



CHICAGO JOURNALS



The Scaling of Intake Rate in Mammalian Herbivores

Author(s): Lisa A. Shipley, John E. Gross, Donald E. Spalinger, N. Thompson Hobbs, Bruce A. Wunder

Source: *The American Naturalist*, Vol. 143, No. 6 (Jun., 1994), pp. 1055-1082

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2462895>

Accessed: 14/10/2011 06:59

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

THE SCALING OF INTAKE RATE IN MAMMALIAN HERBIVORES

LISA A. SHIPLEY,* JOHN E. GROSS,† DONALD E. SPALINGER,* N. THOMPSON
HOBBS,‡ AND BRUCE A. WUNDER§

*Texas Agricultural Experiment Station, Texas A&M University, 1619 Garner Field Road, Uvalde, Texas 78801; †Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523; ‡Mammals Research Section, Colorado Division of Wildlife, 317 West Prospect, Fort Collins, Colorado 80526; §Department of Biology, Colorado State University, Fort Collins, Colorado 80523

Submitted July 31, 1992; Revised August 6, 1993; Accepted August 24, 1993

Abstract.—The rate of food intake exerts an important influence on many aspects of herbivore ecology, including diet and habitat choices, social organization, and predator avoidance. When food is spatially concentrated, short-term dry matter intake rate (I , g/min) is determined largely by morphology of the mouth and mechanics of food consumption. Morphology (tooth size and jaw musculature) and mechanics (cropping and chewing processes) are hypothesized to scale with body mass (M) for mammalian herbivores. By using a simple model of processes regulating short-term I , we developed and tested hypotheses on the scaling of these parameters in 12 species of mammalian herbivores whose masses ranged from 0.05 kg to 547 kg. Specifically, this model predicts that I is controlled by the size of bite taken, by the time required to crop a bite, and by the rate at which food in the mouth can be processed. Maximum bite size scaled with $M^{0.72}$, whereas cropping time did not scale with body mass and averaged 0.015 min/bite across species. Food processing in the mouth scaled with $M^{0.70}$. We concluded that the maximum intake rate of mammalian herbivores will scale closely with $M^{0.71}$. This conclusion was corroborated by 39 published observations of the maximum I of mammalian herbivores. Thus, the scaling of I coincides closely with the scaling of daily energy requirements.

The process of finding and harvesting food dominates the lives of mammalian herbivores. Rates of food consumption by herbivores determine how much time they must invest in feeding to meet their metabolic requirements for energy and nutrients. Thus, the food intake rate determines the time that is available to invest in other activities—such as resting, mating, or avoiding predators. Moreover, food intake rate and its effect on the rate at which food supplies are depleted from habitats often regulate the spatial scale on which herbivores use habitats (Bell 1970; Jarman 1974; Senft et al. 1987; Coughenour 1991). Consequently, food intake rate emerges as a highly influential process in many aspects of herbivore ecology.

The rate of food intake by mammalian herbivores is controlled over several timescales. Over an animal's lifetime, nutrient intake is regulated to meet the costs of maintenance and production. On daily scales, intake rate is limited by digestion and excretion, by the amount of time an animal can invest in feeding, and by the short-term rate of consumption achieved while the animal feeds. On yet a finer scale (i.e., min), consumption rate is limited by the spatial and morpho-

logical properties of plants and by the cropping and masticating capabilities of animals. Here, we focus on the dynamics of short-term dry matter intake rate (I) and the scaling of I with body mass (M). (App. A contains a list of symbols and their definitions.) We intentionally ignore satiation and digestive processes that may regulate intake over longer time frames.

Our focus at a high temporal frequency necessarily restricts the spatial scale of foraging to patches of food. Although plant density may vary widely between patches, by our definition plant density remains relatively constant within patches. Free-ranging herbivores commonly feed in patches in which plants are spaced closely together—for example, in grass swards or in stands of leafy shrubs. When food is distributed this way, I is regulated by the geometry and size of the plant and the mouth morphology of the herbivore, which regulates bite size (S) and the rate of cropping and chewing food (Spalinger et al. 1988; Gross et al. 1993a, 1993b). If mouth dimensions scale with M , then it follows that I in spatially concentrated patches will also scale with M .

Several workers have developed hypotheses on the scaling of I on the basis of mouth and tooth dimensions. These hypotheses reflect two prevailing viewpoints. One view emphasizes the importance of mastication (Gould 1975; Creighton 1980; Lucas and Luke 1984; Fortelius 1985; McArthur and Sanson 1988) and largely ignores the mechanics of cropping. As a result, the scaling of I is believed to be controlled by the morphology of the molars and the masticatory musculature. The alternative viewpoint has emphasized the importance of cropping bites (e.g., bite size and plant height) and has thus focused on the consequences of incisor morphology and mouth dimensions (Clutton-Brock and Harvey 1983; Illius and Gordon 1987). However, this approach has ignored the chewing process. No general scaling relationship has emerged from either perspective, in part because each has failed to unify the processes of cropping and masticating food into a single mechanistic model of I . Furthermore, neither approach has provided an objective method for defining the conditions under which I is regulated by mouth morphology and not by travel velocity (which has its own scaling properties; Pennycuik 1975) or by plant morphology and density.

A model of I appropriate to this problem has been derived (Spalinger and Hobbs 1992) that quantifies the densities of plants for which the model is applicable. This model (hereafter, the “processing model”) offers a means for linking the mechanics of food cropping and processing in the mouth with the morphology of plants. Therefore, the model provides a basis for organizing concepts about the scaling of I when food is concentrated in space. Here, we report experimental tests of alternative hypotheses on the scaling of chewing and cropping components of I in 12 herbivore species ranging over four orders of magnitude in body size. We integrated these scaling relationships into a comprehensive model and examined its ability to predict the I of herbivores.

DEVELOPMENT OF HYPOTHESES

The processing model for I (Spalinger and Hobbs 1992) is based on the assumption that herbivores cannot simultaneously chew food and crop new bites—

cropping and chewing are viewed as competing processes. Consequently, during the time spent feeding (T_f , min), the animal will spend some time cropping bites (T_c , min) and some time processing (i.e., chewing, lubricating, swallowing; T_p , min) the food cropped, such that

$$T_f = T_c + T_p. \quad (1)$$

If we define the mass (g) of food prepared for swallowing during T_f as M_f , then

$$I = \frac{M_f}{T_c + T_p}. \quad (2)$$

We can express both M_f and T_c as linear functions of T_p as follows. If we define R_{\max} as the maximum rate of food processing (g processed/min) that an animal could sustain if it could continuously chew without pausing to crop new bites (e.g., if food were somehow infused to the molars without cropping actions), then $R_{\max} \cdot T_p = M_f$. Similarly, if the average time expended to crop a bite (i.e., remove plant tissue and deliver it to the molars for chewing) is \bar{h} (min/bite), with S measured in grams per bite, then the total time spent cropping is represented by the equation

$$T_c = \frac{R_{\max} T_p \bar{h}}{S}. \quad (3)$$

Substituting these relationships into equation (2) and simplifying gives the processing model:

$$I = \frac{R_{\max} S}{R_{\max} \bar{h} + S}. \quad (4)$$

Scaling of Model Parameters

We used equation (4) to organize competing hypotheses about the mechanisms controlling the I of herbivores when plants are concentrated in space (table 1). Where possible, we used these competing hypotheses to derive alternative scaling relationships for the parameters in equation (4). These hypotheses are based on the assumption that I is controlled by the mechanical actions of mouth parts that are approximately geometrically similar or isometric with M (kg; e.g., linear measures vary with $M^{0.33}$, area measures vary with $M^{0.67}$, and volume measures vary with $M^{1.0}$; Pennycuick 1992, but see also McMahon 1984). However, hypotheses about isometric scaling should be viewed as a simplification of a general relationship between a process (such as intake rate) and M . We emphasize that important variation in this relationship results from the specific evolutionary histories of individual species.

First, we considered the processes that control R_{\max} and the relationships with M that these processes should produce. In the processing model, R_{\max} represents the maximum rate at which food is prepared for swallowing by the grinding action of the molars; it encompasses the process of loading food onto the surface of the molars and breaking food into particles of sufficient size for swallowing (P_{crit} , g/

TABLE 1

HYPOTHESES ON THE SCALING OF THE COMPONENTS OF INTAKE RATE OF MAMMALIAN HERBIVORES IN RELATION TO BODY MASS

Competing Hypotheses	Source	Criteria for Rejection
1.1. Oral processing rate (R_{\max} , g/min) is a linear function of the occlusal surface area of the molars (A_m , mm ²), and both R_{\max} and A_m scale identically and isometrically with body mass (M , kg).	Gould 1975	The scaling of R_{\max} differs from the scaling of A_m , or R_{\max} correlates poorly with A_m . One or both do not scale $\propto M^{0.67}$.
1.2. Oral processing rate is the quotient of chewing frequency (C_f , chews/min) and chewing investment (C_i , chews/g).	Fortelius 1985	The scaling of R_{\max} differs from the scaling of C_f/C_i , or R_{\max} correlates poorly with C_f/C_i .
1.2.1. Chewing frequency (C_f) scales similarly to other physiological rhythms.	Fortelius 1985	C_f fails to scale $\propto M^{-0.25}$.
1.2.2. Chewing frequency is entrained by the mechanics of an oscillating pendulum in which the pendulum is jaw length (L_j , mm).	This article	C_f fails to scale $\propto M^{-0.17}$ and $L_j^{-0.50}$.
1.2.3. Chewing investment (C_i) is inversely related to the volume of food loaded between the molars.	Fortelius 1985	C_i fails to scale $\propto M^{-1.0}$, or differs from the scaling of molar loading volume.
2. Cropping time (\bar{h} , min/bite) is the time period of a physiological rhythm.	This article	\bar{h} fails to scale $\propto M^{0.25}$.
3. Maximum bite size (S_{\max}) is a function of mouth volume.	Clutton-Brock and Harvey 1983	S_{\max} fails to scale $\propto M^{1.0}$.

particle). We emphasize, however, that R_{\max} does not include the functions of the mouth that are necessary to crop plant tissue. Two hypotheses describe the mechanisms controlling the rate of oral processing and, hence, the scaling of R_{\max} . First, oral processing may be simply a function of the occlusal surface area of the molars (A_m , mm²) (Pilbeam and Gould 1974; Gould 1975; Creighton 1980; Lucas and Luke 1984). If this is true, both A_m and R_{\max} should scale with $M^{0.67}$ (hypothesis 1.1, table 1). Alternatively, Fortelius (1985) suggested that the oral processing rate is the quotient of two scalable mechanisms: chewing frequency (C_f , chews/min) and chewing investment (C_i , our term for the number of chews expended/g of food processed). Therefore, $R_{\max} = C_f/C_i$. The C_i expresses the amount of effort an animal must expend to prepare particles for swallowing. It integrates a mechanical process—the efficiency with which molars shear or break food particles—and a predominantly volitional threshold—the extent to which particles must be reduced in size before they can be swallowed.

