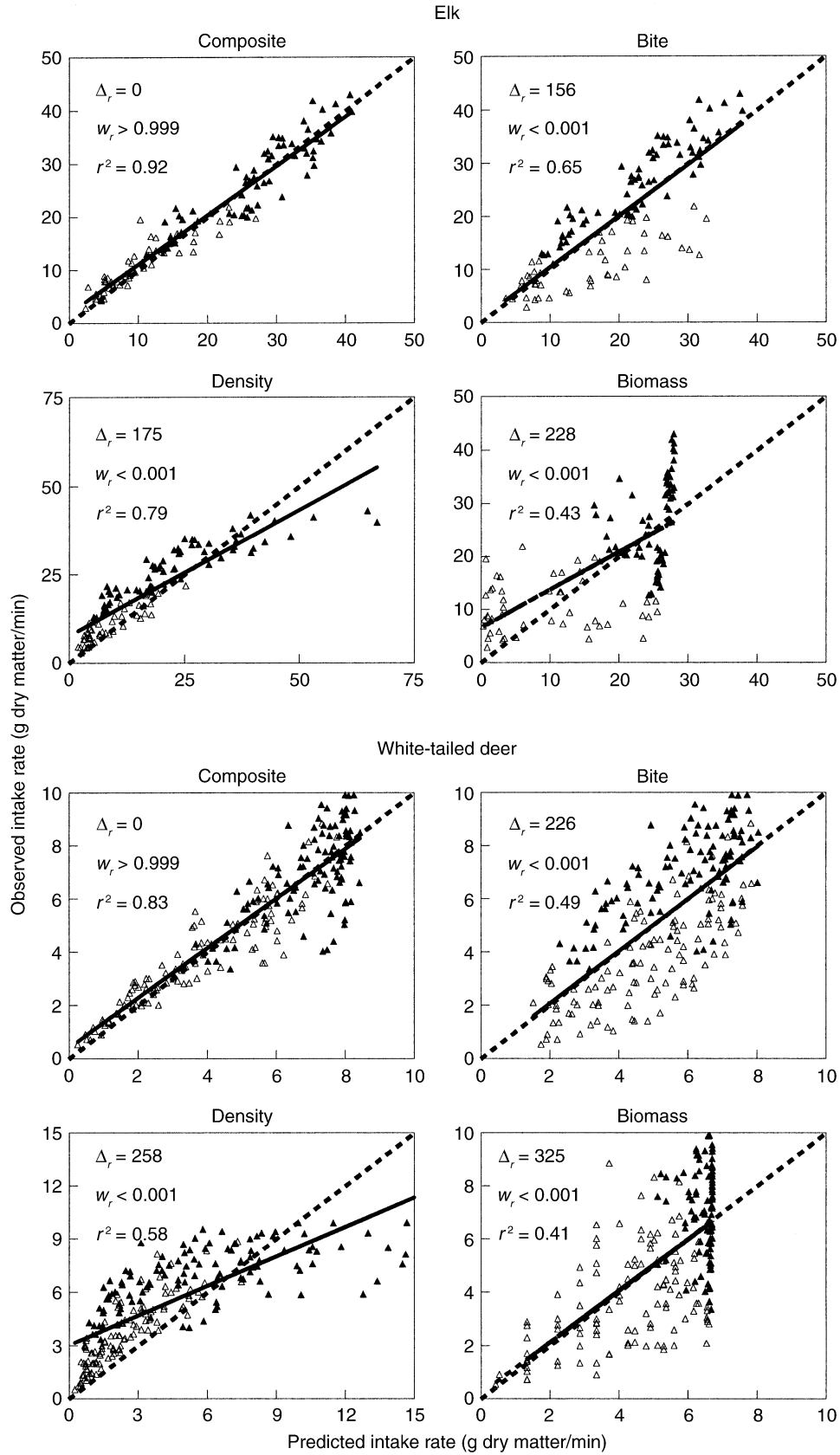
the composite model do not represent both mechanisms regulating functional response. To facilitate plotting residuals, we rearranged Eq. 1 such that independent variables are on one side of the equation and parameters are on the other side:

$$\frac{d}{S} = \frac{V_{\max}}{R_{\max}}. \quad (9)$$

Thus, if mechanisms regulating functional response change above and below the threshold, we would expect a change in the sign of residuals plotted against  $d/S$  at the point  $V_{\max}/R_{\max}$  for the bite mass and density models, but not for the composite.

In all species, the mean of residuals for the observed vs. predicted regression significantly exceeded zero for all models but the composite when  $d/S \leq V_{\max}/R_{\max}$  (Table 3, Figs. 4–6). Similarly, in all species, the mean of residuals was significantly less than zero for all models but the composite when  $d/S > V_{\max}/R_{\max}$  (Table 3, Figs. 4–6). Note that this trend is upheld whether estimates of  $V_{\max}$  and  $R_{\max}$  were measured directly or were estimated from the fit of the composite model (Figs. 4–6).

FIG. 1. Observed rates of dry matter intake by elk and white-tailed deer plotted against predictions of four models of herbivore functional response. The dashed line gives values for observed = predicted. The solid line shows the linear regression of predictions on observations. Solid symbols represent concentrated patches where the distance between plants  $\leq V_{\max}S/R_{\max}$ . Open symbols represent dispersed patches where the distance between plants  $> V_{\max}S/R_{\max}$ . The quantity  $V_{\max}$  is the velocity of foraging in the absence of cropping (in meters per minute);  $S$  is the bite size cropped (in grams); and  $R_{\max}$  is the rate of processing of food in the mouth in the absence of cropping (in grams per minute).



