

## Optimal foraging and community structure: implications for a guild of generalist grassland herbivores

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**Summary.** A particular linear programming model is constructed to predict the diets of each of 14 species of generalist herbivores at the National Bison Range, Montana. The herbivores have body masses ranging over seven orders of magnitude and belonging to two major taxa: insects and mammals. The linear programming model has three feeding constraints: digestive capacity, feeding time and energy requirements. A foraging strategy that maximizes daily energy intake agrees very well with the observed diets. Body size appears to be an underlying determinant of the foraging parameters leading to diet selection. Species that possess digestive capacity and feeding time constraints which approach each other in magnitude have the most generalized diets. The degree that the linear programming models change their diet predictions with a given percent change in parameter values (sensitivity) may reflect the observed ability of the species to vary their diets. In particular, the species which show the most diet variability are those whose diets tend to be balanced between monocots and dicots. The community-ecological parameters of herbivore body-size ranges and species number can possibly be related to foraging behavior.

**Key words:** Optimal foraging – Herbivory – Grass lands – Body size – Competition

Optimal foraging ecology (Schoener 1971; Pyke et al. 1977) has been widely applied in the study of autecology (Krebs and Davies 1978; Rapport and Turner 1975, 1977). However, it has been little used in addressing problems dealing with the study of higher order ecological relationships such as competition, predation and trophic dynamics (Brown 1981). The exception has been the use of foraging strategies in studying competition (Werner 1977; Belovsky 1984a). Nonetheless, an analysis of foraging behavior for the majority of members of a single trophic level within a community and how this might relate to community structure has not appeared in the literature.

This paper examines the foraging ecology of 14 herbivorous species at the National Bison Range, Montana. These species range in body mass over seven orders of magnitude ( $2 \times 10^{-4}$ – $6 \times 10^2$  kg), include members of two very different classes (Insecta and Mammalia) and four orders (Orthoptera, Rodentia, Lagomorpha, Artiodactyla), and account for over 90% of the herbivore biomass and plant

consumption in the community. Using these species, a series of questions was addressed:

- 1) Can the diets of all 14 species be accounted for by a single model?
- 2) Do all the species have the same foraging strategy [i.e., time-minimizing or energy-maximizing *sensu* Schoener (1969); Hixon (1982)]?
- 3) How does body mass influence the importance of different foraging parameters?
- 4) Can the range of body sizes and number of species of herbivores in a community be explained by foraging considerations?

Belovsky (1978, 1984b, c) has shown that the optimization technique of linear programming can explain diet selection by three herbivores (moose: *Alces alces*, snowshoe hare: *Lepus americanus*, beaver: *Castor canadensis*). Furthermore, linear programming techniques have been shown (Belovsky 1984d) to be biologically and mathematically most appropriate for modelling herbivore foraging. This technique enables the inclusion of constraints operating on the forager's feeding choices that arise from their physiology, anatomy or behavioral repertoire. Foods that are patchily rather than randomly or uniformly distributed can be easily handled in the model. Finally, linear constraint values can be determined in a non-circular fashion; this is far more difficult to accomplish if constraints are non-linear. Furthermore, the solution for non-linear constraints requires the use of non-linear programming techniques, which are more complicated.

The linear programming model of herbivore foraging (Belovsky 1978, 1984b, c, d) is composed of four feeding constraint equations which reflect limits on the animal's foraging and its ability to achieve different foraging goals. These equations are characterized by:

- 1) digestive capacity and its fill by different food plants,
- 2) daily foraging time and its utilization by the cropping of different food plants,
- 3) daily energy requirements and their fulfillment by energy provided by different food plants, and
- 4) daily nutrient requirements and their satisfaction by the nutrient contents of different food plants.

With the above constraints, linear programming can be used to predict diets that maximize or minimize various goals. The two most commonly examined goals are either the achievement of greatest daily energy intake (energy maximizer) or satisfaction of minimum energy requirements in the least feeding time (time minimizer). A time minimizer

presumably achieves the greatest fitness by spending its time in other activities than feeding (e.g. mating, caring for young, hiding from predators, etc.) after it satisfies some minimal nutritional need. An energy maximizer presumably achieves the greatest fitness by ingesting the greatest amount of energy or other nutrients. In addition, a forager might seek to minimize filling its digestive tract and still satisfy minimal nutritional requirements, since a full digestive tract is mass that must be transported and may reduce the forager's ability to run away from predators. The importance of these alternate feeding goals or strategies has been presented elsewhere (Schoener 1969, 1971, 1983; Pyke et al. 1977; Belovsky 1984d; Hixon 1982).

### Study site

The necessary data to construct linear programming models of herbivore foraging were collected during the summers (May–Sept.) of 1978–1982 at the National Bison Range, Montana. The Bison Range is an intermountain Palouse prairie ranging in elevation from 800 to 1,600 m above sea level. The area, although overgrazed in the past (pre-1960's) by bison (*Bison bison*), is today maintained to represent the original vegetation and is perhaps undergrazed. The vegetation is dominated by monocots (70% by biomass), with forbs and woody plants (dicots) comprising 20% and 10% by biomass, respectively (Belovsky unpubl. data). The common monocots are *Agropyron spicatum*, *Festuca idahoensis*, *Festuca scabrella*, *Koeleria cristata* and *Poa pratensis*. Common forbs are *Lupinus* sp., *Achillea* sp., *Balsamorhiza sagitata*, *Penstemon* sp., *Arnica soraria*, and *Tragopogon dubiosus*, while common woody plants are *Artemisia frigida*, *A. ludoviciana*, *A. dracunculoides* and *Symphoricarpos occidentalis*. Over the Bison Range, the average plant biomass of new growth is 189 g/m<sup>2</sup> (s.e. = 22.1, n = 40) (Belovsky unpubl. data).

### Methods and model parameters

*The vegetation.* Belovsky (1978, 1984d) points out that the linear programming model predicts diet choices between plants which differ in their impact on foraging constraints and which are spatially located in separate patches (i.e., they cannot be searched for simultaneously). On the Bison Range in summer, plants appear to fall into two classes, monocots (predominantly graminoids) and dicots (forbs and deciduous leaves), based upon their nutritional value, digestive capacity utilization and distribution in the environment.

Nutritional characteristics were estimated by digesting 0.5 g dried samples (10 samples/species) of vegetation in HCl and pepsin, an approximate measure of digestibility for herbivores (Terry and Tilley 1964). Digestive capacity utilization was measured as bulk (wet wt/dry wt) for 10 samples/species. For these plant traits, monocots were far more similar to each other than to forbs or deciduous leaves, while forbs and deciduous leaves were very similar to each other (ANOVA, Table 1). Therefore, monocots were considered one food plant class, while dicots (forbs and deciduous leaves) were considered another.