The C_f and C_i are each hypothesized to scale with M (hypothesis 1.2, table 1). Fortelius (1985, 1988, 1990) suggested that C_f declines with increasing M , scaling

approximately with $M^{-0.25}$, as do cardiac rhythm and other physiological rates (Peters 1983; Schmidt-Nielsen 1984; hypothesis 1.2.1, table 1). Alternatively, we proposed that the scaling of C_f is a predictable outcome of the mechanics of an oscillating pendulum, similar to the stride frequency of mammals (Pennycuik 1975; McMahon 1977). The C_f can thus be viewed mechanistically as the oscillation of a pendulum, with the mandible of the jaw equivalent to the length of the pendulum. The dependence of C_f on jaw length (L_j , mm) results from the fact that oscillation frequency is related to pendulum length^{-0.50} (McMahon 1977). If L_j scales isometrically with M (e.g., varies with $M^{0.33}$), then C_f will scale with $M^{-0.17}$ (i.e., $[M^{0.33}]^{-0.50}$; hypothesis 1.2.2, table 1).

With respect to C_i , Fortelius (1985, 1988, 1990) proposed that the rate at which food is comminuted is proportional to the mass or volume of food placed between the molars (which we term "molar loading volume"). This volume would be proportional to the product of A_m and the depth of food placed between the teeth (i.e., bolus thickness, L_d , mm) and thus would scale as $M^{0.67} \times M^{0.33} = M^{1.0}$. Fortelius argued that, if the amount of food processed per chew scaled simply with A_m (as implied in hypothesis 1.1), then the food layered between the teeth would be of uniform thickness regardless of body size—it would be the same for elephants as for lemmings. Molar loading volume represents the volume of food processed per chew, and thus C_i (number of chews expended/g food ingested) is the inverse of this parameter. We therefore hypothesized that C_i would scale with $M^{-1.0}$ (hypothesis 1.2.3, table 1). Fortelius's hypothesis regarding C_i assumes that (i) stress delivered to the food particles occluded between the molars is independent of M , and (ii) that the initial size of particles entering the mouth (P_{init}) and the particle size swallowed both scale isometrically with M ($\propto M^{1.0}$; see App. B for a more detailed treatment of C_i). Fortelius's hypothesis is appealing because it implies that R_{max} will scale with $M^{0.75}$ (e.g., $C_f/C_i \propto M^{-0.25}/M^{-1.0} = M^{0.75}$), which is equivalent to the interspecific scaling of metabolic rate (Peters 1983).

The second parameter of the processing model (eq. [4]), \bar{h} , represents the time required to crop a bite. The time expended by an animal to crop bites likely depends on animal characteristics, such as the size of the muzzle and incisors (Janis and Ehrhardt 1988), the mobility of the soft tissues, such as the tongue and lips (Hiiemae 1984), and the stress produced during occlusion of the incisors. In general, however, we would expect \bar{h} to scale to about $M^{0.25}$ (hypothesis 2, table 1) in accordance with other time periods in biological cycles (Peters 1983; Schmidt-Nielsen 1984).

We turn now to the scaling of bite size. Because the actual bite size cropped by an animal depends on both mouth morphology and plant architecture (Cooper and Owen-Smith 1986; Illius and Gordon 1987), we restricted our hypotheses to the scaling of the largest bite sizes allowed by mouth morphology (S_{max} , g). Clutton-Brock and Harvey (1983) and Owen-Smith (1985) hypothesized that, when it is not restricted by plant height or width, bite size should scale in proportion to mouth volume ($M^{1.0}$). Consistent with these ideas, we hypothesized that S_{max} , and thus maximal intake rate (I_{max} , g/min), will generally be set by mouth volume (which varies with $M^{1.0}$; hypothesis 3, table 1).

TABLE 2
NUMBER AND CHARACTERISTICS OF HERBIVORES USED TO DETERMINE THE SCALING
OF INTAKE RATE WITH BODY MASS

Herbivore Species	No.	Mass (kg)	Digestive Strategy	Typical Forage
Collared lemming (<i>Dicrostonyx groenlandicus</i>)	13	.05	Hindgut	Grass
Black-tailed prairie dog (<i>Cynomys ludovicianus</i>)	5	.75	Hindgut	Grass/forbs
Domestic rabbit (<i>Oryctolagus cuniculus</i>)	5	2.9	Hindgut	Browse
White-tailed deer (7 mo) (<i>Odocoileus virginianus</i>)	4	25	Ruminant	Browse
Collared peccary (<i>Tayassu tajacu</i>)	3	27	Monogastric (complex)	Cactus/concentrate
White-tailed deer (adult; <i>O. virginianus</i>)	4	46	Ruminant	Browse
Axis deer (<i>Axis axis</i>)	3	53	Ruminant	Grass/browse
Woodland caribou (<i>Rangifer tarandus</i>)	2	104	Ruminant	Lichens/grass/browse
Grizzly bear (<i>Ursus arctos</i>)	3	161	Monogastric	Grass/fruit/(omnivore)
Elk (<i>Cervus elaphus</i>)	3	265	Ruminant	Grass/browse
Moose (<i>Alces alces</i>)	2	309	Ruminant	Browse
Domestic horse (<i>Equus caballus</i>)	3	432	Hindgut	Grass
Domestic cattle (<i>Bos taurus</i>)	4	547	Ruminant	Grass

A Composite Scaling Model

A general model for the scaling of I can be derived by substituting the individual scaling functions of R_{\max} and \bar{h} into equation (4). If S_{\max} is also substituted for S , the model predicts I_{\max} . We will refer to this model as the composite scaling model. Our approach to predicting I as a function of M differs from purely empirical approaches (e.g., Peters 1983; Barton 1992), because we derived our prediction of the I - M relationship from the scaling of individual mechanisms rather than from simple, empirical correlations of M and I . Hence, if the scaling relationships of model components (i.e., R_{\max} , \bar{h} , S_{\max}) are correct, and if equation (4) accurately represents I in spatially concentrated patches, then our composite scaling model should predict I_{\max} solely on the basis of M .

MATERIAL AND METHODS

Overview of Experimental Approach

We tested hypotheses 1–3 (table 1) by estimating R_{\max} , \bar{h} , S_{\max} , C_f , C_i , L_j , and A_m for 12 species of herbivores ranging in M from 0.05 kg to 550 kg. These animals represented a variety of feeding styles (e.g., browser, grazer) and digestive strategies (e.g., monogastric, ruminant, hindgut-fermenter; table 2). Hypothesized scaling relationships (table 1) were compared with those we observed. We then derived a composite scaling model by substituting the best-fit scaling relationships for R_{\max} , \bar{h} , and S_{\max} from our experiments into equation (4). We compared the predictions of this model to the highest previously published values

of intake rates of herbivores differing in M (table 3). Although the variety of feeding styles and unequal taxonomic distribution complicate statistical analyses, we used a broad range of animals to increase our confidence in any scaling patterns that might emerge.

Measuring R_{\max} and \bar{h}

We estimated values for R_{\max} and \bar{h} for the species of mammalian herbivores listed in table 2 by offering them fresh alfalfa (*Medicago sativa*) in hand-constructed patches at Texas Agricultural Experiment Station, Texas A&M University, Uvalde, Texas; Colorado State University, Fort Collins, Colorado; and Washington State University, Pullman, Washington. Experimental animals were habituated to experimental protocols before data were collected. We offered all animals fresh alfalfa (neutral detergent fiber content was 32% of dry mass) to assure that I was similarly constrained in all animals and not influenced by potential differences in the fibrousness and morphology of forages. Details of these experiments were reported elsewhere (Gross et al. 1993b) and are therefore only summarized here.

To obtain estimates of R_{\max} (g/min) and \bar{h} (min/bite), we measured the influence of bite size on intake rate by creating a simple foraging environment in which we could independently control the size and distribution of bites of alfalfa. We attached alfalfa to plywood boards by inserting plant stems through holes in the boards and fastening them from underneath with rubber stoppers. Because lemmings were too small for the experimental apparatus, we placed alfalfa "plants" (defined as single or multiple stems of alfalfa anchored at a single location) at 1-cm intervals along a plastic strip (commonly used as a binder for report covers) which held the alfalfa securely by pressure. For all herbivores, alfalfa plants were distributed uniformly in concentrated patches (i.e., spaced so that the animal could reach the next plant within the swing of its neck and before finishing chewing the previous bite). We ran a series of trials in which we offered uniform plant sizes within trials but varied plant size among trials by changing the height or number of stems offered. Animals responded to this variation in plant size by varying the bite size taken. This variation in bite size, in turn, caused variation in intake rate.

Trials were conducted with 2–13 individuals of each species (white-tailed deer fawns and adults were treated separately). Each trial lasted from 1–5 min. To assure a consistent appetite in the experimental animals, we fasted the larger animals (> 20 kg) overnight and the smaller species for 6–7 h before the foraging trials. All animals were maintained on a pelleted, complete ration between trials.

During each trial we measured the time spent foraging and the number of bites cropped by an individual animal. We defined a bite as a single cropping motion of the jaws or mouth that severed a mass of tissue from a plant. To count bites taken by lemmings, we videotaped trials and viewed them in slow motion. The mass of food eaten was calculated as the difference between the mass of food offered and the mass remaining after the trial, corrected for dry matter. The variable S (g/bite) was estimated as the quotient of the number of bites taken and the dry mass of food eaten, and I (g/min) was estimated as the quotient of the