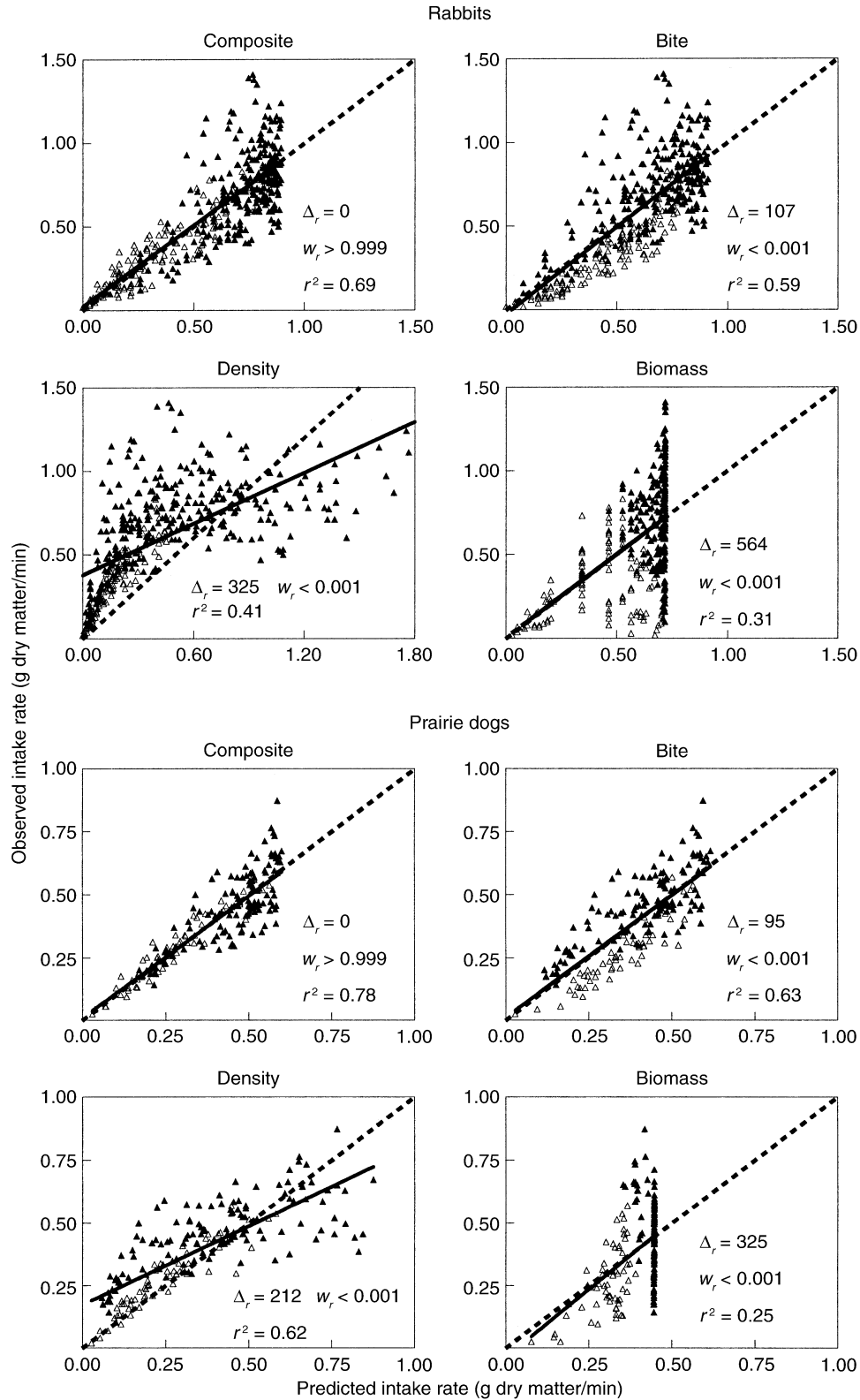


FIG. 2. Observed rates of dry matter intake by rabbits and prairie dogs plotted against predictions of four models of herbivore functional response. The dashed line gives values for observed = predicted. The solid line shows the linear regression of predictions on observations. Solid and open symbols are as in Fig. 1.