Distribution of monocots and dicots in the environment was determined by sampling at 10 sites (0.16 ha) reflecting different slopes, aspects and elevation at the Bison Range. Sixteen to 40 0.01 m<sup>2</sup> plots were located randomly at each

**Table 1.** Comparison of the characteristics of different plant growth forms as foods for herbivores using ANOVA

	Sample Size	$\bar{x} \pm S.D.$	F-value with categories above
Food Bulk (wet wt/dry wt):			
Grasses	16	1.64 ± 0.35	
Forbs:			
Herbs	23	2.70 ± 0.75	38.46***
Deciduous leaves	16	2.63 ± 0.42	41.10***, 0.11 <sup>a</sup>
Food Digestibility (% dry matter soluble in acid + pepsin):			
Grasses	21	21.17 ± 5.42	
Forbs:			
Herbs	30	42.05 ± 10.25	74.17***
Deciduous leaves	17	48.06 ± 10.25	107.81***, 3.90 <sup>a</sup>

<sup>a</sup> N.S.; \*\*  $P < 0.05$ ; \*\*\*  $P < 0.001$

**Table 2.** Data on the distribution of grasses and forbs at 10 sites at the National Bison Range, Montana. A one-sided test was used because a negative association and positive skewness were hypothesized, i.e., monocots and dicots are patchily distributed in different portions of the environment

Site	n	Skewness coefficient		Spearman Rank correlation
		Grass	Forb	
1	40	2.58**	3.20**	−0.33**
2	36	0.54*	3.28**	−0.59**
3	40	0.16	1.05**	−0.26**
4	30	2.65**	3.05**	−0.10
5	40	1.59**	2.65**	−0.01
6	18	1.01*	1.57**	−0.27
7	18	−0.57	1.05**	−0.34*
8	16	0.71	2.79**	−0.36*
9	16	1.07**	1.14**	−0.32*
10	16	0.12	1.60**	−0.50*

\*  $P < 0.10$ , one-sided; \*\*  $P < 0.05$ , one sided

site; the vegetation was clipped, separated to monocot and dicot, dried, and weighed. Skewness coefficients for the distribution of monocot and dicot biomasses at each site were computed; a positive coefficient indicates a "patchy" distribution within each food class (Table 2). Spearman Rank correlations were computed for the association of monocot and dicot abundances at each site to determine whether monocots and dicots occur together (Table 2). For monocots, 9/10 sites had positive skewness coefficients (binomial probability:  $P < 0.001$ ) and 6/10 areas were statistically significant ( $P < 0.10$ ). For dicots, 10/10 sites had significant positive skewness coefficients, (binomial probability:  $P < 0.001$ ). These results indicate that dicots are strongly distributed in patches, while monocots are less so but still not randomly or uniformly distributed. Furthermore, 10/10 sites had a negative rank correlation between monocots and dicots (binomial probability:  $P < 0.001$ ), and for 7/10 sites the association was significant ( $P < 0.10$ ). Therefore, monocots and dicots are distributed patchily and their

patches do not occur together, requiring non-simultaneous search by herbivores if they are to feed on both.

*The foragers.* Model parameters reflecting the consumption of monocot and dicot foods were collected for four orthopterans (*Melanoplus femur-rubrum*, *M. sanguinipes*, *Dissosteira carolina* and *Circotettix undulatus*) and ten mammals (*Microtus pennsylvanicus*, *Spermophilus columbianus*, *Sylvilagus nuttalli*, *Marmota monax*, *Antilocapra americana*, *Odocoileus virginianus*, *Odocoileus hemionus*, *Ovis canadensis*, *Cervus elaphus* and *Bison bison*). The data collection methods have been provided in detail elsewhere (Belovsky 1978, 1981a, b, c, 1984b, c, d; Belovsky and Jordan 1978, 1981) and, unless previously unreported, will only be summarized here. During each month, data were collected for each species if the species was active (*i.e.*, the adult grasshoppers are not active until late July; *Spermophilus columbianus* and *Marmota flaviventris* are hibernating by August). All parameter values appear in Table 3 along with the standard errors and sample sizes if the values were obtained from this study.

*Constraint equation 1. Digestive capacity.* Digestive capacity is measured as the product of the volume of the forager's organ(s) used for the breakdown of plant tissues (Table 3, parameter 2), and digestive turnover through the organ(s) (Table 3, parameter 3). For ruminants, the organs are the rumen-reticulum; for other tetrapods, they are the caecum and stomach; and for insects, the midgut and foregut. Organ capacity is obtained by killing animals and weighing the contents (wet weight) after the animals have fed *ad libitum*.

Digestive turnover can be measured by a number of methods. Animals can be fed foods 'labelled' with an indigestible marker (radioactive isotopes, *e.g.*, Mautz and Petrides 1971; cotton thread, *e.g.*, Campling et al. 1961) to measure rate of appearance of the marker in feces. Another method is to sacrifice a set of animals, who have had food provided *ad libitum*, and measure changes in digestive organ contents over a period of time (Storr 1963). Both techniques were used in my studies.

The 'labelled' food technique (cotton thread: see Belovsky 1984b) was used for *Marmota flaviventris* and *Sylvilagus nuttalli*. The sacrifice technique was used for *Spermophilus columbianus*, *Microtus pennsylvanicus* and orthopterans. Digestive turnover rate was determined using feeding trials for these species, where a mixed diet of monocots and dicots was provided *ad libitum*, and then 50 animals were sacrificed (5 every 30 min). The digestive turnovers for the other larger mammals (> 3 kg) were taken from the literature, as determined using 'labelled' foods. Digestive turnover is measured as  $24 \text{ h} \div \text{mean retention time}$ , where mean retention time (Moen 1973) is the expected time that a food particle is resident in the digestive tract.

The fill of digestive capacity by plants is measured as the ratio of wet (fresh) to dry weight. These values for monocots and dicots were based upon 10 samples for each plant species, 16 and 39 species, respectively (Table 1).

*Constraint equation 2. Feeding time.* To solve the linear programming model, the estimate of daily feeding time must represent a maximum value potentially available to the forager (Belovsky 1978, 1984d). A thermal physiology model has been employed to compute this value in previous studies (Belovsky 1981b, 1984b) for herbivores. This esti-

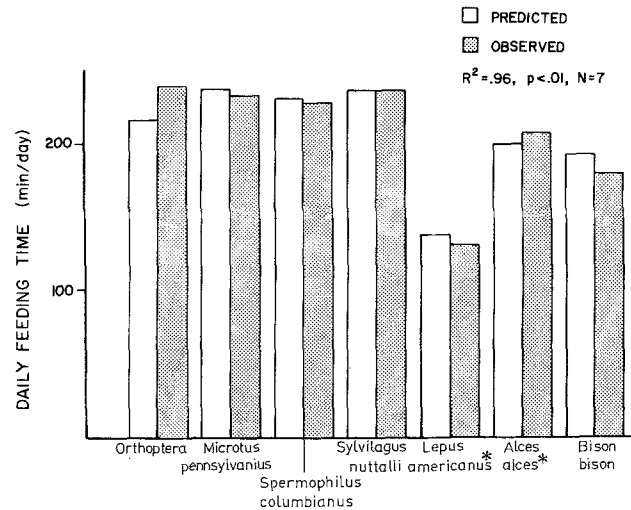


Fig. 1. A comparison of the thermal physiology-based estimate of daily feeding time and the observed daily feeding time are presented for 7 species of herbivores. Two species (marked with an asterisk) are included from a forest environment (Belovsky 1981b, 1984b), indicating that the observation that daily feeding time is dependent on climate and the forager's thermal physiology may be a general condition

mate represents the maximum time the forager can feed given climate, its thermal physiology and different habitats that it can use in the environment. The model is constructed under the assumption that climate and periods when the digestive organ is unfilled set the upper limit for feeding time.