TABLE 3

MAXIMUM BITE SIZES AND INTAKE RATES OF HERBIVORES FEEDING ON A VARIETY OF FRESH FORAGES

Animal	Body Size (kg)	Maximum Bite Size (g)	Maximum Intake Rate (g/min)	Forage Type*	Source
Bank vole	.0401	B	Lundberg 1988
Brown lemming	.0511	G	Batzli et al. 1981
Cotton rat	.1516	G	Randolph et al. 1991
Snowshoe hare	1.0	.33	.66	B	Shipley and Spalinger 1992
Howler monkey	6.7	.45	5.7	B	Ofstedal 1991
Vervet monkey	7	.05	2.3	B	Wrangham and Waterman 1981
Domestic lamb	40	.20	5	B	Flores et al. 1989
Impala	40	.44	7.5	B	Dunham 1980
Domestic sheep	40	.15	5.7	G	Penning et al. 1991
Domestic sheep	42	.20	6.4	G	Black and Kenney 1984
Mule deer	42	.46	7.9	B	Wickstrom et al. 1984
Domestic sheep	43	.42	7.5	G	Allden and Whittaker 1970
Black-tailed deer	48	.42	9.1	B	Spalinger et al. 1988
White-tailed deer	53	1.10	15.6	B	Shipley and Spalinger 1992
Domestic goat	60	.43	4.8	G	Peinado-Lucena et al. 1992
Domestic goat	60	3.57	...	B	Peinado-Lucena et al. 1992
Mule deer	60	...	3.3	B	Collins and Urness 1983
Domestic sheep	65	.42	...	G	Burlison et al. 1991
Reindeer	70	...	24.9	B	Trudell and White 1981
Topi	80	.43	...	G	Murray 1991
Caribou	85	.67	13.7	B	Shipley and Spalinger 1992
Wildebeest	90	.50	...	G	Murray 1991
Hartebeest	100	.30	...	G	Murray 1991
Elk	160	1.80	21.9	B	Wickstrom et al. 1984
Elk	225	.36	12.6	G	Hudson and Nietfeld 1985
Elk	231	...	17.2	G	Collins and Urness 1983
Domestic cattle	241	.63	...	G	Erlinger et al. 1990
Moose	247	2.45	26	B	Shipley and Spalinger 1992
Elk	250	...	22.5	G	Collins et al. 1978
Elk	250	.86	21	G	Hudson and Watkins 1986
Domestic cattle	300	...	29	G	Vulink and Drost 1991
Domestic cattle	330	.80	...	G	Erlinger et al. 1990
Moose	340	1.43	25.1	B	Renecker and Hudson 1986
Moose	350	3.75	21.2	B	Risenhoover 1987
Moose	350	...	29	G	Åström et al. 1990
Moose	360	...	16.7	B	Belovsky and Jordan 1978
Domestic cattle	400	1.22	74.1	G	Arthur 1984
Domestic cattle	450	.47	...	G	Stobbs 1973
Domestic cattle	463	...	37.5	G	Hodgson and Jamieson 1981
Domestic cattle	471	1.46	49	B	Dougherty et al. 1989
Bison	650	1.47	68.8	G	Hudson and Frank 1987
Domestic cattle	750	.81	24.3	G	Ungar et al. 1991
Giraffe, female	800	2.20	26.9	B	Pellew 1984
Giraffe, male	1,200	3.27	35.4	B	Pellew 1984
Asian elephant	3,000	...	129.6	B	Owen-Smith 1988
African elephant	3,000	...	72	B	Owen-Smith 1988
African elephant	3,000	...	102.4	B	Lindsay 1991

* G represents grasses and B represents either herbaceous and woody browses or forbs.

dry mass eaten and the time spent feeding. With S as an independent variable and I as a dependent variable, we used nonlinear regression (SAS Institute 1985) to estimate the parameters R_{\max} and \bar{h} of equation (4) for each herbivore species (Gross et al. 1993b).

Measuring Maximum Bite Size

We measured maximum bite size for each species by offering each animal successively larger plants. We expected that, if S were a function of mouth volume, then it would increase linearly with plant size offered until S_{\max} was obtained, at which point bite size would remain constant as plant size increased further. Previous work revealed a clearly asymptotic bite size for only three species (lemmings, prairie dogs, and elk; Gross et al. 1993b). The bite size of rabbits, white-tailed deer, moose, and cattle failed to reach an asymptote, presumably because these animals were able to chew bites that extended outside their mouths. In addition, the bite size of white-tailed deer fawns, axis deer, caribou, grizzly bears, and horses declined relative to plant size at the largest plant sizes offered, but an asymptotic bite size or S_{\max} was not clearly demarcated. To deal with these inconsistencies, we simply estimated the S_{\max} for each species as the largest single bite size measured in any trial. This approach was admittedly crude, so we extended our analysis by using 34 published observations of the largest bites obtained by mammalian herbivores (table 3).

Measuring Chewing Frequency and Chewing Investment

We measured chewing frequency and chewing investment from video recordings of each foraging trial replayed in slow motion. We defined a chew as an up and down cycle of the jaw during which the molars occluded in the absence of any cropping (i.e., cropping motions were not counted). The chewing frequency for each animal was determined as the average rate of chewing for at least five measurements per trial by timing at least five successive chews occurring without interruption for cropping. The chewing investment was calculated as the total number of chews taken during the trial divided by the total dry mass eaten.

Measuring Mouth Morphology and Body Size

To obtain measures of mouth morphology, we made impressions of the upper row of molars for each animal. Tooth impressions were made by first immobilizing the animal with xylazine hydrochloride (Rompun) or with a xylazine hydrochloride/ketamine mixture and then by propping the animal's mouth open with a wooden wedge. We spread Alginate dental impression material (Healthco International, Boston, Mass.) into an aluminum tray shaped to fit the upper molar row and placed the tray on the upper molars while the impression material hardened. While the animals were sedated, the width of the lower incisors (between the outermost edges of the fourth incisors on the left and right ramus; Illius and Gordon 1990) and the jaw length (between the angular process of the mandible and the point of insertion of the first incisor into the gums) were measured to the nearest 1 mm. Because lemmings and prairie dogs were too small to handle this way, we took impressions and jaw measurements from the skulls of a few of the

individuals from the same research population. To create positive models of the teeth, we poured Microstone dental stone (Whip Mix Corporation, 361 Farmington Ave., Louisville, Ky.) into the hardened impressions. From these models, we measured the surface area of the molars as the sum of the product of maximum width and length (measured with calipers to the nearest 0.1 mm) of each premolar and molar on the upper row on one side of the jaw. Lemmings and rabbits were weighed to the nearest 0.1 g, prairie dogs to the nearest 1 g, and all other species to the nearest 0.5 kg.

Calculating the Scaling Coefficients

The scaling of R_{\max} , \bar{h} , S_{\max} , C_f , C_i , and mouth morphology with M was first analyzed by using ordinary least-squares linear regression (SAS Institute 1985) on \log_e -transformed data fitted to the model $Y = aM^b$ (transformed to the linear model $\log_e Y = \log_e a + [b]\log_e M$), where Y is a variable, a is a scaling coefficient, and b is a scaling exponent. Because we wished to compare I interspecifically, mean values for each herbivore species were used in the regressions. If a significant relationship existed between M and the dependent variable, ordinary least-squares slopes were converted to reduced major-axis slopes by dividing the ordinary least-squares slopes by the correlation coefficient (Rayner 1985; McAr-dle 1988; LaBarbera 1989). Standard errors and slopes estimated from reduced major-axis regression were used to construct confidence estimates and test against the hypothesized slopes (Hayami and Matsukuma 1970). Residual variation was examined for normality and uniform distribution along the regression line. A correction factor was calculated to compensate for bias when converting the intercept from \log_e back to normal scale (Sprugel 1983; LaBarbera 1989).

White-tailed deer fawns (7 mo old) were treated as an individual species in these analyses. Although this potentially confounds ontogenetic and phylogenetic scaling relationships, many of our tests focused on the mechanics of food intake. In these tests the source of variation, whether ontogenetic or phylogenetic, was unimportant. However, for scaling relationships based on body size, we compared slopes of regression with and without including the fawns. Including the fawns did not change the slopes, intercepts, or correlation coefficients of any of the relationships by more than half a percentage point (0.5%). Consequently, the analyses reported here included the fawns.

Testing the Composite Scaling Model

To examine the predictive ability of the composite scaling model, we obtained 39 previously published values of the highest intake rates recorded for herbivores that ranged in M from 0.04 kg to 3,000 kg (table 3). We examined model predictions by comparing the scaling exponent of I_{\max} (i.e., the slope of the \log_e/\log_e regression of I on M) observed for these herbivores with the scaling of I_{\max} predicted by the composite scaling model (derived from eq. [4] and the reduced major-axis scaling parameters for R_{\max} , \bar{h} , and S_{\max}). We also determined the correlation of predicted versus observed I_{\max} when we used our composite scaling model to predict intake solely on the basis of herbivore M . We considered this a robust test of the model, because (i) the values of I reported in the literature were derived by using several different techniques, (ii) the animals ate a wide variety

TABLE 4

SCALING OF THE COMPONENTS OF INTAKE RATE WITH BODY MASS OF 12 SPECIES OF MAMMALIAN HERBIVORES USING THE LOG_e TRANSFORMATION OF THE MODEL $Y = aM^b$

COMPONENT (Y)	ORDINARY LEAST-SQUARES REGRESSION						REDUCED MAJOR-AXIS REGRESSION	
	$\log_e a$	(SE)	C. F.*	b	(SE)	r^2	$\log_e a$	$b \pm \text{C.I.}$
R_{\max} , g/min	-.29	(.17)	1.01	.69	(.04)	.97	-.35	.70 \pm .07
h , min/bite	-4.44	(.22)	1.02	.03	(.05)	.03
S_{\max} , g	-2.34	(.20)	1.02	.71	(.04)	.96	-2.34	.72 \pm .08
C_f , chews/min	5.61	(.10)	1.01	-.18	(.02)	.87	5.66	-.19 \pm .04
C_i , chews/g	5.82	(.21)	1.02	-.83	(.04)	.97	5.88	-.85 \pm .08
A_m , mm ²	4.10	(.18)	1.02	.61	(.04)	.95	4.05	.62 \pm .07
L_j , mm	3.92	(.08)	1.01	.35	(.02)	.97	3.90	.35 \pm .03
Incisor width, mm	1.76	(.11)	1.01	.41	(.02)	.96	1.73	.42 \pm .05
C_f/C_i , g/min	-.20	(.17)	1.01	.65	(.04)	.96	-.23	.66 \pm .07

NOTE.—Reduced major-axis slopes may be calculated by dividing ordinary least-squares slopes by the correlation coefficient r (Rayner 1985).

* C. F., Correction factor for the logarithmic transformation bias of a (C. F. = $\exp(\text{SE}^2/2)$, Sprugel 1983), where $a = \text{C. F.} \times \exp(\log_e a)$.

of foods, and (iii) studies included a range of body sizes that greatly exceeded those of the animals used in our experiments.

RESULTS

Oral processing rates ranged from 0.15 g/min in lemmings to 74.2 g/min in cattle. The R_{\max} of the 12 herbivore species scaled in proportion to $M^{0.70}$ (table 4; fig. 1), and A_m scaled in proportion to $M^{0.62}$ (table 4; fig. 2). Neither scaling exponent differed significantly from 0.67, the hypothesized exponent for A_m (R_{\max} : $Z = .84$, $P = .40$; A_m : $Z = 1.34$, $P = .18$; hypothesis 1.1), and they did not differ from each other ($Z = 1.47$, $P = .14$). However, A_m accounted for only 54% of the variance in R_{\max} (fig. 3), and thus we concluded that R_{\max} is not solely a function of A_m (hypothesis 1.1, table 1). In contrast, the quotient of C_f (chews/min) and C_i (chews/g) accounted for 91% of the variation in R_{\max} (fig. 4; Gross et al. 1993b) and scaled with nearly the same exponent of M ($M^{0.65}$; $Z = .75$, $P = .45$; table 4). We concluded that hypothesis 1.2 is better able to account for the observations of R_{\max} than is hypothesis 1.1 (table 1).