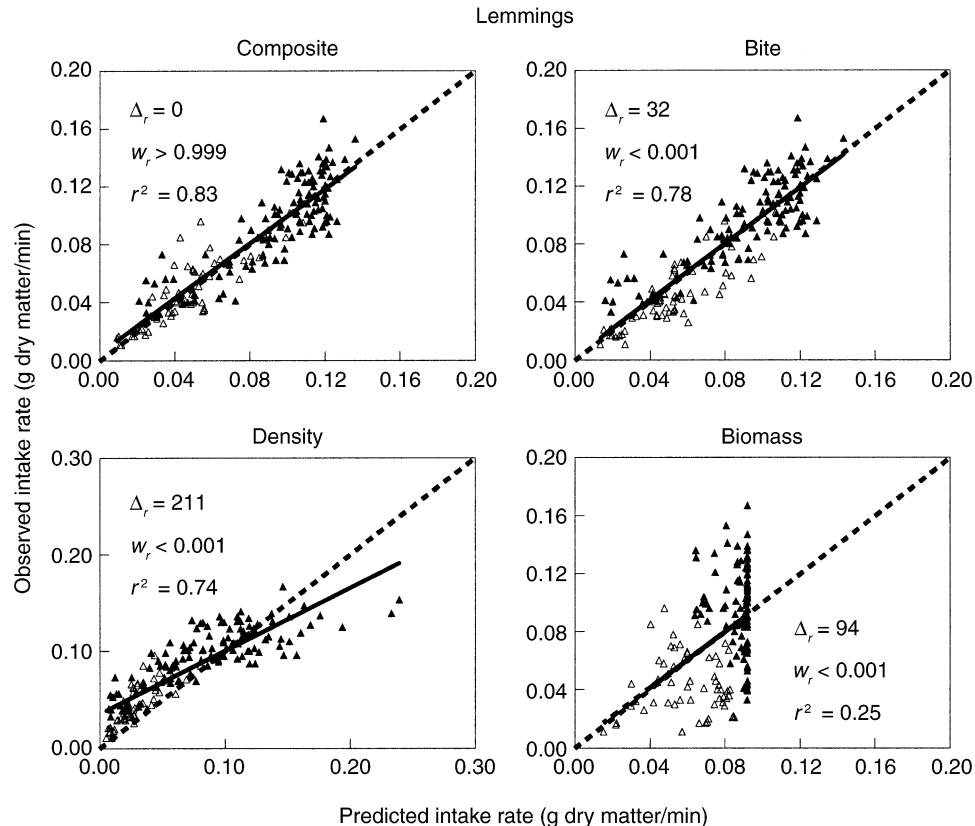


FIG. 3. Observed rates of dry matter intake by lemmings plotted against predictions of four models of herbivore functional response. The dashed line gives values for observed = predicted. The solid line shows the linear regression of predictions on observations. Solid and open symbols are as in Fig. 1.

There remains the possibility that the parameters fit in the composite model do not portray the biological quantities represented in the model's mechanisms. To test that possibility, we compared maximum-likelihood estimates (MLE) of  $V_{\max}$  and  $R_{\max}$  with direct measures of foraging velocity and processing rate (Table 4). Confidence intervals on model parameters overlapped confidence intervals on direct measurements for all species except the estimate of  $R_{\max}$  for elk and the estimate of  $V_{\max}$  for white-tailed deer.

#### DISCUSSION

Information theoretics provided strong evidence that the composite model offered the best approximation of functional response of herbivores feeding in patches composed of plants varying in density and size. Moreover, consistent with the hypothesis of a threshold defining mechanisms that regulate functional response (Eqs. 6, 7), plots of the residuals in the observed vs. predicted regression against the ratio of plant spacing to bite mass ( $d/S$ ) showed qualitatively different behavior above and below measured values for  $V_{\max}/R_{\max}$  (Figs. 3 and 4) for all models but the composite. Negative residuals (Figs. 4–6) are expected for the bite mass model above this threshold because, in this case,

plants are dispersed in space and the bite mass model fails to account for travel time between plants, producing predictions that exceed observations (Figs. 1–3). Similarly, the density model overestimated intake rate below the threshold because it failed to represent time costs of processing, producing a slope  $< 1$  in the observed vs. predicted regressions (Figs. 1–3). In each case, the parameter estimation procedure was forced to compensate for bias on one or the other side of the threshold (Figs. 4–6), leading to positive residuals when plants were concentrated in space (e.g.,  $d/S \leq V_{\max}/R_{\max}$ ) and negative residuals when they were dispersed (e.g.,  $d/S > V_{\max}/R_{\max}$ ). We would not expect any consistent bias in the biomass model related to  $d/S$ , and the observed bias was very small relative to the bite mass and density models.

The superior performance of the composite model when plant density and mass varied among food patches reveals that faithful portrayal of the short-term intake rate of herbivores foraging in spatially heterogeneous environments must account for the operation of at least two mechanisms. The first mechanism is cropping plant tissue and processing it for swallowing (Spalinger and Hobbs 1992). This mechanism prevails when forage consumed by herbivores is concentrated in space. Un-



TABLE 3. Average residuals in a regression of observations on predictions for competing models in patches where plants are concentrated and dispersed.

| Species and density | Composite model |          |          | Bite model |          |          |
|---------------------|-----------------|----------|----------|------------|----------|----------|
|                     | Residual        | <i>t</i> | <i>P</i> | Residual   | <i>t</i> | <i>P</i> |
| Elk                 |                 |          |          |            |          |          |
| Concentrated        | 0.37            | 0.92     | 0.362    | 3.81       | 9.48     | 0.000    |
| Dispersed           | -0.49           | -1.41    | 0.165    | -5.03      | -6.58    | 0.000    |
| Deer                |                 |          |          |            |          |          |
| Concentrated        | 0.08            | 0.70     | 0.485    | 1.11       | 8.83     | 0.000    |
| Dispersed           | -0.08           | -1.20    | 0.231    | -1.08      | -8.78    | 0.000    |
| Rabbits             |                 |          |          |            |          |          |
| Concentrated        | 0.00            | 0.24     | 0.811    | 0.05       | 4.39     | 0.000    |
| Dispersed           | -0.01           | -0.84    | 0.404    | -0.12      | -15.49   | 0.000    |
| Prairie dogs        |                 |          |          |            |          |          |
| Concentrated        | 0.00            | 0.14     | 0.885    | 0.04       | 5.09     | 0.000    |
| Dispersed           | 0.00            | -0.40    | 0.687    | -0.08      | -12.70   | 0.000    |
| Lemmings            |                 |          |          |            |          |          |
| Concentrated        | 0.00            | 0.64     | 0.523    | 0.01       | 3.22     | 0.002    |
| Dispersed           | 0.00            | -1.23    | 0.224    | -0.01      | -6.19    | 0.000    |