Computing a daily feeding time for 14 species over a five-year period based upon a thermal physiology model is very time consuming and is in progress (Belovsky, unpubl. data). At this time, however, a comparison of the observed daily feeding time and that predicted from the thermal model indicates that agreement is quite good (Fig. 1) for 5 species spanning the range of body sizes in the study.

Extrapolation of these findings to the remaining species is further substantiated by the observation that all 14 species demonstrate a common response in summer to increased daily air temperatures by reducing daily feeding time (Belovsky and Slade 1986). Therefore, observed daily feeding times were employed as estimates of maximum daily feeding times.

Under the worst scenario, if the observed daily feeding time is less than the thermal-based maximum value, which does not seem to be the case here, analysis of the foraging model is still illustrative. First, solutions to the time-minimizing goal are always independent of the daily feeding time constraint and this is usually the case for the digestive capacity-minimizing goal. Consequently, the model's predictions of these two goals are unaffected. On the other hand, if the energy-maximizing solution and the forager's observed behavior agree, then we are presented potentially with a case where the forager is an energy maximizer within a daily feeding time that is restricted by factors other than climate (*e.g.*, required time for care of young, avoiding predators, etc.). These additional limits on feeding time may not be all-consuming as assumed in the time-minimizer hypothesis and this observation would indicate that the time-minimizing and energy-maximizing goals are not strict al-

**Table 3.** Parameters measured to use in the linear-program diet optimization model for Bison Range herbivores during summer. Standard errors and ranges of sample sizes are given only for values from this study

Parameters and sample size range	Herbivore species				
	<i>Dissosteira carolina</i> ♀	<i>Circotettix undulatus</i> ♀	<i>Melanoplus sanguinipes</i> ♀	<i>Melanoplus femur-rubrum</i> ♀	<i>Microtus pennsylvanicus</i>
1. Weight (kg) (sample size)	$1.6 \times 10^{-3}$ $\pm 7.0 \times 10^{-4}$ (6)	$7.7 \times 10^{-4}$ $\pm 1.68 \times 10^{-4}$ (8)	$3.59 \times 10^{-4}$ $\pm 4.4 \times 10^{-5}$ (114)	$2.04 \times 10^{-4}$ $\pm 2.5 \times 10^{-5}$ (54)	0.035
2. Digestion organ volume (g-wet wt) (sample size)	$5.2 \times 10^{-2}$ $\pm 4.2 \times 10^{-3}$ (6)	$4.2 \times 10^{-2}$ $\pm 4.2 \times 10^{-3}$ (8)	$2.32 \times 10^{-2}$ $\pm 7.09 \times 10^{-3}$ (114)	$1.69 \times 10^{-2}$ $\pm 3.72 \times 10^{-3}$ (54)	4.0 <sup>e</sup> $\pm 0.6$ (26)
3. Digestive turnover (times/day) (animal days: 3–65)	3.87	3.60	3.50	4.09	7.8
4. Feeding time (min/day) (animal h: 110–3290)	239.0 <sup>z</sup>	239.0 <sup>z</sup>	239.0 <sup>z</sup>	239.0 <sup>z</sup>	231.0 <sup>d,z</sup>
5. Cropping rate (min/g-dry wt) monocot (min: 140–160)	1,100.0 $\pm 130.0$	2,860.0 $\pm 330.0$	6,250.0 $\pm 830.0$	10,000.0 $\pm 203.0$	21.17 <sup>d</sup> $\pm 2.86$
dicot (forbs & leaves) (min: 160–820)	280.0 $\pm 50.0$	580.0 $\pm 100.0$	7,140.0 $\pm 720.0$	7,690.0 $\pm 1,000.0$	10.97 <sup>d</sup> $\pm 4.58$
6. Bulk (wet/dry wt) monocot (sample size: 64)	1.64 $\pm 0.09$	1.64 $\pm 0.09$	1.64 $\pm 0.09$	1.64 $\pm 0.09$	1.64 $\pm 0.09$
dicot (forbs and leaves) (sample size: 156)	2.67 $\pm 0.13$	2.67 $\pm 0.13$	2.67 $\pm 0.13$	2.67 $\pm 0.13$	2.67 $\pm 0.13$
7. Energy content (KJ/g-dry wt) monocot (animal days: 6–20)	7.04 <sup>a</sup>	7.04 <sup>a</sup>	7.04 <sup>a</sup>	7.04 <sup>a</sup>	8.84
dicot (forbs and leaves) (animal days: 4–20)	9.76 <sup>a</sup>	9.76 <sup>a</sup>	9.76 <sup>a</sup>	9.76 <sup>a</sup>	9.63
8. Average energy requirement (2 × basal: KJ/day)	0.854 <sup>b</sup>	0.528 <sup>b</sup>	0.297 <sup>b</sup>	0.214 <sup>b</sup>	70.60 <sup>g</sup>

<sup>a</sup> Bailey and Mukerji 1976, 1977; Smith 1959; Dyer and Bokhari 1976; Gyllenberg 1970; Husain et al. 1946; Bernays and Chapman 1972; Davey 1954; Dadd 1960

<sup>b</sup> Reichle 1968

<sup>c</sup> Kostelecka-Myrcha and Myrcha 1964; Lee and Horvath 1969; Belovsky 1984d

<sup>d</sup> These values determined from captive animals; Belovsky 1984d

<sup>e</sup> Data collected in 1980

<sup>f</sup> Data collected in 1978

<sup>g</sup> Packard 1968; Wiegert 1961

<sup>h</sup> Karasov 1981

<sup>i</sup> Bailey 1965

<sup>j</sup> O'Gara 1970; and 2 measurements from our study

<sup>k</sup> Berwick 1968; and 3 measurements from our study

<sup>l</sup> Short 1964; Short et al. 1969; Prins and Geilan 1971

<sup>m</sup> Short 1963; Short et al. 1965, 1966; Prins and Geilan 1971; Allo et al. 1973; Schoonveld et al. 1974; Dean et al. 1975

<sup>n</sup> Assumed same as white-tail deer (Mautz and Petrides 1971)

ternatives as often conceptualized. Rather, they might represent endpoints of a continuum.

The feeding time values (time actually spent cropping foods) in this study (Table 3, parameter 4) were empirically determined by observing individual animals feed over the summer period in the field (Belovsky and Slade 1986). The only exception to this was *Microtus pennsylvanicus* which was observed in 0.2 m<sup>2</sup> terraria with vegetation-covered sod present (Belovsky 1984d). This was necessary because *Microtus* could not be observed feeding in the field. A complete review of these data appears elsewhere (Belovsky and Slade 1986).

Cropping rate values (Table 3, parameter 5) are a major measurement required for this study because they are generally not available from the literature and are the most difficult to measure in the field. Determination of cropping rates requires the measurement of two parameters: the number or area of food items an herbivore ingests per unit time, i.e., leaves, blades, or cm<sup>2</sup> consumed per minute, and the

mean dry weight of an item of food. The number or area of items ingested per minute must be multiplied by the weights per item to obtain cropping rates (g/minute).