The C_f scaled with $L_j^{-0.55}$ and $M^{0.19}$ (table 4). The exponents were nearly identical to the values of $L_j^{-0.50}$ ($Z = .82$, $P = .41$) and $M^{-0.17}$ ($Z = .96$, $P = .34$) that were predicted by the oscillating pendulum model (hypothesis 1.2.2, table 1). The L_j scaled with $M^{0.35}$, which was similar to the expected isometric scaling of $M^{0.33}$ ($Z = 1.46$, $P = .45$). In contrast, the exponent of M for C_f was significantly different from -0.25 predicted by the physiological rate model ($Z = 2.99$, $P = .003$; hypothesis 1.2.1, table 1). Therefore, the oscillating pendulum model was a better predictor of C_f than the physiological rate model. The C_i (chews/g) scaled with $M^{-0.85}$ (table 4; fig. 5), which was significantly higher than the hypothesized

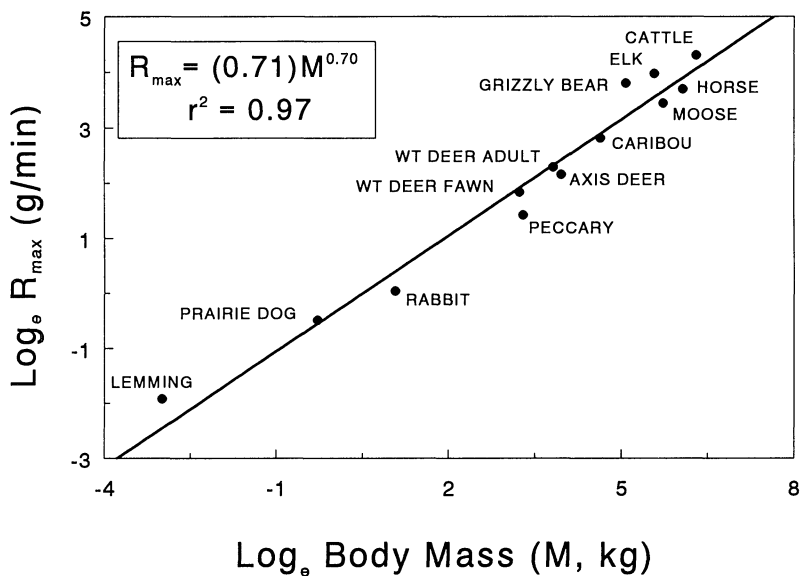


FIG. 1.—The R_{\max} was strongly correlated with M for the 12 species of mammalian herbivores used in our experiments (white-tailed deer fawns and adults were treated separately).

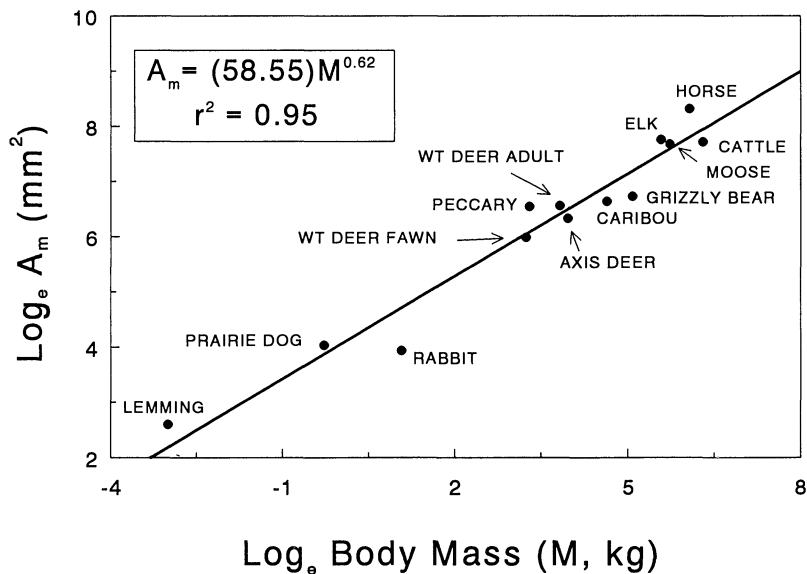


FIG. 2.—The A_m was a function of M for herbivorous mammals

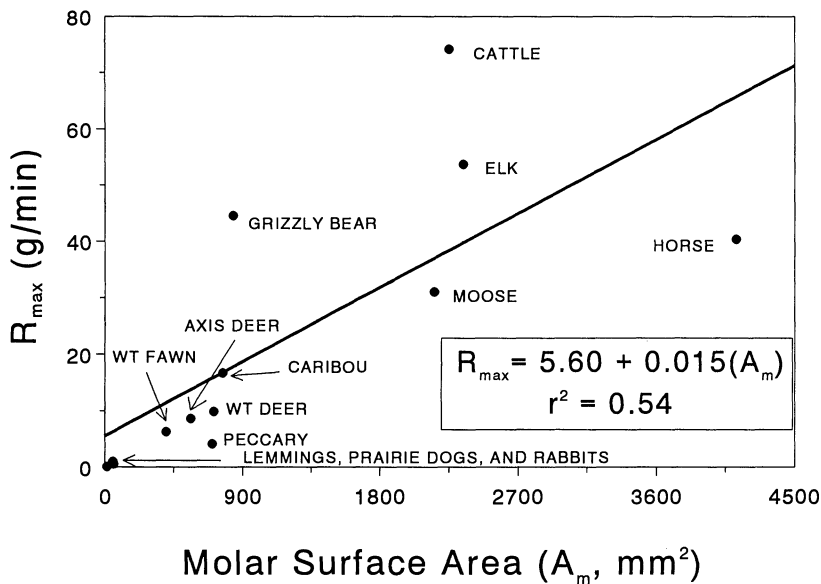


FIG. 3.—The R_{max} was correlated with the A_m of the herbivores used in our study

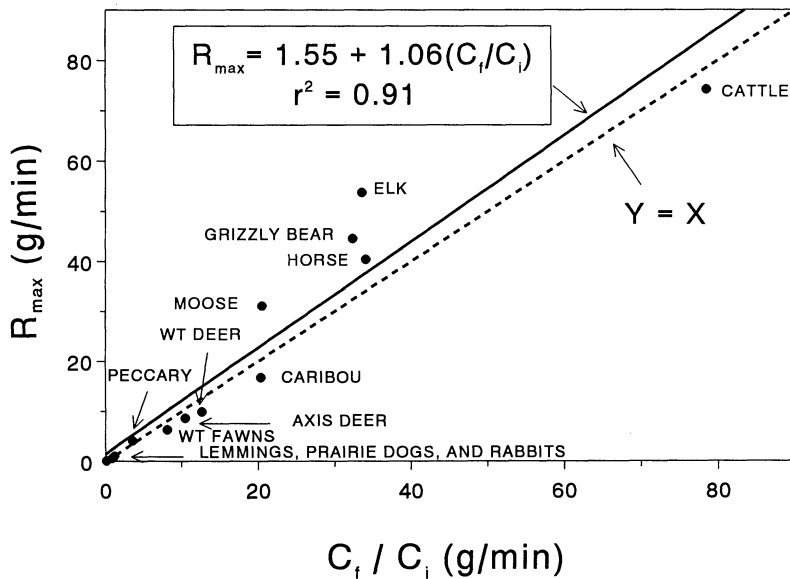


FIG. 4.—The R_{max} was strongly correlated with the quotient of C_f (chews/min) and C_i (chews expended/g ingested) of mammalian herbivores in our experiments. The dotted line represents the equality $Y = X$.

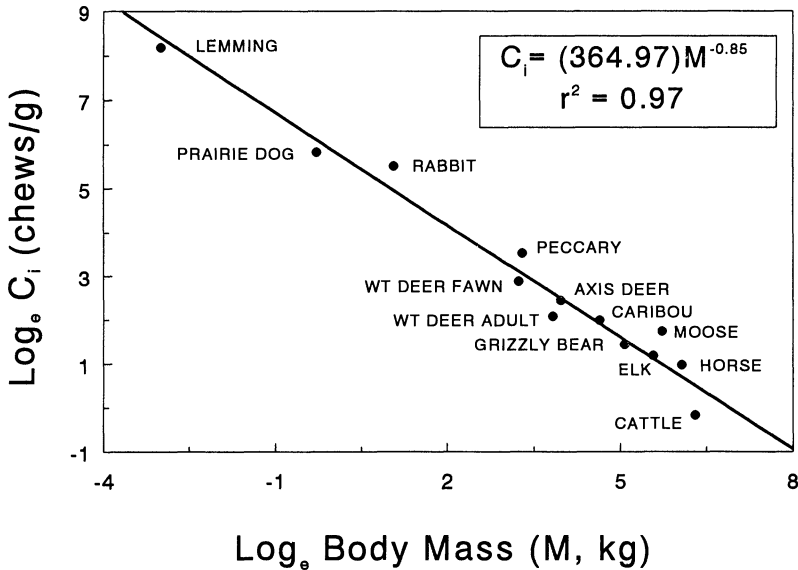


FIG. 5.—The C_i (chews expended/g ingested) was a function of M of the captive herbivores used in our experiments.

exponent of -1.0 , (hypothesis 1.2.3, table 1; $Z = 3.66$, $P = .0002$). However, the original hypothesis assumed that A_m would scale with $M^{0.67}$, and we were unable to measure the depth of food loaded on the molars by our experimental animals. Because the A_m of our animals actually scaled with $M^{0.62}$, we would expect molar loading volume (the product of A_m and bolus thickness) to scale with $M^{0.95}$. The scaling of C_i does not differ significantly from this value ($Z = 1.64$, $P = .10$).

Cropping time averaged 0.015 min/bite across species ($SE = 0.025$, range = 0.007–0.037 min/bite) and did not vary with M as was predicted by hypothesis 2 (tables 1, 4; fig. 6). The longest \bar{h} 's were observed in those herbivores with protruding muzzles, such as the moose (0.037 min/bite) and peccaries (0.027 min/bite; fig. 6). The S_{max} obtained by our experimental animals scaled with $M^{0.72}$ (table 4). This exponent differed significantly from the hypothesized exponent of 1.0 ($Z = 6.65$, $P < .0001$; hypothesis 3, table 1). In comparison, the largest bite size recorded for herbivores in previously published studies (table 3) scaled with $M^{0.59}$ ($SE = .09$, $r^2 = .65$) for animals eating grass, and $M^{0.63}$ ($SE = .11$, $r^2 = .55$) for animals eating shrubs or forbs (fig. 7).