Notes: The quantity  $V_{\max}$  is the velocity of foraging in the absence of cropping (meters per minute);  $S$  is the bite size cropped (grams);  $R_{\max}$  is the rate of processing food in the mouth in the absence of cropping (grams per minute); and  $d$  is the distance between plants (meters). Concentrated patches are those where  $d \leq V_{\max}S/R_{\max}$  based on direct measurements of  $V_{\max}$  and  $R_{\max}$ . Dispersed patches are those where  $d > V_{\max}S/R_{\max}$ . Significant differences between the mean of residuals and zero indicate bias in the model predictions.

† Test of the hypothesis that the average residual  $\neq 0$ .

der these conditions, heterogeneity in the arrangement of leaves in the plant canopy regulates the mass of bites that can be cropped from the plant, and bite mass, in turn, regulates intake rate.

The second mechanism is the effect of travel time on the herbivore's rate of encounter with potential bites of forage (Spalinger and Hobbs 1992). This mechanism prevails when plants are dispersed in space. Under these conditions, variation in the spatial arrangement of plants within patches controls encounter rate, and encounter rate, in concert with bite mass, regulates intake rate. It is particularly important to recognize that when the first mechanism operates, then differences in measured heterogeneity in the spatial arrangements of plants will not induce changes in herbivore intake rate. That is, when the spacing among plants  $\leq d^*$  and herbivores can navigate directly from plant to plant, then their intake rate will be insensitive to variation in plant density and spatial pattern. Thus, it follows that the quantity  $d^*$  represents an important threshold for the functional expression of heterogeneity (Kotliar and Wiens 1990, Kolasa and Rollo 1991). When plant spacing  $\leq d^*$ , then variation in plant density or spatial pattern will have no consequences for herbivore intake rate.

This threshold provides a useful way to scale the effects of plant pattern for animals of different size. It is possible to approximate thresholds for heterogeneity for animals of different mass ( $M$ , in kilograms) using scaling relationships for  $S$ ,  $V_{\max}$ , and  $R_{\max}$ . The maximum bite size consumed by mammals ( $S_{\max}$ , in grams) scales as  $S_{\max} = 0.096M^{0.72}$ , whereas  $R_{\max} = 0.70M^{0.70}$

(Shipley et al. 1994). Given that foraging velocity ( $V_{\max}$ , in meters per minute) scales as  $V_{\max} = 52.16M^{0.04}$  (Shipley et al. 1996) and assuming no differences in acceleration among animals of different mass (but see Shipley et al. 1996), thresholds for heterogeneity can be approximated as a function of body mass as  $d^* = SV_{\max}/R_{\max} = 7.1M^{0.06}$  (Fig. 7).

Three important results can be inferred from this relationship (Fig. 7). First, when bite masses approach the maximum consumable by a species and animals can navigate directly from bite to bite, then variation in the spatial pattern of plants at the level of the patch will influence intake rate if, and only if, plants are highly dispersed in the environment. Under these conditions, the distance between plants must exceed 6–10 m for variation in pattern to modify intake rate. Thus, the density of apparent plants will be most likely to influence intake rate in environments with very low productivity or when animals are feeding on very rare plants in productive environments. Second, it follows from this scaling relationship that animals of different size experience heterogeneity in a remarkably similar way (Fig. 7). Orders of magnitude increases in herbivore body mass are associated with small changes in the threshold for heterogeneity. This follows from the scaling of foraging velocity: per unit body mass, small animals travel far more rapidly when foraging than do large ones (Shipley et al. 1996). Finally, this relationship illustrates an interaction between scales in determining the influence of heterogeneity. Heterogeneity at the scale of the leaf determines bite mass, and bite mass, in turn, influences the effect of plant spacing at

TABLE 3. Extended.

| Density model |                |                | Biomass model |               |                |
|---------------|----------------|----------------|---------------|---------------|----------------|
| Residual      | <i>t</i>       | <i>P</i>       | Residual      | <i>t</i>      | <i>P</i>       |
| 2.54<br>-3.36 | 4.53<br>-10.97 | 0.000<br>0.000 | 2.05<br>-2.70 | 2.19<br>-2.59 | 0.032<br>0.012 |
| 0.66<br>-0.64 | 4.30<br>-5.88  | 0.000<br>0.000 | 0.60<br>-0.58 | 3.69<br>-3.54 | 0.000<br>0.001 |
| 0.07<br>-0.15 | 4.78<br>-11.97 | 0.000<br>0.000 | 0.04<br>-0.09 | 2.78<br>-4.70 | 0.006<br>0.000 |
| 0.03<br>-0.06 | 3.03<br>-7.03  | 0.003<br>0.000 | 0.01<br>-0.02 | 0.88<br>-1.80 | 0.380<br>0.076 |
| 0.00<br>-0.01 | 2.78<br>-5.38  | 0.006<br>0.000 | 0.01<br>-0.02 | 3.10<br>-4.81 | 0.002<br>0.000 |

the scale of the patch. If bite masses are small, then plant spacing becomes important at shorter distances than when bites are large.