The number of items ingested per minute was measured by observing herbivores larger than 100 g at close range (<25 m and usually <10 m) with binoculars or spotting scope. For the smaller herbivores (*Microtus pennsylvanicus* and grasshoppers), the number of food items or area ingested was measured by observation of the animals in cages or terraria (0.2 m<sup>2</sup>) containing sections of sod for *Microtus* or several food items for Orthoptera. The food was present for periods of time short enough to prevent food depletion (<20 min duration). The number of bites of a food class was counted in two-minute periods for all the herbivore species except grasshoppers where the area of food items removed in 20 min was measured. Area removed was measured by tracing the food items on graph paper before feeding and comparing the item with the tracing after feeding to estimate the region that had been consumed.

Table 3

Herbivore species								
<i>Spermophilus columbianus</i>	<i>Sylvilagus nuttalli</i>	<i>Marmota flaviventris</i>	<i>Antilocapra americana</i>	<i>Ovis canadensis</i>	<i>Odocoileus virginianus</i>	<i>Odocoileus hemionus</i>	<i>Cervus canadensis</i>	<i>Bison bison</i>
0.35	1.0	2.5	46.0	72.0	80.0	90.0	318.0	636.0
43.0 ±3.22 (48)	92.0 ±5.2 (7)	230.0 ±22.8 (42)	5,942.0 <sup>j</sup>	4,653.0 <sup>k</sup>	4,200.0 <sup>l</sup>	4,386.0 <sup>m</sup>	21,159.0 <sup>s</sup>	87,700.0 <sup>t</sup> ±8,460.0 (11)
7.3	6.9	4.7	1.14 <sup>n</sup>	1.14 <sup>n</sup>	1.14 <sup>n</sup>	1.14 <sup>n</sup>	0.45 <sup>u</sup>	0.3 <sup>v</sup>
228.0 <sup>e,z</sup>	236.0 <sup>f,z</sup>	196.0 <sup>f,z</sup>	218.0 <sup>z</sup>	209.0 <sup>z</sup>	203.0 <sup>z</sup>	199.0 <sup>z</sup>	181.0 <sup>z</sup>	178.0 <sup>z</sup>
3.49 <sup>e</sup> ±0.21	1.61 <sup>f</sup> ±0.233	1.52 <sup>f</sup> ±0.47	0.207 ±0.016	0.128 ±0.008	0.18 ±0.013	0.18 ±0.016	0.029 ±0.002	0.010 ±8 × 10 <sup>-5</sup>
1.37 <sup>e</sup> ±0.10	0.38 <sup>f</sup> ±0.048	0.29 <sup>f</sup> ±0.021	0.08 ±0.007	0.086 ±0.005	0.10 ±0.007	0.09 ±0.007	0.056 ±0.005	0.045 ±0.007
1.64 ±0.09	1.64 ±0.09	1.64 ±0.09	1.64 ±0.09	1.64 ±0.09	1.64 ±0.09	1.64 ±0.09	1.64 ±0.09	1.64 ±0.09
2.67 ±0.13	2.67 ±0.13	2.67 ±0.13	2.67 ±0.13	2.67 ±0.13	2.67 ±0.13	2.67 ±0.13	2.67 ±0.13	2.67 ±0.13
9.46 10.22	10.51 11.35	11.01 11.93	9.63 <sup>n</sup> 10.05 <sup>n</sup>	12.14 <sup>y</sup> 12.48 <sup>y</sup>	9.63 <sup>n</sup> 10.05 <sup>n</sup>	9.63 <sup>n,r</sup> 10.05 <sup>n,r</sup>	10.22 <sup>x,w</sup> 16.67 <sup>x,w</sup>	12.40 <sup>w</sup> 14.66 <sup>w</sup>
196.4 <sup>h</sup>	586.26	1,624.79 <sup>i</sup>	8,618.1 <sup>o</sup>	11,377.7 <sup>p</sup>	9,853.4 <sup>q</sup>	10,766.3 <sup>r</sup>	46,352.6 <sup>x</sup>	74,250.4

<sup>o</sup> Wesley et al. 1970, 1973

<sup>p</sup> Chappel and Hudson 1978a, 1980

<sup>q</sup> Silver et al. 1971

<sup>r</sup> Short 1981

<sup>s</sup> Murie 1951; Prins and Geilan 1971; Nagy and Regelin 1975; Church and Hines 1978; and data from this study

<sup>t</sup> Meagher 1973; and ten from our study

<sup>u</sup> Maloij and Kay 1971; Staines 1976; Milne et al. 1976; Dean et al. 1980

<sup>v</sup> Schaefer et al. 1978

<sup>w</sup> Peden 1971; Richmond et al. 1977; Schaefer et al. 1978; Hawley et al. 1981

<sup>x</sup> Nelson and Leege 1982

<sup>y</sup> from *Ovis aries*, Milne 1976; Arman and Hopcraft 1975; Blaxter 1962

<sup>z</sup> Belovsky and Slade 1986

Only observations which entailed the herbivore's cropping of a single food class were used to compute cropping rates. Mixed observations do not allow determination of the food-cropping rates for each of the food categories in an independent manner.

To obtain the number of items ingested per minute, the bites/minute values must be multiplied by the number of items/bite. The number of items/bite is often a difficult measure to obtain in the field for bison, elk, bighorn sheep, deer, pronghorn antelope, marmots, cottontails and ground squirrels. Fortunately, semi-tame animals were present at the study site. These were animals either raised in captivity and turned free or naturally unafraid of humans because of the absence of hunting. Semi-tame animals permitted very close observations at times (< 2 m) which enabled measurement of the items/bite. This was not a problem for the species observed in captivity.

By observing the herbivores in the field or in captivity at close range (< 20 m), the plants on which they fed could

be relocated and the size of the items consumed was measured using calipers (width for monocot blades and diameter for dicot stems or petioles). These plant measurements ('eaten remainder') were matched using calipers to a plant of similar size which was then clipped, and the portion equivalent to that consumed ('matched bite') was separated, saved, dried and weighed to provide the weight/item. For grasshoppers, the known area of a food item was collected, dried and weighed to measure the conversion of area ingested to weight.

For the estimates of cropping rate, based on the products of the above values, a standard deviation must be computed. Because bites/min, items/bite and weight/item are too difficult to measure simultaneously for a given individual forager, a simple measure of standard deviation using the products of these values is not possible. For the product of independent variables, the standard deviation was estimated as:  $[(\text{VAR}(XY) = \text{VAR}(X)\text{VAR}(Y) + E(X)\text{VAR}(Y) + E(Y)\text{VAR}(X))]$  (Snedecor and Cochran 1967; Travis 1982).

This formula, however, provides an overestimate of the standard deviation because the bites/min, items/bite and weight/item are not independent measures and they covary negatively (Hudson and Nietfeld 1985; Wickstrom et al. 1984). Negative covariation reduces the standard deviation estimate based upon an assumption of independence (Snedecor and Cochran 1967; Travis 1982). I could not compensate for negative covariation because the three parameters were not measured simultaneously in my study.

*Constraint equation 3). Energetic requirements.* Each herbivore's energy requirements were taken from metabolic studies in the literature. If studies were not available in the literature, the energy expenditures were computed using the standard body weight-metabolic function (Kleiber 1961; Hemmingen 1960), increased two times for an active life (Moen 1973). This metabolic value was chosen to reflect a minimum intake needed for an individual's survival and replacement reproduction (one surviving offspring/lifetime), the basis for the time-minimizer foraging goal (Schoener 1971). Furthermore, this minimum value should not be confused with observed measures of energy budgets or maximum physiological values, rather it reflects a hypothetical value. These energy requirements appear in parameter 8 of Table 3.