By substituting the scaling coefficients for S_{max} , R_{max} , and the mean \bar{h} derived from our experiments into equation (4), we predicted the scaling of I_{max} of mammalian herbivores:

$$I_{max} = \frac{0.71 M^{0.70} \times 0.09 M^{0.72}}{0.71 M^{0.70} \times 0.015 + 0.09 M^{0.72}} \approx 0.63 M^{0.71}. \quad (5)$$

Because both S_{max} and R_{max} scaled approximately to $M^{0.71}$, the quotient of equa-

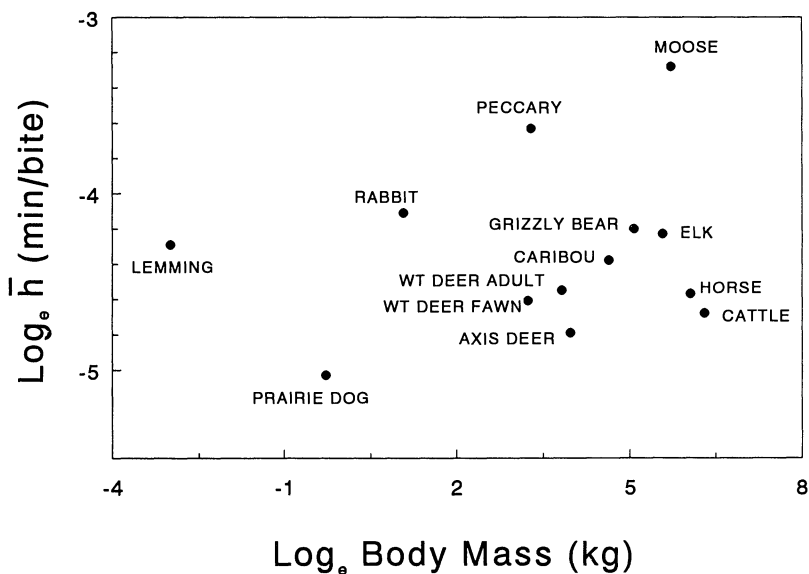


FIG. 6.—The \bar{h} (min/bite) was independent of M in mammalian herbivores

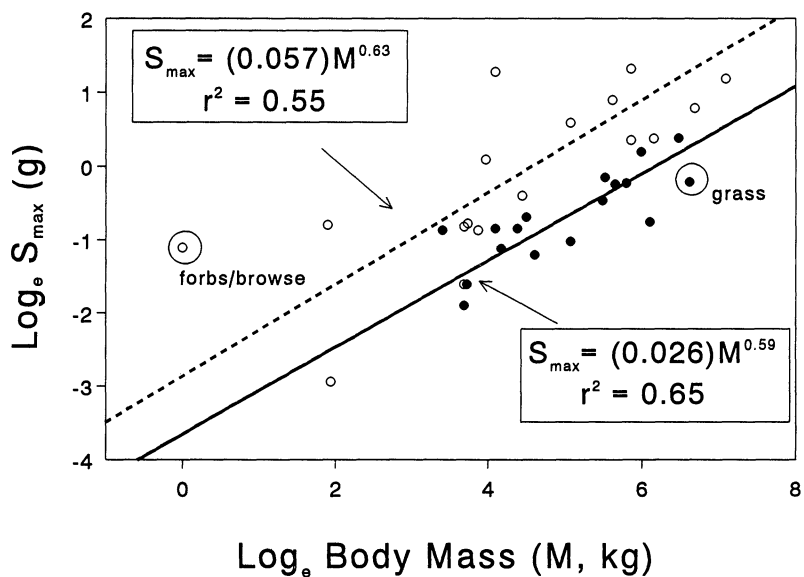


FIG. 7.—Published values for S_{\max} of 34 herbivores of a variety of species (table 3) are plotted against M . Open circles and the broken line represent bite sizes of browns and forbs, and closed circles and the solid line represent bite sizes of grasses.

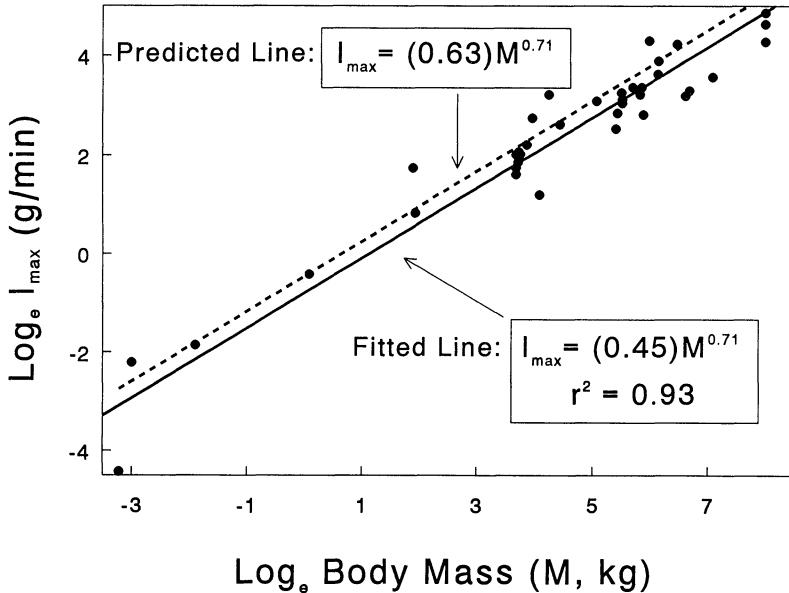


FIG. 8.—Published values for I_{\max} of 39 herbivores of a variety of species (table 3) is plotted as a function of M (solid line), and the relationship predicted by the composite scaling model (eq. [5]) is represented by a dashed line.

tion (5) can be simplified to $0.63M^{0.71}$. The highest values of intake rate of 39 herbivores from a variety of independent studies scaled with the same exponent as predicted by the composite scaling model— $0.45M^{0.71}$ ($r^2 = 0.93$; fig. 8). The composite scaling model (eq. [5]) explained 78% of the variation in the highest intake rates recorded for these 39 herbivores.

DISCUSSION

Scaling of the Mechanical Components of Intake Rate

We investigated the scaling of three components of short-term dry matter intake rate (R_{\max} , \bar{h} , and S_{\max} ; eq. [4]) in animals feeding in concentrated patches of plants. Pilbeam and Gould (1974) and Gould (1975) hypothesized that an animal's capacity for processing foods in the mouth is a simple function of the occlusal surface area of the molars, and, thus, oral processing rate should scale as $M^{0.67}$. Our results suggest that their prediction of the scaling of R_{\max} is correct but that the mechanism they propose is incomplete. Both R_{\max} (g/min) and A_m scaled closely to $M^{0.67}$ (table 4), but they did not correlate strongly with each other ($r^2 = .54$; fig. 3). The alternative model of Fortelius (1985; $R_{\max} = C_f/C_i$; hypothesis 1.2, table 1) provided a more complete explanation of the scaling of R_{\max} and accounted for 91% of the variation in R_{\max} (fig. 4). These results suggest that the A_m alone does not control R_{\max} and emphasize that departures of R_{\max} from the interspecific scaling can result from any factor that influences C_f or C_i . The R_{\max}

can thus be better estimated by measuring both A_m and L_j and by calculating C_f and C_i .

The scaling of C_f seems to be better explained by mechanics than by physiological rhythms. A superior fit was provided by the oscillating pendulum model to our observations of C_f than was provided by the physiologically based abstraction adopted by Fortelius (1985). The L_j , which hypothetically entrains chewing rate, is approximately isometric among animals and scales nearly to $M^{0.33}$ (table 4). The negative exponent relating pendulum length to oscillation frequency simply means that shorter jaws can cycle faster than longer jaws. Natural selection for rapid food processing would thus seem to place a premium on shorter jaws. However, jaw length, like all the morphological parameters, is subject to multiple selection pressures, the outcome of which presumably results in a combination of traits appropriate to the animal's specific diet and feeding strategy. For example, the relatively long jaw of the moose would at first seem maladapted, tending to slow chewing frequency and reduce the force between the incisors and upper palate so as to increase cropping time. However, the moose's long muzzle may be adaptive by enabling the moose to strip extremely large bites from the stems of its preferred browses (e.g., willow shoots).

The C_i (chews/g) scaled in proportion to $M^{-0.85}$ (table 4; fig. 5). Although C_i did not scale as the inverse of M , as hypothesized ($C_i \propto M^{-1.0}$; hypothesis 1.2.3, table 1), our data nevertheless support the idea that C_i scales as a function of the volume of food placed on the teeth (molar loading volume). The A_m scaled with $M^{0.62}$, but we could not measure bolus thickness and must assume that it scales isometrically with M ($\propto M^{0.33}$). The product of A_m and the expected bolus thickness scaled nearly as the inverse of C_i ($\propto M^{0.95}$).

However, we acknowledge that the mechanisms controlling C_i may be substantially more complex than this hypothesis suggests (see App. B). We did not measure muscular force or occlusal stress, and it is possible that jaw muscle mass does not scale isometrically with body mass. Moreover, hypothesis 1.2.3 (table 1; App. B) assumes that particles enter the mouth and are swallowed at a size proportional to $M^{1.0}$. Because the maximum bite size obtained by our animals scaled with $M^{0.72}$ (table 4), the particle size entering the mouth likely scales with an exponent less than 1.0. In addition, empirical evidence suggests that the particle size swallowed may not be isometric to M either. For example, cattle swallow food particles that are about 1.5–2 times larger than those of sheep (Ulyatt et al. 1986), yet cattle are about 10 times larger in M . Similarly, esophageal samples of browse leaves swallowed by elk (169 kg) and mule deer (42 kg) were similar in size, scaling roughly as $M^{0.29}$ (D. E. Spalinger and C. T. Robbins, unpublished data), and particle sizes in the stomach and feces of cattle, horses, ponies, goats, sheep, and rabbits scaled with $M^{0.14}$ and $M^{0.19}$, respectively (Uden 1978).

Our analyses of chewing investment also revealed differences in the way herbivores process foods. For example, A_m was relatively larger in horses and peccaries than it was in ruminants (figs. 2, 3), yet horses and peccaries invested more chewing per gram of food relative to body size than did ruminants (figs. 3, 5). However, horses maintained an R_{\max} very near that of ruminants, whereas the R_{\max} of peccaries was considerably lower (figs. 1, 3). Because the jaw muscles

of horses are three times heavier than those of ruminants of similar size (Janis 1976; Fortelius 1985), we would expect horses to comminute food with a greater force and thus either exhibit a higher R_{\max} or take fewer chews per gram than we observed. However, the matter is more complex than it appears: horses are hindgut-fermenters and thus may be required to chew foods more thoroughly during feeding (i.e., swallow smaller particles) than ruminants, which are able to rechew ingested materials during rumination. Although the same restrictions may apply to peccaries, their unique jaw and tooth structure may also be responsible for their relatively large C_i and A_m and their low R_{\max} (figs. 1, 2, 5). The peccary's exaggerated canines allow only orthal (up and down) as opposed to transverse (sideways grinding) chewing, and their bunodont molars lack the sharp, shearing ridges typical of grazing and browsing herbivores (Sowls 1978; Kiltie 1981). Consequently, low occlusal stress may limit the rate at which peccaries can process herbaceous foods.

In contrast to horses and peccaries, grizzly bears had a relatively small A_m yet invested a similar number of chews per gram and maintained a higher R_{\max} than expected for their M (compare figs. 1, 2, 3, 5). Because omnivorous bears do not ferment plants' cell walls, they may maximize feeding and nutrient assimilation rates by investing less in particle breakdown, swallowing large particles, and relying on a "plug-flow" digestive system in which rapid turnover is of extreme importance (Penry and Jumars 1986; Pritchard and Robbins 1990).