Similar to the findings of Gross et al. (1993b), our statistical estimates of values for  $R_{\max}$  closely resembled direct measurements. MLE values for  $V_{\max}$  also resembled the velocities that we observed during foraging in the absence of cropping. However, these measured velocities were lower than estimates of  $V_{\max}$  reported in our previous studies (Shipley et al. 1994) because our earlier work estimated velocity at infinite distance to standardize comparisons among species. In the work reported here, many observations were taken at relatively short distances and, hence, did not allow for full acceleration after the animal paused to crop.

Plants were arranged in a uniform pattern in our experiments and, consequently, the distance among plants was constant within a patch of a given density. That is, there was a one-to-one relationship between density and distance among plants, and all patches had plant spacing above or below  $d^*$ . In natural environments, however, plants within patches are more likely to be randomly distributed or aggregated in "subpatches." In this case, there will be a relationship between the expected value of the distance between plants and their density, but there are likely to be distances within the patch above and below  $d^*$ , regardless of the expected value of  $d^*$ . This problem can be overcome by treating the distances among plants as a probability distribution of distances (e.g., Viswanathan et al. 1999). Call that distribution  $g(x)$ , where  $x$  specifies a move distance and  $g(x)$  gives the probability that the animal will make a move of that distance. We can use this distribution to account for the proportion of moves greater and less than  $d^*$  and can weight the time components in the denominator of intake rate by this pro-

portion. This provides a way to represent functional response in heterogeneous environments:

$$I = \frac{nS}{nh + (n-1) \left( \frac{S \int_0^{d^*} g(x) dx}{R_{\max}} \right) + \frac{\int_{d^*}^{\infty} xg(x) dx}{V_{\max}}} \quad (10)$$

where  $n$  = number of bites consumed from each plant. The left-hand integral in the denominator gives the probability that a given move is  $\leq d^*$ . The second integral gives the expected value of the distance of moves  $> d^*$ . Thus, the denominator of Eq. 10 is the sum of nonoverlapping time intervals spent cropping bites (term 1), processing bites (term 2), and traveling between two plants (term 3). The numerator is the mass removed from a plant. We note that the variable  $n$  is not likely to be a constant, and probably will respond dynamically to  $D$  (Laca et al. 1993, Distel et al. 1995, Shipley and Spalinger 1995), and variation in  $S$  that occurs as patches are depleted (Laca et al. 1994, Distel et al. 1995, Ginnett et al. 1999). The nature of this response will probably influence patch residence time and, as such, offers an important area for future development of foraging theory for herbivores.

The support for the bite mass model does not mean that it is superior to other similar models. Pastor et al. (1999) offered a refinement of the bite mass model incorporating animal decisions on sequencing of cropping and chewing bites. Their model allows cropping time to respond asymptotically to variation in bite mass and animal decisions on allocation of bites to chewing and processing. Similarly, Ginnett and Demment (1995) found that cropping time increased with in-