The net energy content of food plants (Table 3, parameter 7) was measured as the product of gross energy content of the average plant within a food class and its average digestibility to the herbivore. Monocot and dicot gross energy contents were, respectively, 18.4 KJ/g-dry wt and 20.1 KJ/g-dry wt (Golley 1961; unpublished work, Bison Range files). For species in a given plant class, these values were found to be fairly constant (Golley 1961).

Measurements of the food plant's digestibility to each herbivore are often available in the literature. When not available, the digestibility measures for each herbivore were made using captive animals. Digestibility was measured as dry matter disappearance of the food (1-dry wt of feces/dry wt of ingested food). These measurements only had to be made for the smaller herbivores (marmot, cottontail, ground squirrel, *Microtus* and grasshopper species). This was accomplished by feeding captive animals various plant species in each food class in *ad libitum* quantities. The dry weight of food ingested was measured as well as fecal production over 24 h to compute digestibility.

*Constraint equation 4). Nutrient requirements.* No nutrient constraint seemed necessary to explain these herbivores' foraging. Either sodium (Botkin et al. 1973; Belovsky and Jordan 1981; Belovsky 1981c; Jordan et al. 1973; Weeks and Kirkpatrick 1976; Denton et al. 1961; Denton 1956, 1957, 1965; Bott et al. 1964; Scoggins et al. 1970; Bakko 1977; Weir 1972, 1973; Jarman 1972; Aumann 1965; Aumann and Emlen 1965; Hutchinson and Deevey 1949; Kimmins 1970) or protein (Schwartz et al. 1977; Bell 1969, 1971; Gwynne and Bell 1968; Owen-Smith and Novellie 1982; Klein 1962; Klein and Schönheyder 1970; Moen 1973; Murphy and Coates 1966) often are considered to be potentially important as limiting nutrients to herbivores.

The sodium and protein content of plant species at the study site were taken from the literature for sites with similar environmental conditions. The average sodium content for a number of plant species at the Bison Range was 400 times greater than for plant species in areas where sodium

appeared to influence herbivore foraging (0.04% vs. 0.0001% by weight). Crude protein averaged 12.3% over the summer and 17.7% over the period of peak parental investment in reproduction; approximately 6–7% is required for maintenance and 13–16% for growth and reproduction (French et al. 1955). Only during the period of peak parental investment (lactation) might protein be constraining. Therefore, nutrient impacts on foraging were not considered important in this study. If a model without nutrient constraints fails to predict diet choice, then a protein constraint would be a possible addition for further study.

*Herbivore diet.* The observed herbivore diets were measured using microhistological analysis of the plant fragments in feces or stomach contents (Sparks and Malechek 1968). The proportion of monocots and dicots was determined for each sample. Each herbivore's diet for the summer was computed as the average of its average monthly diets. The monthly estimates were based upon a minimum of 15 samples. Generally, stomach samples were used for herbivores smaller than *Spermophilus columbianus* (350 g), stomach and fecal samples were used for *Spermophilus columbianus* and *Marmota flaviventris* (2.5 kg), and fecal samples were primarily used for *Sylvilagus nuttalli* and larger herbivores (> 3 kg).

Diet values obtained by microhistological analysis were scaled by relative digestibility to account for differential appearance of monocots or dicots (Smith and Shandruk 1979). This was accomplished by scaling the observed counts of monocots and dicots by their dry matter digestibility for each herbivore species (Table 3, parameter 7). Although there are some difficulties with this technique in estimating species composition of an herbivore's diet (Smith and Shandruk 1979), it appears adequate for predicting diet composition by food classes which is the goal of the model.

These measures of an herbivore's diet are well suited for testing the linear programming solutions, because they do not employ any of the observations used for estimating the model parameters as do other diet-estimating techniques (e.g., cropping rates times feeding times).

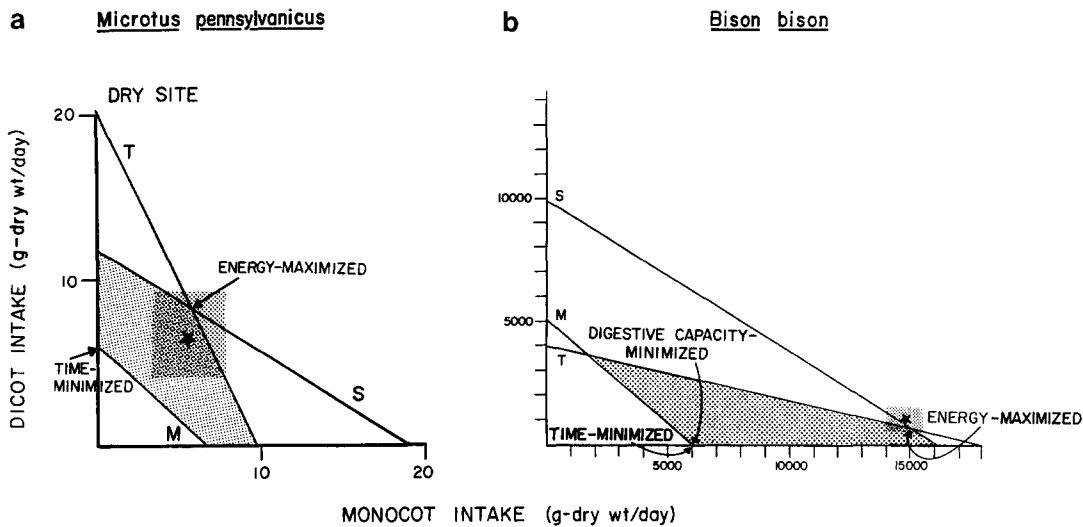
*The linear programming model.* The digestive capacity, daily feeding time and energy-requirement constraints can be written as:

$$C > \text{or} < a_1g + a_2d$$

where  $C$  is the foraging constraint and  $a_1$  or  $a_2$  converts the dry matter intake of monocots ( $g$ ) or dicots ( $d$ ), respectively, into the units of  $C$ . Because there are only two food classes (monocots and dicots), the linear programming solutions to the various goals, if they exist, occur at the intersections of two constraint equations or of a constraint equation and an axis (Belovsky 1978, 1984d). One of the three constraints drops out of the analysis for each of the three goals because it becomes the goal or object of foraging: for energy maximization, the energy constraint drops out; for feeding time minimization, the daily foraging constraint drops out; and for digestive capacity minimization, the digestive constraint drops out. For a review of linear programming techniques, see Strum (1972).