Even though \bar{h} lacked a consistent relationship with body size (table 4; fig. 6), it clearly varied among animals. It is perhaps surprising that this variation did not correspond to any general feeding strategy (grazer, browser) or incisor morphology (e.g., the presence of upper incisors; table 2; fig. 6). We conclude that variance in \bar{h} probably reflects differences in feeding behaviors and styles relative to the food we offered and the fact that not all species are equally adapted to eating alfalfa-like plants. For example, \bar{h} was substantially greater for moose and peccaries (fig. 6). Moose are adapted to feeding primarily on browses (Peek et al. 1976) and rarely eat terrestrial herbs; peccaries are adapted to feeding on forages, such as prickly pear cacti, seed pods, and hard-shelled nuts (Sowls 1978). Both moose and peccaries have long muzzles that may interfere with cropping short-statured herbs. Prairie dogs, on the other hand, cropped bites relatively quickly (fig. 6). Because they feed mostly on low-growing forbs and succulent grasses (Koford 1958), prairie dogs may be particularly adapted to minimizing \bar{h} .

The dependence of intake rate on bite size (the third component of the processing model, eq. [4]) is well documented (Stobbs 1973; Collins and Urness 1983; Wickstrom et al. 1984; Renecker and Hudson 1986; Hudson and Frank 1987; Illius and Gordon 1987; Risenhoover 1987; Vivås and Sæther 1987; Spalinger et al. 1988; Shipley and Spalinger 1992; Gross et al. 1993*b*). Bite size is determined by the way that physical characteristics of plants (e.g., leaf size, bulk or mass density, branching patterns, and spinescence; Cooper and Owen-Smith 1986; Burlison et al. 1991; Penning et al. 1991; Laca et al. 1992) interact with the size and morphology of an animal's mouth (e.g., incisor width and mouth gape; Illius and Gordon 1987). We attempted to isolate the influence of animal size on bite size by examining the scaling of the largest bites our animals could obtain. The maxi-

mum bite size in our experiments scaled with $M^{0.72}$ rather than with $M^{1.0}$, the predicted scaling of mouth volume (hypothesis 3, table 1), and regression of previously published values for S_{\max} yielded an even lower scaling exponent (≈ 0.60 for both grasses and browses; fig. 7).

The S_{\max} may not be a function of mouth volume for several reasons. First, some animals can defeat the constraints of mouth size by using idiosyncratic behaviors, such as sweeping up vegetation with the tongue (e.g., cattle; Hodgson 1985) or the trunk (e.g., elephants; Owen-Smith 1988), or by prehending a bite larger than will fit in the mouth and feeding this mass through the diastema directly to the molars (e.g., snowshoe hares; Shipley and Spalinger 1992; Gross et al. 1993b). Second, animals may choose to consume bites smaller than the maximum allowed by mouth morphology because there may be an optimum bite size at which chewing is most efficient (Fortelius 1990; Vivås et al. 1991). If bites were harvested in sizes proportional to mouth volume, the masticating capability of the molars might be overloaded (i.e., because A_m scales with an exponent of $M < 1.0$). Therefore, the scaling of S_{\max} may be more related to how much plant tissue can be handled by the grinding surfaces of the teeth (A_m) or efficiently chewed and removed from the mouth (R_{\max}) than to how much will actually fit in the mouth.

Finally, bite size may be regulated by the trade-offs between nutritional quality and cropping larger bites. In our experiments, plant quality remained relatively constant with plant size, but in natural habitats larger bites are generally of lower quality because they contain more stem or senescent leaves. Consequently, nutrient digestibility is reduced (Vivås and Sæther 1987). Furthermore, if a larger bite results in substantially greater fibrousness, then intake rate may decline because fibrousness reduces R_{\max} (Spalinger et al. 1988; Shipley and Spalinger 1992). For these reasons, herbivores may not be adapted to maximum bite size but, instead, may optimize bite size relative to both nutrient and I constraints (Lundberg and Åström 1990; Vivås et al. 1991).

Effects of Plant Morphology on the Scaling of Intake Rate

Plant architecture interacts with mouth morphology to control the size of the bite the animal can take in a single cropping motion and often restricts bites to sizes much smaller than will fit in the mouth. If bite size can be measured or predicted on the basis of plant geometry, then the scaling of the intake rate can be determined by substituting actual bite size or the scaling relationship for bite size into the composite scaling model.

Some foods are packaged in a certain bite size that must be taken by all foragers (e.g., acorns), and thus bite size is constant regardless of herbivore size. In grassland communities, however, bite size is constrained by both mouth morphology and plant size. Sward height and density interact with the dimensions of the animal's mouth to determine bite size. When grass tillers become very short, the only unrestricted bite dimension lies along the cropping surface formed by the incisors and mouth gape (Illius and Gordon 1987). Therefore, the scaling of bite size in this habitat may be predicted from the scaling of the width of the incisor row (Clutton-Brock and Harvey 1983; Owen-Smith 1985; Illius and Gordon 1987).

Because incisor row width scales with an exponent between 0.29 (Taylor et al. 1987) and 0.42 (this study, table 4), bite size is more constrained for larger animals as grass height declines. However, this constraint is partially offset because short swards often have a higher mass density (g/cm^3) than tall swards, an effect recognized in grazing lawns subject to intense herbivory (McNaughton 1984). In such habitats it is difficult to predict the consequences of body size on intake rate unless the relationship between sward height and mass density is specified.

In contrast to grasses, many plants offer a mass that is substantially greater than the herbivore's potential maximum bite size, yet the herbivore's bite size is still constrained. Shrubs, for example, have plant parts that are spatially diffuse, exhibiting recursive branching and irregular form. Therefore, the plant's mass is not equivalent to its volume, and, consequently, bite size is scale-dependent. Fractal geometry may provide a means to assess this relationship. For instance, Morse et al. (1985) found that plant surface area scaled as

$$A_p = \alpha L^{1.5}, \quad (6)$$

where A_p is the surface area projection of the plant, L is the scaling length (cm; Milne 1991), 1.5 is the fractal dimension, and α is the mass density coefficient. Morse et al. (1985) measured surface area, not mass density; but plant parts, such as leaves, are of uniform and nearly constant thickness, and mass density should consequently scale at approximately the same fractal dimension. Thus, equation (6) becomes

$$M_p = \alpha L^{1.5}, \quad (7)$$

where M_p is the mass of the plant (g). Because M_p is not euclidian in its geometry, if the spatial volume obtained by an animal in a single bite scales isometrically (or nearly so) with M , then actual bite size will fall shy of maximum bite size. Analytically, we can equate the scaling length of equation (7) with the bite dimension of the herbivore. For isometric mouth dimensions, L would scale with M as

$$L = \alpha M^{0.33}, \quad (8)$$

where α is the scaling coefficient. If the width of the incisor row is the appropriate metric for scaling bite size (Illius and Gordon 1987), then, for our herbivores, the scaling length of a bite would be

$$L = 0.58M^{0.42}. \quad (9)$$

Substituting equation (9) into equation (7), we obtain

$$M_p = 0.44\alpha M^{0.62}, \quad (10)$$

which expresses the plant mass obtained in a single bite (and, hence, $M_p = S$) as a function of herbivore M . Because M_p scales with an exponent that is less than the scaling exponent of S_{\max} , larger herbivores may be less efficient than small herbivores when consuming such plants. However, the exact outcome depends on the values of α and the fractal dimension, which are characteristics of each plant. In spite of this, it is intriguing that the scaling of the plant mass obtained in a bite from equation (10) is very close to the scaling of the S_{\max} of

herbivores reported in the literature (e.g., scaling $\propto M^{0.59}$ for grazers and $\propto M^{0.63}$ for herbivores consuming browse and forbs; fig. 7).

Scaling of Maximum Intake Rate and Metabolic Rate

Our composite scaling model of intake rate (eq. [5]), which combines the scaling of R_{\max} and S_{\max} , and the interspecific mean \bar{h} , suggests that the maximum intake rate of animals feeding on spatially concentrated food resources will scale to approximately $M^{0.71}$. The highest intake rates of a variety of herbivores feeding under free-ranging and experimental pasture conditions scaled identically to this predicted value ($\propto M^{0.71}$; fig. 8). In addition to their role as predictors, scaling relationships are important because they provide insight into the constraints on the behavior and evolution of organisms. If animals are to survive and reproduce, clearly their long-term rate of energy consumption must equal their rate of energy expenditure. Therefore, it is satisfying that the scaling of I_{\max} with $M^{0.71}$ is nearly identical to the interspecific scaling of energy requirements (e.g., $M^{0.75}$; Kleiber 1932; Brody et al. 1934; and $M^{0.71}$: Nagy 1987; McNab 1988). Maximum intake rate results from morphological features and mechanical processes of the mouth that scale isometrically (or nearly so) with M . Therefore, I_{\max} itself scales isometrically with M . This begs the question, Does mouth structure scale to meet metabolic demand and thus is it only incidentally isometric with body size, or is metabolic demand entrained because of an evolutionary "blueprint" that scales body parts isometrically?

CONCLUSIONS

The processing model (Spalinger and Hobbs 1992) implies that short-term intake rate in spatially concentrated patches of food is determined by the bite size obtained by an animal, by the rate at which the herbivore can process and swallow food, and by the handling time associated with cropping a bite of food. Our experiments have shown that bite size and oral processing rate scale with herbivore body mass, while cropping time varies with animal species but not with body mass. The oral processing rate scaled with $M^{0.70}$, and the maximum bite size scaled with $M^{0.72}$. The maximum bite size of herbivores eating natural forages scaled somewhat lower at $M^{0.59}$ for grasses and $M^{0.63}$ for browses and forbs. The differences in scaling parameters may reflect the effect of plant geometry on plant mass density. Because both the oral processing rate and maximum bite size scaled approximately to $M^{0.71}$, maximum intake rates were also predicted to scale with $M^{0.71}$. The maximum intake rates of a variety of herbivores foraging in free-ranging or experimental pastures scaled with $M^{0.71}$, which was the same as the predicted value. Hence, the scaling of short-term intake rate corresponds closely with the scaling of metabolic rate.

ACKNOWLEDGMENTS

We wish to thank the many people who provided valuable assistance in conducting trials and caring for animals, especially M. Kotzman, C. K. Pape, and

M. D. Shipley. We appreciate the generosity of C. T. Robbins in sharing his animals and facilities at Washington State University. We also thank M. Fortelius, N. Owen-Smith, and V. L. Roth for their helpful comments on the manuscript. This study was supported by United States National Science Foundation grants BSR-9006738/9007882 and DEB-9221844/9221610, the Texas Agricultural Experiment Station, and the Colorado Division of Wildlife.