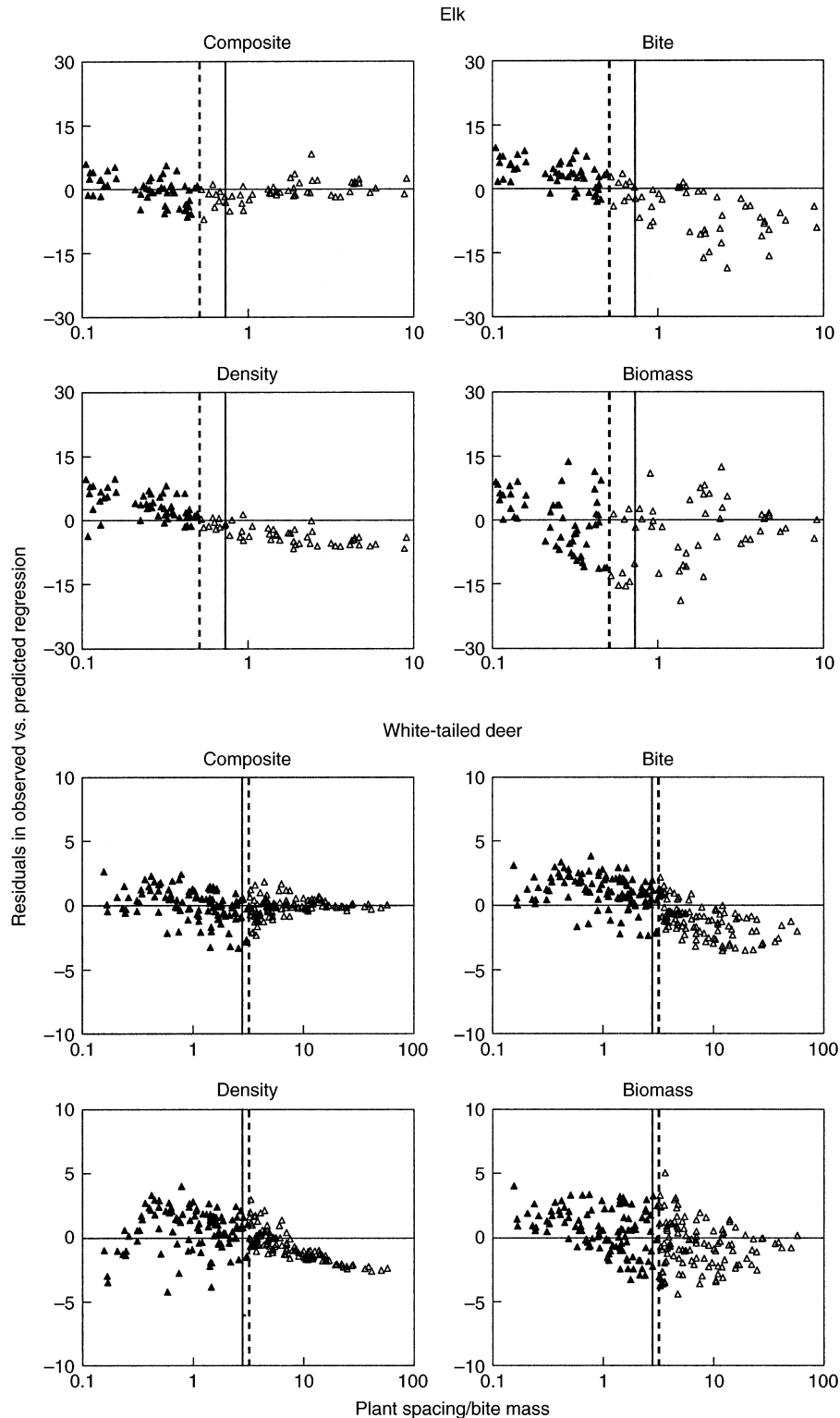


FIG. 4. Residuals from the regression of observations on predictions for elk and white-tailed deer plotted against the ratio of distance between plants (in meters) divided by bite mass (in grams). Note the log scale. The hypothesis that two processes regulate herbivore functional response (Eqs. 6 and 7) predicts a systematic change in residuals for the bite mass and density models at the threshold  $d/S = V_{\max}/R_{\max}$  separating dispersed patches (open symbols) from concentrated patches (solid symbols). The dashed vertical line estimates this threshold based on measured values of  $V_{\max}$  and  $R_{\max}$ . The solid vertical line estimates this threshold based on maximum-likelihood estimates of  $V_{\max}$  and  $R_{\max}$ .

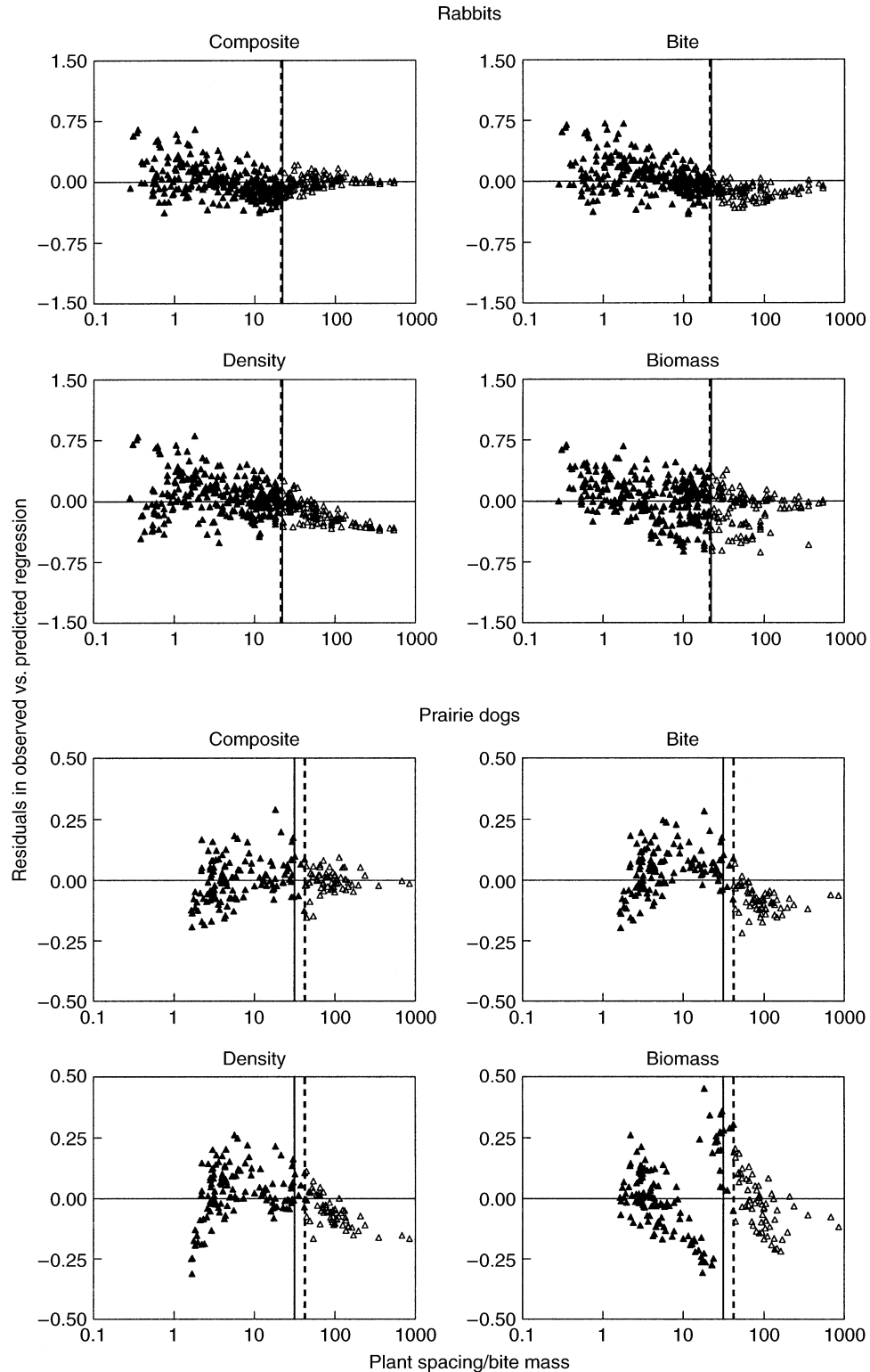


FIG. 5. Residuals from the regression of observations on predictions for rabbits and prairie dogs plotted against the ratio of distance between plants (in meters) divided by bite mass (in grams). Note the log scale. See Fig. 4 for the hypothesis and explanation of symbols and lines.