## Results and discussion

*Foraging by each species.* The data necessary to construct the linear programming model for each of the 14 Bison

**TIME (T):**

$$231 \text{ min/day} \geq 21.17g + 10.97f$$

**DIGESTIVE CAPACITY (S):**

$$31.2 \text{ g-wet/day} \geq 1.64g + 2.67f$$

**MAINTENANCE + REPRODUCTIVE METABOLISM (M):**

$$70.6 \text{ KJ/day} \leq 8.84g + 9.63f$$

**TIME (T):**

$$178 \text{ min/day} \geq 0.01g + 0.045f$$

**DIGESTIVE CAPACITY (S):**

$$26310 \text{ g-wet/day} \geq 1.64g + 2.67f$$

**MAINTENANCE + REPRODUCTIVE METABOLISM (M):**

$$74250.4 \text{ KJ/day} \leq 12.40g + 14.66f$$

**Fig. 2a, b.** Linear programming solutions are graphically presented for *Microtus* **a** and bison **b**. The lighter shaded region represents the region of feasible diets that satisfies the forager's constraint equations. The time-minimizing, energy-maximizing and digestive-capacity-minimizing solutions are presented for comparison with the observed diet (★). The 95% confidence region of the observed diet is presented by the darker shaded rectangle. The *Microtus* possesses the largest confidence interval of all the species studied and the bison has the lowest

Range herbivores appear in Table 3. Examples of time-minimizing, energy-maximizing, and digestive capacity-minimizing solutions to the linear programming model appear in Fig. 2, along with the observed diets for two of the 14 species, bison and *Microtus*. These two species were chosen as examples since they provide comparisons between the model's predictions and the observed diets for conditions with the greatest potential error (*Microtus*) and with the lowest potential error (bison). Therefore, these two examples represent the best and worst possible cases of the 14 species studied. *Microtus* have a large potential error in their observed diets because they were measured using stomach contents, and for such a small species its small digestive capacity can be filled in a single meal which may not reflect the daily diet (Belovsky 1984a).

Figure 3 presents a comparison of the linear programming model's predictions for time-minimizing and energy-maximizing diets with the observed diets for the 14 species. The 45° angle line in the plots represents perfect prediction of the observed diets by the model. The comparison indicates that the energy-maximized solution to the model predicts the observed diet very well ( $r^2 = 0.99$ ,  $n = 14$ ,  $P < 0.001$ ), even though the time-minimized solution also provides a statistically significant correlation ( $r^2 = 0.50$ ,  $n = 14$ ,  $P < 0.05$ ). Another alternative strategy of digestive capacity minimization provides a poor fit with observed diets ( $r^2 = 0.06$ ,  $n = 14$ , n.s.).

The diet resulting if the herbivores choose their foods at random, that is, take foods as they are encountered, would be a constant of approximately 70% monocots by

weight ( $r^2 = \text{undefin.}$ ,  $n = 14$ , n.s.). This is not observed. In conclusion, the energy-maximized linear programming model gives the best fit by far for diet in these herbivores.

To further examine the model's predictions, a  $\chi^2$  goodness of fit test can be used to compare the predicted and observed diets for each of the 14 species. For each species' diet determination, a known number of plant fragments had been counted in the stomach or fecal analysis. Each fragment is approximately equal in size since the samples are ground through a given-sized screen. Consequently, the number of fragments counted were considered as independent samples. An expected value for each  $\chi^2$ -cell was computed as the predicted diet proportion times the total number of fragments counted, which is compared with the observed fragments counted for the cell. The  $\chi^2$ -test has one degree of freedom since it has two cells (monocots and dicots).

A  $\chi^2$ -test was employed for several reasons, rather than a  $t$ -test, to compare the observed mean diet and standard deviation to a predicted value as portrayed in Fig. 2. First, the computation of a mean and standard deviation is misleading since it would require the averaging of monthly values which would unrealistically inflate the standard deviation by expressing diet variation between months and not samples. Second, the standard deviation may be inflated if it measures the variation between stomach contents that arise from meal and not diet choice (see above). Third, the  $t$ -test would tend to underestimate differences between the predicted and observed diets due to the small sample sizes based on monthly averages and their large standard

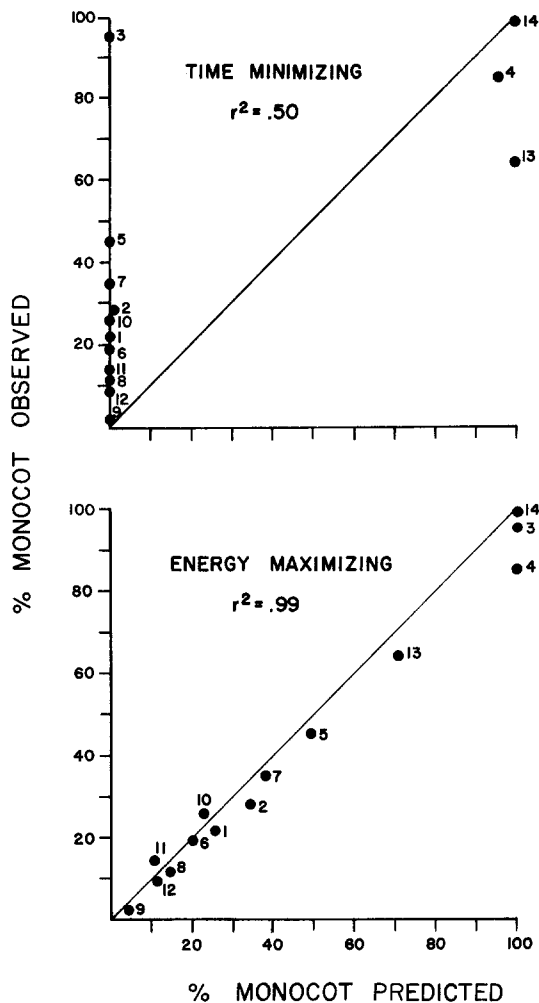


Fig. 3. The time-minimized and energy-maximized diets predicted by the linear programming model versus the observed diets are presented, demonstrating that time-minimizers are predicted to be either monocot or dicot specialists. The energy-maximizing diet explains the observed diets better. Each number represents a different species: 1 *Melanoplus femur-rubrum*, 2 *Melanoplus sanguinipes*, 3 *Circotettix undulatus*, 4 *Dissosteira carolina*, 5 *Microtus pennsylvanicus*, 6 *Spermophilus columbianus*, 7 *Sylvilagus nuttalli*, 8 *Marmota flaviventris*, 9 *Antilocapra americana*, 10 *Ovis canadensis*, 11 *Odocoileus virginianus*, 12 *Odocoileus hemionus*, 13 *Cervus canadensis* (or *elaphus*), and 14 *Bison bison*

deviations. Therefore, a  $\chi^2$ -test was more likely to find the model predictions different from the observed diets.

Based upon the  $\chi^2$ -test, the time-minimized diet is significantly different from the observed diet for all species but bison and *Dissosteira carolina*, but their observed feeding times are much greater than that predicted for time minimization. Only the observed diet for elk (*Cervus elaphus*) was not significantly different ( $P > 0.05$ ) from a random diet. Three of the 14 diets predicted to minimize digestive capacity were not different from observed (*Dissosteira carolina*, *Circotettix undulatus*, and *Bison bison*); however, the observed feeding times for these species were very different from those of a digestive-capacity minimizer. None of the energy-maximized diets were different from observed.