APPENDIX A

DEFINITIONS OF SYMBOLS USED

α	Mass density coefficient (g/cm^2)
a, b, c	Scaling coefficients
A_m	Occlusal surface area of the molars (mm^2)
A_p	Surface area projection of a plant
b	Scaling exponent
C	Number of chews expended
C_f	Chewing frequency (chews/min)
C_i	Chewing investment (chews expended/g food processed)
\bar{h}	Time expended to crop a bite (min/bite)
I	Short-term dry matter intake rate (g/min)
I_{\max}	Maximum short-term dry matter intake rate (g/min)
k_p	Proportion of food particles broken per chew
L	Length
L_d	Depth of particles loaded onto molars; bolus thickness (mm)
L_j	Jaw length (mm)
M	Body mass (kg)
M_f	Mass of food prepared for swallowing (g)
M_p	Mass of a plant (g)
P_c	Particle size after C chews (g)
P_{crit}	Critical particle size of food necessary for swallowing (g)
P_{init}	Initial particle size of food upon entering the mouth (g)
R_{\max}	Maximum rate of food processing in the mouth in the absence of cropping (g/min)
S	Bite size (g/bite)
S_{\max}	Maximum bite size an animal can obtain (g/bite)
T_c	Time spent cropping while feeding (min)
T_f	Time spent feeding (min)
T_p	Time spent processing foods in the mouth (min)
X, Y	Variables

APPENDIX B

THE MECHANICS OF FOOD COMMINATION

Chewing investment (chews invested/g food) is a simplistic term representing a complex process that includes the mechanics of loading food onto the grinding surfaces of the molars, reducing food particles to a size suitable for swallowing (i.e., breakage; Lucas and Luke 1984), and forming a bolus (Fortelius 1985). Fortelius (1985) provided an excellent discussion of the processes and constraints that determine C_i . Here, we synthesize and clarify Fortelius's hypothesis (1.2.3, table 1) and offer a simple model to illustrate the dynamics and scaling of C_i .

Oral processing serves two primary roles. First, it prepares forages for digestion by severing protective layers (e.g., cutin, cell wall) and exposing cellular contents to digestive enzymes (Pond et al. 1984; Ulyatt et al. 1986). Second, it reduces particles to a size that ensures unrestricted flow through the digestive system (Schoonveld et al. 1974; Poppi et al. 1981; Spalinger and Robbins 1992). The diameter of the gut lumen sets an absolute

upper limit to particle size, but animals invariably swallow particles much smaller than this to enhance digestion rate and prevent impaction (Ulyatt et al. 1986; McArthur and Sanson 1988; Wilson et al. 1989).

Particle comminution also incurs a cost to the herbivore. The rate of food processing in the mouth (eq. [4]) decreases in direct proportion to the amount of time invested in reducing particle size during feeding. Moreover, the efficiency of particle breakage is likely a process of diminishing return, decreasing as particle size is reduced (Lucas and Luke 1984). Our evaluation of C_i is further hampered because some herbivores may optimize digestive efficiency by swallowing relatively large particles to retard passage of digesta and thereby maximize the extent of digestion of refractory substrates, such as cellulose (De Boever et al. 1990; Spalinger and Robbins 1992).

These arguments illustrate that the size of a particle swallowed by a herbivore is the outcome of a complex series of constraints and objectives. However, even if C_i (and thus the particle size swallowed) is under volitional control, there should exist a general scaling of particle size. As a first approximation, we suggest that particle size swallowed (g/particle) scales with gut volume (or particle diameter scales with gut lumen diameter), which scales roughly to $M^{1.0}$ (Parra 1978).

Particle comminution involves two processes: the loading of particles between the molars, and the breakage of those particles. The mass of particles loaded per chew is a function of the occlusal surface area of the molars, the morphology of the molars, and bolus thickness. The process of breakage is a function of the stress delivered to the loaded particles and the size of the particles. The mass of particles of initial size X broken to particles of size Y per chewing cycle is proportional to the product of these two processes (i.e., loading \times stress). In principle, we can therefore extract a scaling for the proportion of particles broken/chew (k_p) by defining the scaling of loading and stress.

Stress (force/area of contact) results from the action of the elevator muscles of the jaw producing force on particles trapped between the shearing or compressive surfaces of the molars (Lucas and Luke 1984; Fortelius 1985). The stress produced in chewing is therefore the quotient of the force of the muscles and A_m . The force generated by a muscle is proportional to its cross-sectional area (Wejls 1980; Cachel 1984), and, consequently, if the jaw musculature scales isometrically with M , then force should scale to $M^{0.67}$. Likewise, A_m is hypothesized to scale as a surface area to a volume ($\propto M^{0.67}$), and L_d to $M^{0.33}$ (as a linear measure to a volume). If k_p is the product of loading and stress, then

$$k_p \propto A_m \times L_d \times \frac{\text{Force}}{A_m}. \quad (\text{B1})$$

Therefore, k_p should scale as the product of jaw force and L_d and, hence, scale to $M^{1.0}$. As Fortelius (1985) pointed out, this does not mean that A_m is superfluous to the chewing process. Molar surface area retains adaptive significance for herbivores, because different types of foods may require either higher stress (smaller surface area) for efficient breakage (e.g., brittle foods such as nuts or twigs) or, conversely, higher loading for efficient shearing (more occlusal ridges for foods that are ductile and/or planar in dimension; Lucas and Luke 1984).

In principle, each particle entering the mouth may require multiple mastications, depending on the difference between its P_{init} and P_{crit} . If particle loading is constant (relative to tooth size) and breakage is inversely related to particle size, then we may represent particle reduction as a simple negatively exponential process (fig. B1). The reduction of a unit mass of particles can be described by the equation

$$P_c = P_{\text{init}} e^{-k_p C}, \quad (\text{B2})$$

where C is the number of chews and P_c is the particle size obtained after C chews. Equation (B2) is the solution of the differential equation describing the rate of particle reduction (dP/dC) and thus assumes a stable equilibrium in particle comminution. Equation (B2) can be solved to obtain C_i , the number of chews necessary to obtain this particle size. Thus,

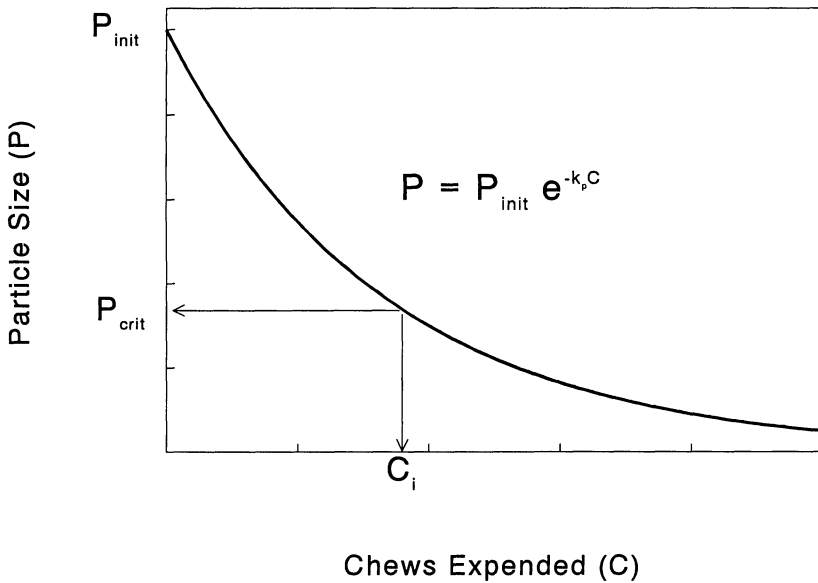


FIG. B1.—The change in particle size of a food item was hypothesized to be a negatively exponential function of the number of chews expended.

$$C_i = \frac{\log_e(P_{init}) - \log_e(P_{crit})}{k_p}. \quad (B3)$$

The parameters and variables in equation (B3) can now be replaced with scaling relations to arrive at a scaling of C_i . We previously hypothesized that k_p would scale to $M^{1.0}$ (eq. [B1]), and that P_{init} and P_{crit} would also scale to $M^{1.0}$. Thus, C_i should scale as

$$C_i \propto \frac{\log_e(bM^{1.0}) - \log_e(cM^{1.0})}{aM^{1.0}}, \quad (B4)$$

which reduces to

$$C_i \propto \frac{\log_e(b) - \log_e(c)}{a} M^{-1.0}. \quad (B5)$$

Because a , b , and c are scaling coefficients, and, thus, constants, we hypothesized that C_i scales as $M^{-1.0}$.

The processes we outlined above have necessarily simplified a very complex physical process. Our intent was to clarify that the hypothesis regarding chewing investment (hypothesis 1.2.3) makes assumptions about the scaling of the size of the particle cropped and swallowed. Because we could measure neither the chewing force nor the particle sizes cropped or swallowed, the "test" of this hypothesis cannot support or refute the hypothesized mechanism or validate the assumptions regarding the scaling of particle size. Such refinements will require further investigation.

LITERATURE CITED

- Allden, W. G., and I. A. McD. Whittaker. 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* 21:755–766.
- Arthur, R. L. 1984. Plant community and forage preferences of cattle on native aspen parkland range. M.S. thesis. University of Alberta, Edmonton.

- Åström, M., P. Lundberg, and K. Danell. 1990. Partial prey consumption by browsers: trees as patches. *Journal of Animal Ecology* 59:287–300.
- Barton, R. A. 1992. Allometry of food intake in free-ranging anthropoid primates. *Folia Primatologica* 58:56–59.
- Batzli, G. O., H.-J. G. Jung, and G. Guntenspergen. 1981. Nutritional ecology of microtine rodents: linear foraging-rate curves for brown lemmings. *Oikos* 37:112–116.
- Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Pages 111–124 in A. Watson, ed. *Animal populations in relation to their food sources*. Blackwell, Oxford.
- Belovsky, G. E., and P. A. Jordan. 1978. The time-energy budget of a moose. *Theoretical Population Biology* 14:76–104.
- Black, J. L., and P. A. Kenney. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. *Australian Journal of Agricultural Research* 35:565–578.
- Brody, S., R. C. Procter, and U. S. Ashworth. 1934. Basal metabolism, endogenous nitrogen, creatinine and neutral sulphur excretions as functions of body weight. University of Missouri Agriculture Experiment Station Research Bulletin 220:1–40.
- Burlison, A. J., J. Hodgson, and A. W. Illius. 1991. Sward canopy structure and the bite dimension and bite weight of grazing sheep. *Grass and Forage Science* 46:29–38.
- Cachel, S. 1984. Growth and allometry in primate masticatory muscles. *Archives of Oral Biology* 29:287–293.
- Clutton-Brock, T. H., and P. H. Harvey. 1983. The functional significance of variation in body size among mammals. *Special Publication American Society of Mammalogists* 7:632–663.
- Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *Journal of Wildlife Management* 47:646–663.
- Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. *Journal of Wildlife Management* 42:799–810.
- Cooper, S. M., and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia (Berlin)* 68:446–455.
- Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44:530–542.
- Creighton, G. K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. *Journal of Zoology (London)* 191:435–443.
- De Boever, J. L., J. I. Andries, D. L. De Brabander, B. G. Cottyn, and F. C. Buysse. 1990. Chewing activity of ruminants as a measure of physical structure: a review of factors affecting it. *Animal Feed Science and Technology* 27:281–291.
- Dougherty, C. T., P. L. Cornelius, N. W. Bradley, and L. M. Lauriault. 1989. Ingestive behavior of beef heifers within grazing sessions. *Applied Animal Behaviour Science* 23:341–351.
- Dunham, K. M. 1980. The feeding behavior of a tame impala *Aepycyros melampus*. *African Journal of Ecology* 18:253–257.
- Erlinger, L. L., D. R. Tolleson, and C. J. Brown. 1990. Comparison of bite size, biting rate and grazing time of beef heifers from herds distinguished by mature size and rate of maturity. *Journal of Animal Science* 68:3378–3587.
- Flores, E. R., F. D. Provenza, and D. F. Balph. 1989. Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. *Applied Animal Behaviour Science* 23:271–278.
- Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zoologica Fennica* 180:1–76.
- . 1988. Isometric scaling of mammalian cheek teeth is also true metabolic scaling. Pages 459–462 in D. E. Russell, J.-P. Santoro, and D. Sigogneau-Russell, eds. *Teeth revisited: proceeding of the VIIth international symposium on dental morphology*, Paris 1986. *Mémoires du Muséum National D'Histoire Naturelle*, Paris.
- . 1990. Problems with using fossil teeth to estimate body sizes of extinct mammals. Pages 207–228 in J. Damuth and B. J. MacFadden, eds. *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press, Cambridge.
- Gould, S. J. 1975. On the scaling of tooth size in mammals. *American Zoologist* 15:351–362.
- Gross, J. E., N. T. Hobbs, and B. A. Wunder. 1993a. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? *Oikos* 68:75–81.

- Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993b. Foraging by herbivores in food-concentrated patches: tests of a mechanistic model of functional response. *Ecology* 74:778–791.
- Hayami, I., and A. Matsukuma. 1970. Variation of bivariate characters from the standpoint of allometry. *Palaeontology* 13:588–605.
- Hiiemae, K. 1984. Functional aspects of primate jaw morphology. Pages 257–281 in D. J. Chivers, B. A. Wood, and A. Bilsborough, eds. *Food acquisition and processing in primates*. Plenum, New York.
- Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society* 44:339–346.
- Hodgson, J., and W. S. Jamieson. 1981. Variations in herbage mass and digestibility, and the grazing behaviour and herbage intake of adult cattle and weaned calves. *Grass and Forage Science* 36:39–48.
- Hudson, R. J., and S. Frank. 1987. Foraging ecology of bison in aspen boreal habitats. *Journal of Range Management* 40:71–75.
- Hudson, R. J., and M. T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. *Journal of Range Management* 38:80–82.
- Hudson, R. J., and W. G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. *Canadian Journal of Zoology* 64:1705–1708.
- Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56:989–999.
- . 1990. Variation in foraging behavior in red deer and the consequences for population demography. *Journal of Animal Ecology* 59:89–101.
- Janis, C. M. 1976. The evolutionary strategy of the Equidae and the origin of rumen and cecal digestion. *Evolution* 30:757–774.
- Janis, C. M., and D. Ehrhardt. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society* 92:267–284.
- Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215–267.
- Kiltie, R. A. 1981. The function of interlocking canines in rain forest peccaries (Tayassuidae). *Journal of Mammalogy* 62:459–469.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia* 6:315–353.
- Koford, C. B. 1958. Prairie dogs, white-faces, and blue grama. *Wildlife Monographs* 3:1–78.
- LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* 20:97–117.
- Laca, E. A., E. D. Ungar, N. Seligman, and M. W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science* 47:91–102.
- Lindsay, W. K. 1991. Food intake rates and habitat selection of elephants in Amboseli, Kenya. Pages 88–92 in J. B. Kayanja and E. L. Edroma, eds. *African wildlife: research and management*. International Council of Scientific Unions, Paris.
- Lucas, P. W., and D. A. Luke. 1984. Chewing it over: basic principles of food breakdown. Pages 283–301 in D. J. Chivers, B. A. Wood, and A. Bilsborough, eds. *Food acquisition and processing in primates*. Plenum, New York.
- Lundberg, P. 1988. Functional response of a small mammalian herbivore: the disc equation revisited. *Journal of Animal Ecology* 57:999–1006.
- Lundberg, P., and M. Åström. 1990. Low nutritive quality as a defense against optimally foraging herbivores. *American Naturalist* 135:547–562.
- McArdle, B. H. 1988. The structural relationship: regression in biology. *Canadian Journal of Zoology* 66:2329–2339.
- McArthur, C., and G. D. Sanson. 1988. Tooth wear in eastern grey kangaroos (*Macropus giganteus*) and western grey kangaroos (*Macropus fuliginosus*), and its potential influence on diet selection, digestion and population parameters. *Journal of Zoology (London)* 215:491–504.
- McMahon, T. A. 1977. Scaling quadrupedal galloping: frequencies, stresses, and joint angles. Pages 143–151 in T. J. Pedley, ed. *Scale effects in animal locomotion*. Academic Press, London.

- . 1984. Muscles, reflexes, and locomotion. Princeton University Press, Princeton, N.J.
- McNab, B. K. 1988. Complications inherent in scaling the basal rate of metabolism in mammals. *Quarterly Review of Biology* 63:25–54.
- McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* 124:863–886.
- Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. Pages 199–235 in M. G. Turner and R. H. Gardner, eds. *Quantitative methods in landscape ecology*. Springer, New York.
- Morse, D. R., J. H. Lawton, M. M. Dodson, and M. H. Williamson. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature (London)* 314:731–733.
- Murray, M. G. 1991. Maximizing energy retention in grazing ruminants. *Journal of Animal Ecology* 60:1029–1045.
- Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57:111–128.
- Oftedal, O. T. 1991. The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 334:161–170.
- Owen-Smith, R. N. 1985. Niche separation among African ungulates. Pages 167–171 in E. S. Vrba, ed. *Species and speciation*. Transvaal Museum Monograph 4. Transvaal Museum, Pretoria.
- . 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.
- Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pages 205–229 in G. G. Montgomery, ed. *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C.
- Peek, J. M., D. L. Ulrich, and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeast Minnesota. *Wildlife Monographs* 48:1–66.
- Peinado-Lucena, E., M. Sánchez-Rodríguez, A. G. Gómez-Castro, C. Mata-Moreno, and J. A. Gallego-Barrera. 1992. Dry matter intake per mouthful by grazing dairy goats. *Small Ruminant Research* 7:215–223.
- Pelley, R. A. 1984. Food consumption and energy budgets of the giraffe. *Journal of Applied Ecology* 21:141–159.
- Penning, P. S., A. J. Parsons, R. J. Orr, and T. T. Treacher. 1991. Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. *Grass and Forage Science* 46:15–28.
- Pennycuik, C. J. 1975. On the running of the gnu (*Connochaetes taurinus*) and other animals. *Journal of Experimental Biology* 63:775–799.
- . 1992. *Newton rules biology*. Oxford University Press, Oxford.
- Penry, D., and P. Jumars. 1986. Chemical reactor analysis and optimal digestion. *BioScience* 36:310–315.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Pilbeam, D., and S. J. Gould. 1974. Size and scaling in human evolution. *Science (Washington, D.C.)* 186:892–907.
- Pond, K. R., W. C. Ellis, and D. E. Akin. 1984. Ingestive mastication and fragmentation of forages. *Journal of Animal Science* 58:1567–1574.
- Poppi, D. P., K. J. Minson, and J. H. Ternouth. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. II. Factors controlling the retention of feed in the reticulo-rumen. *Australian Journal of Agricultural Research* 32:109–121.
- Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68:1645–1651.
- Randolph, J. C., G. N. Cameron, and J. A. Wrazen. 1991. Dietary choice of a generalist grassland herbivore: *Sigmodon hispidus*. *Journal of Mammalogy* 72:300–313.
- Rayner, J. M. V. 1985. Linear relations in biomechanics: the statistics of scaling functions. *Journal of Zoology (London)* 206:415–439.
- Renecker, L. A., and R. J. Hudson. 1986. Seasonal foraging rates of free-ranging moose. *Journal of Wildlife Management* 50:143–147.

- Risenhoover, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. diss. Michigan Technological University, Houghton.
- SAS Institute. 1985. SAS user's guide: statistics. SAS Institute, Cary, N.C.
- Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge University Press, Cambridge.
- Schoonveld, G. G., J. G. Nagy, and J. A. Bailey. 1974. Capability of mule deer to utilize fibrous alfalfa diets. *Journal of Wildlife Management* 38:823–829.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.
- Shipley, L. A., and D. E. Spalinger. 1992. Mechanics of browsing in dense food patches: influence of plant and animal morphology on intake rate. *Canadian Journal of Zoology* 70:1743–1752.
- Sowls, L. K. 1978. Collared peccary. Pages 191–205 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America*. Stackpole, Harrisburg, Pa.
- Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* 140:325–348.
- Spalinger, D. E., and C. T. Robbins. 1992. The dynamics of particle flow in the rumen of mule deer (*Odocoileus hemionus hemionus*) and elk (*Cervus elaphus nelsonii*). *Physiological Zoology* 65:379–402.
- Spalinger, D. E., T. A. Hanley, and C. T. Robbins. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology* 69:1166–1175.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64:209–210.
- Stobbs, T. H. 1973. The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. *Australian Journal of Agricultural Research* 24:809–819.
- Taylor, C. S., J. I. Murray, and A. W. Illius. 1987. Relative growth of incisor arcade breadth and eating rate in cattle and sheep. *Animal Production* 45:453–458.
- Trudell, J., and R. G. White. 1981. The effect of forage structure and availability on food intake, biting rate, bite size, and daily eating time of reindeer. *Journal of Applied Ecology* 18:63–81.
- Uden, P. 1978. Comparative studies on rate of passage, particle size, and rate of digestion in ruminants, equines, rabbits, and man. Ph.D. diss. Cornell University, Ithaca, N.Y.
- Ulyatt, M. J., D. W. Dellow, A. John, C. S. W. Reid, and G. C. Waghorn. 1986. Contribution of chewing during eating and rumination to clearance of digesta from the rumino-reticulum. Pages 498–515 in L. P. Milligan, W. L. Grovum, and A. Dobson, eds. *Control of digestion and metabolism in ruminants*. Prentice Hall, Englewood Cliffs, N.J.
- Ungar, E. D., A. Genizi, and M. W. Demment. 1991. Bite dimensions and herbage intake by cattle grazing short hand-constructed swards. *Agronomy Journal* 83:973–978.
- Vivås, H. J., and B.-E. Sæther. 1987. Interactions between a generalist herbivore, the moose *Alces alces* and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. *Journal of Animal Ecology* 56:509–520.
- Vivås, H. J., B.-E. Sæther, and R. Andersen. 1991. Optimal twig-size selection of a generalist herbivore, the moose *Alces alces*: implications for plant-herbivore interactions. *Journal of Animal Ecology* 60:395–408.
- Vulink, J. T., and H. J. Drost. 1991. A causal analysis of diet composition in free ranging cattle in reed-dominated vegetation. *Oecologia (Berlin)* 88:167–172.
- Wejjs, W. A. 1980. Biomechanical models and the analysis of form: a study of the mammalian masticatory apparatus. *American Zoologist* 20:707–719.
- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285–1301.
- Wilson, J. R., M. N. McLeod, and D. J. Minson. 1989. Particle size reduction of the leaves of a tropical and a temperate grass by cattle. I. Effects of chewing during eating and varying times of digestion. *Grass and Forage Science* 44:55–63.
- Wrangham, R. W., and P. G. Waterman. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *Journal of Animal Ecology* 50:715–731.