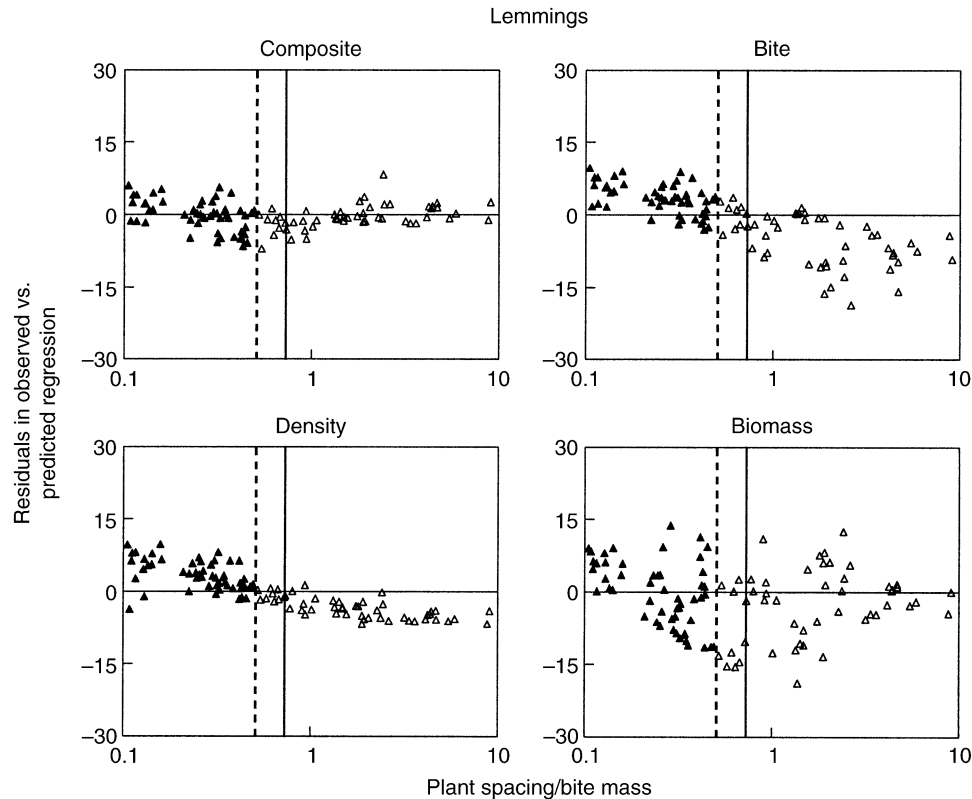


FIG. 6. Residuals from the regression of observations on predictions for lemmings plotted against the ratio of distance between plants (in meters) divided by bite mass (in grams). Note the log scale. See Fig. 4 for the hypothesis and explanation of symbols and lines.

TABLE 4. Comparison of maximum-likelihood estimates of model parameters with direct measurements of those parameters.

| Species and<br>parameter | Estimate<br>based on<br>best model | Average<br>of direct<br>measure-<br>ments† | 95% confidence limits<br>on measurement |       |
|--------------------------|------------------------------------|--|---|-------|
|                          |                                    |  | Lower                                   | Upper |
| Elk                      |                                    |  |   |       |
| $R_{\max}$               | 53.3                               | 33.63                                      | 21.74                                   | 45.52 |
| $V_{\max}$               | 27.1                               | 24.5                                       | 16.13                                   | 32.87 |
| White-tailed deer        |                                    |  |   |       |
| $R_{\max}$               | 8.85                               | 12.33                                      | 8.00                                    | 16.66 |
| $V_{\max}$               | 27.1                               | 35.7                                       | 27.53                                   | 43.87 |
| Rabbit                   |                                    |  |   |       |
| $R_{\max}$               | 1.05                               | 1.16                                       | 1.00                                    | 1.32  |
| $V_{\max}$               | 19.9                               | 25.3                                       | 16.75                                   | 33.85 |
| Prairie dog              |                                    |  |   |       |
| $R_{\max}$               | 0.71                               | 0.86                                       | 0.70                                    | 1.02  |
| $V_{\max}$               | 29.9                               | 26.8                                       | 21.26                                   | 32.34 |
| Lemming                  |                                    |  |   |       |
| $R_{\max}$               | 0.15                               | 0.15                                       | 0.14                                    | 0.16  |
| $V_{\max}$               | 13.1                               | 11.1                                       | 7.12                                    | 15.08 |

<sup>†</sup> Mean and variance based on differences among individual animals.

creasing mass of bites consumed by giraffes (*Giraffa camelopardalis*), and they provided a model incorporating this response. Because of structural similarities among the models, the maximum-likelihood estimates of model parameters yield identical predictions of intake rate and likelihoods. As a result, differences in AIC values among these models would only reflect the differences in the number of parameters among the models. This simply means that these models cannot be usefully compared with the data provided by our experiments. Parameter estimates in structurally similar models need to be compared with direct observations of parameter values, which allows tests of the biological interpretation of those parameters.