Even though the elk's observed diet is not different from random foraging, it also is not different from the energy-

Table 4. Predicted and observed feeding times for pronghorn antelope with different reproductive statuses are presented, along with sample sizes and t-test values

	Energy maximizer	Time minimizer	Observed
Doe or non-reproductive buck	218 min/day	69 min/day	218 min/day
Subordinate reproductive buck	218 min/day $t = 0.42$	69 min/day $t = 1.1$	$177 \pm 94$ min/day ( $n = 11$ )
Dominant reproductive buck	218 min/day* $t = 7.2$	69 min/day $t = 0.80$	$84 \pm 17$ min/day ( $n = 5$ )

\*  $P < 0.05$

maximized diet. This suggests that given the elk's feeding characteristics and the Bison Range environment, the best elk diet might be provided by eating foods as they are encountered, but this still provides an energy-maximizing diet. In the three cases in which the predicted diets that minimize digestive capacity or the two cases in which the predicted time-minimizing diets are not different from the observed diet, the energy-maximizing prediction still provides as good or a better fit. Therefore, all 14 herbivores appear to forage as energy maximizers, even though they are very different in body size, digestive physiology and taxonomic affiliation.

Because all the herbivores examined here appear to be energy maximizers, the question arises why herbivores might be energy maximizers rather than time or digestive-capacity minimizers. Perhaps herbivores are energy maximizers to survive either long-term (winter) or short-term (reproductive) energetic deficiencies (Belovsky 1984d). These deficiencies might arise from either low food abundance or the low digestibility of plants with a low nutritional quality per unit bulk. The latter requires herbivores to process foods relatively slowly to extract nutrients while the food bulk rapidly fills digestive capacity. The net result to the animal may be the inability to acquire adequate energy intake in some short time period and consequently the need to store energy reserves. Therefore, herbivores may consistently need to acquire as much energy as possible.

One might wonder whether a time minimizer is a realistic, observable alternative, or simply a "straw-man". For this purpose, male and female pronghorn antelope were observed during the mating season (approximately September 7–31), and their daily foraging time was recorded. Solving the linear programming model and comparing the solutions with the observed feeding times (Table 4), we find that dominant males which perform most of the mating (Kitchen 1974) appear to be time minimizers, while females and non-reproductive males are still energy maximizers. Subordinate but reproductive males are intermediate in their daily feeding time. This occurs because males spend large portions of their time fending off other males from their herds of females rather than feeding. Therefore, a time-minimizing strategy is observable.

Another question of concern is whether the observed and/or predicted diets vary between years. It is possible that the forager selects a diet which is close to some opti-



**Table 5.** The 1980 daily feeding-time and cropping-rate constraints for two herbivores at the Bison Range are presented. Sample sizes are presented in parentheses

	Feeding time (min/day)	Cropping rate (min/g-dry wt)	
		Monocot	Dicot
<i>Sylvilagus nuttalli</i>	236 (71 animal h)	0.71 ± 0.11 (81 min)	0.46 ± 0.06 (57 min)
<i>Marmota flaviventris</i>	242 (323 animal h)	0.67 ± 0.29 (134 min)	0.35 ± 0.03 (242 min)

**Table 6.** The predicted time-minimized and energy-maximized diets are presented for two species in 1980 for comparison to their 1978 diets

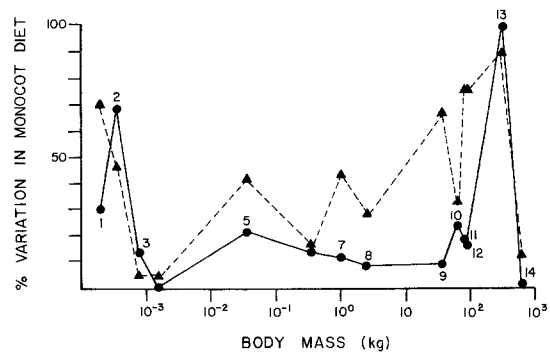
	Energy- maximized	Time- minimized	Observed	
			1980	1978
<i>Sylvilagus nuttalli</i>				
% Monocot	84	0*	80	35
% Dicot	16	100*	20	65
<i>Marmota flaviventris</i>				
% Monocot	45	0*	42	12
% Dicot	55	100*	58	88

\* $P < 0.05$

imum over time but cannot vary its diet selection as conditions change. Table 5 presents the foraging model parameters for the cottontail and marmot in 1980, a year with higher rainfall and plant biomass than 1978, the year reported for them in Table 3. Solution of the linear programming models for these animals in 1980 indicates that the predicted diets are very different from those in 1978 (Table 6) and the foragers modify their diet choice accordingly to remain energy maximizers. Belovsky (1984a) indicated, using *Microtus*, that predicted and observed diet choices varied between habitats, in a like fashion. Therefore, the foragers appear to be able to respond to changing environments.

As Belovsky (1978, 1984d) points out, one needs to be concerned with the sensitivity of a foraging model's predictions, as well as goodness of fit, since excessive sensitivity can reduce one's confidence in predictions. Sensitivity refers to how large of a change in the model's predictions arises from a change in model parameters. If a model's predictions change by a large amount then the model is considered very sensitive. In past applications of the linear programming model to herbivore foraging (Belovsky 1978, 1984b, c, d), when any one constraint was varied by 10%, a deviation in the predicted diet of less than 10% was observed.

The same sensitivity analysis was applied to the herbivores in this study. However, increasing and decreasing any one constraint value for a species (C) by 10% produced widely differing model predictions for the energy-maximized diets. The maximum deviation in each species' predicted diet with a 10% variation in any one constraint equation is plotted against herbivore body mass for the 14 species in Fig. 4. The constraint producing this deviation was considered the most sensitive for the species' model. Four species had maximum diet deviations less than 10%, 5 had



**Fig. 4.** Species body mass is plotted against the percent variation in the summer diets (maximum % monocot intake minus minimum % monocot intake) predicted by the energy-maximized solution to the linear programming model when the parameters are allowed to vary by 10% (sensitivity analysis) (●). This represents the plasticity of different species or body sizes in their diets. The maximum variation in diet found in the literature or this study (Allen 1968; Alldredge et al. 1974; Anderson et al. 1965; Anthony 1976; Anthony and Smith 1974; Barmore 1969; Bartmann et al. 1982; Beale and Smith 1970; Becker 1972; Berwick 1968; Blood 1967; Boeker et al. 1972; Bookhout 1965; Brown 1961; Bryant et al. 1979; Buechner 1947; Buechner 1950; Buechner 1952; California Wildlife Investigations Laboratory, N.d.; Chamrad and Box 1968; Cliff 1939; Cole 1969; Collins and Urness 1983; Collins et al. 1978; Constan 1972; Couey 1946; Cowan 1945; Cowan 1947; Currie et al. 1977; Dailey 1980; DeNio 1938; Deschamp et al. 1979; Dirschl 1963; Dorn 1970; Drawe 1968; Dusek 1975; Everitt and Drawe 1974; Everitt and Gonzalez 1979; Ferrel and Leach 1949; Ferrel and Leach 1950a; Ferrel and Leach 1950b; Free et al. 1970; Gordon 1968; Greer et al. 1970; Halloran 1943; Halls 1978; Hanley 1980; Hanley and Hanley 1982; Hansen and Clark 1977; Hansen and Dearden 1975; Harper 1962; Harper et al. 1967; Hill and Harris 1943; Hlavachick 1968; Hobbs et al. 1983; Hobbs et al. 1981; Hubbard and Hansen 1976; Hungerford 1970; Jameson 1947; Joern 1979; Johnson 1979; Johnson and Hansen 1979; Keller 1975; Klebenow 1965; Korschgen et al. 1980; Krausman 1978; Kufeld 1973; Kufeld et al. 1973; Lauer and Peek 1976; Leach 1956; Leach and Hiehle 1957; Leopold et al. 1951; Lovaas 1958; MacCracken and Hansen 1981; Mackie 1970; Martinka 1968; Mason 1952; McCollough et al. 1980; McCulloch 1969; McCulloch 1973; McCulloch 1978; McCullough 1980; McMahan 1964; Meagher 1973; Mitchell and Smoliak 1971; Morris and Schwartz 1957; Mulkern et al. 1969; Neff 1974; Nellis and Ross 1969; Nelson and Burnell 1975; O'Gara and Greer 1970; Oldemeyer et al. 1971; Peden 1976; Peden et al. 1974; Pickford and Reid 1943; Reynolds et al. 1978; Schwartz and Nagy 1976; Schwartz et al. 1977; Seegmiller and Ohmart 1981; Severson and May 1967; Severson et al. 1968; Sexson et al. 1981; Shank 1982; Short 1977; Smith 1952; Smith 1965; Smith and Shandruk 1979; Smith et al. 1979; Smith and Julander 1953; Spalinger 1980; Stevens 1966; Stevens 1974; Stormer and Bauer 1980; Taber and Dasmann 1958; Taylor 1972; Telfer 1967; Telfer 1972; Todd 1975; Ueckert 1968; Ueckert et al. 1972; Urness 1981; Uzzell 1958; Wallmo 1981; Wallmo and Regelin 1981; Wallmo et al. 1973; Wilkins 1957; Willms and McLean 1978; Willms et al. 1979; Willms et al. 1980; Zimmerman 1965) is plotted for comparison (▲), indicating that the sensitivity analysis of the linear programming model reflects observed sensitivity (Spearman Rank Correlation = 0.69,  $P < 0.005$ ). The numbers refer to the species in Fig. 3 and provide a ranking by body size. The smaller peaks in monocot consumption at species 5 and 7 may be real but were considered either as sampling variation or of minor importance