We observed a generally positive relationship between biomass and intake rate of herbivores. However, the biomass model competed poorly against the composite and bite mass models. The poor performance of the biomass model resulted, in part, from its tendency to overestimate intake rates of small plants at high density, which produced what appears to be a “vertical line” in the plots of observed vs. predicted intake rate. This arrangement of points was produced by predictions that were approximately asymptotic on the fictional response curve when biomass was high, but bite size was variable, a bias that has been well documented



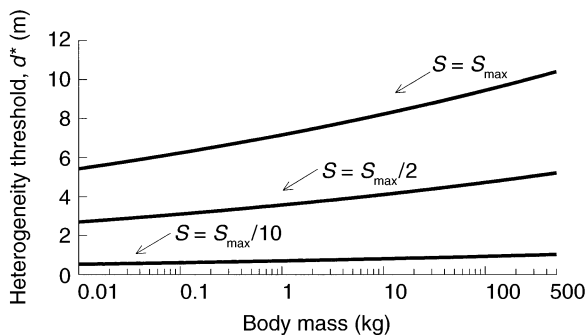


FIG. 7. The distance  $d^*$  (in meters) specifies a threshold determining the scales that regulate the functional response of herbivores navigating directly from plant to plant. When the distance between plants  $\leq d^*$ , then heterogeneity in the spatial arrangement of leaves regulates functional response. When the distance between plants  $> d^*$ , then the functional response is regulated by plant density and leaf characteristics controlling bite mass. An interaction between scales occurs because the value of  $d^*$  depends on plant characteristics that affect achieved bite mass ( $S$ , in grams) relative to the maximum bite mass obtainable by the animal ( $S_{\max}$ , in grams).

in other experimental work (Gross et al. 1993a). The biomass model will underestimate intake when bite size is large and density is low (Gross et al. 1993a).

However, despite the lack of fit in the biomass model, we acknowledge that comparing the alternatives treated here is problematic because these different models have fundamentally different purposes. The primary purpose of the bite mass, density, and composite models is to represent hypotheses about mechanisms that regulate herbivore functional response, and in so doing, to increase understanding of the foraging process. In contrast, the biomass model is primarily empirical; it does not represent mechanism at all. In most studies, its purpose is to predict intake rate, given empirical parameter estimates that are appropriate to the particular site being studied. In this predictive role, the biomass model has served admirably to increase understanding of processes operating at a higher level of organization than functional response, for example, dynamics of aggregation and patch selection by ungulates, (Hobbs and Swift 1988, Fryxell 1991, Wilmschurst et al. 1995, 2000), interspecific competition (Hobbs et al. 1996), and relationships between individual animal condition and population dynamics (Hobbs 1989). Moreover, as pointed out by Bergman et al. (2000), the biomass model is particularly valuable in this role because its independent variable is directly related to a fundamentally important attribute of plant communities, their aboveground productivity.

Although their purposes are different, there remains valuable interplay between empirical, predictive models (like the biomass model) with mechanistic ones (like the composite model). Understanding mechanisms can help one to define when empirical prediction is feasible and when it is not. For example, although

biomass can be a superb predictor of herbivore intake rate (Alden and Whittaker 1970, Wickstrom et al. 1984, Hobbs et al. 1996, Bergman et al. 2000), there are cases in which it fails badly (Spalinger et al. 1988, Spalinger and Hobbs 1992, Gross et al. 1993a). These conflicting observations can be reconciled by the dual mechanisms controlling intake rate, as revealed by the strong evidence supporting the composite model. The same biomass of plant tissue within a patch can be expressed by many small plants or by a few large ones. Thus, although two patches may have identical biomasses, differences in plant mass and canopy geometry may compel animals to consume bites of different mass, and these differences can produce very different intake rates at the same biomass. Biomass will be a sturdy, empirical predictor of intake rate whenever bite mass and biomass are correlated and plants are concentrated in space. In dispersed patches, biomass will be predictive when bite mass is constant and plant density varies. However, when plant characteristics at the scale of the leaf and the scale of the patch change in opposite directions, as they did in our experiments, then biomass will offer only crude estimates of herbivore intake rate (Figs. 1 and 2; see also Spalinger et al. 1988, Gross et al. 1993a).

Biomass and plant density, unlike bite mass, have characteristics that are directly related to patch depletion and, as such, are clearly related to gain functions that are critical to composing most models of patch residence time (Astrom et al. 1990, Shipley and Spalinger 1995, Roguet et al. 1998, Ginnett et al. 1999). It is true that the best approximating models offered here do not consider the effects of patch depletion. However, the functional response can be usefully thought of as the first derivative of the gain function. The shape of the gain function, in turn, can be mechanistically derived from an understanding of the way in which the variables in the functional response change as patches are depleted (e.g., Laca et al. 1994, Ginnett et al. 1999). This is a promising area for future work.

Reliably predicting the food intake rate of foraging herbivores using a single variable like plant biomass, bite mass, or plant density would be convenient for ecologists. However, predicting functional response based on a single characteristic of plants may not be possible in heterogeneous environments. Our findings offer strong support for the partitioning of herbivore functional response into distinct types on the basis of mechanism (Spalinger and Hobbs 1992). The type of mechanism that prevails depends on the effects of heterogeneity in plant tissue expressed in three dimensions in the environment.

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