10–20% deviations, 3 had 20–30% deviations, 1 had a 60–70% deviation and 1 had a 90–100% deviation.

The fact that 5 of 14 species have predicted diet deviations over 20% is disconcerting (Fig. 4). Moreover, given

the confidence intervals for the observed constraints, the probability that their true values fall within 10% of the observed value is only 0.40 (range 0.01–0.80). The daily feeding time and cropping rate constraint equations are generally the most sensitive for the model. The difficulty in reducing the chance of error for this constraint arises because of the inherent spatial variability of food abundance in the environment and little can be done to reduce this factor within reasonable sampling time in the field.

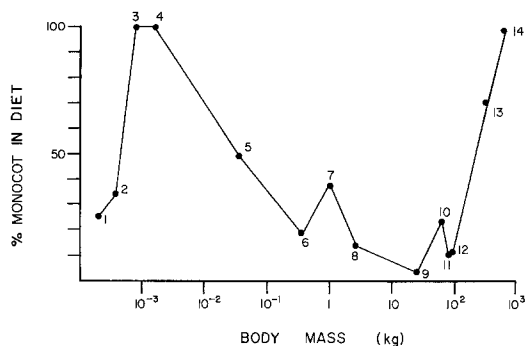
Although the sensitivity of the linear programming model for some species is upsetting from the viewpoint of the modeller, this sensitivity may be biologically important. Figure 4 also contains a plot of the maximum diet deviation reported in the literature or taken from this study for the 14 species (maximum % monocots observed in the diet minus minimum % monocots observed in the diet). The reported variability in these herbivores' diets is correlated with their diet sensitivity predicted by the linear programming model (Spearman Rank Correlation = 0.69,  $n = 14$ ,  $P < 0.001$ ). This high correlation is very surprising since the literature studies do not portray a uniform range of foraging environments for each of the species, making the correlations' strength even more convincing.

The diet sensitivity for the models may reflect the ability of these herbivores to vary their diets with environmental variability. Furthermore, the high level of sensitivity of the models for some species may be unavoidable because they reflect real biological sensitivity. It is also interesting that the species which show the greatest model sensitivity are those whose diets are in a region of transition from monocots to dicots or dicots to monocots (*Circotettix undulatus*, *Microtus pennsylvanicus*, *Cervus elaphus*), i.e., a diet tending to be balanced between monocots and dicots. These foragers generally have daily feeding time and digestive capacity constraints that are very similar in magnitude (see below).

Sensitivity of the model for the feeding time- and digestive capacity-minimizing solutions is far less than that for the energy-maximizing solutions. Sensitivity of the model for these solutions is inconsequential. For example, on average, the forager's energy requirements would have to vary by at least 2.1-fold (range: 1.1- to 6.2-fold) for the feeding time-minimizing goal to change the predicted diet. This amount of variation in the energy constraint would necessitate energy requirements that are approximately 4.2 times basal metabolism (range: 2.2 to 12.4 times), which is equal to or greater than the maximum energy requirements reported in the literature (Moen 1973).

Finally, the model's high sensitivity does not diminish our confidence in the observation that these herbivores appear to forage as energy maximizers. This is because the models for the 14 species serve as independent tests of the alternative foraging hypotheses, making the overall conclusion, in essence, a non-parametric test, freed of the parametric estimates and sensitivity of species by species analyses. Therefore, the conclusion that these herbivores appear to forage as energy maximizers is quite robust.

*Body size: the importance for different foraging constraints and for plant defense.* Since all of the herbivores studied forage as though they are energy maximizers, and the same foraging constraints are operating to delimit this goal (feeding time and digestive capacity), then the only difference between these herbivores' foraging strategies is the constraint values which might scale with body size. We can



**Fig. 5.** Each Bison Range herbivore's summer diet (% monocot), as predicted by the energy-maximized solution to the linear programming model, is plotted against the species' adult body mass (obtained from either this study or Burt and Grossenheider 1964). The numbers associated with each point refer to the species names presented in Fig. 3.

then ask if there is a pattern of diet selection for energy-maximizers with body size. Figure 5 presents the energy-maximized predicted diets expressed as % of monocot in the diet plotted against body mass. Two peaks of monocot consumption (Fig. 5:  $10^{-3}$ – $10^{-2}$  kg and  $10^2$ – $10^3$  kg) and two peaks of dicot consumption (Fig. 5:  $10^{-4}$ – $10^{-3}$  kg and  $10^{-1}$ – $10^2$  kg) are observed. This indicates that there is a wider range of body sizes that selects diets higher in dicots than monocots, 4 orders of magnitude vs 2.

The size classes which are heavy monocot feeders ( $10^{-3}$ – $10^{-2}$  kg and  $10^2$ – $10^3$  kg) are characterized by monocot consumption constrained by digestive capacity and by dicot intake constrained by feeding time or digestive capacity. Body size classes which are predominantly dicot feeders ( $10^{-4}$ – $10^{-3}$  kg and  $10^{-1}$ – $10^2$  kg) are constrained in their monocot consumption by feeding time while dicot consumption is limited by digestive capacity.

Very few body sizes have balanced (near equal) digestive capacity and feeding time constraints for both dicot and monocot ingestion. This condition leads to a diet balanced between monocots and dicots, i.e., equal ingestion of both foods. Consequently, most herbivores will tend to specialize (consume more) on either monocots or dicots.

The feeding time constraint, in general, appears to be limiting since it most often determines which food class does not dominate the diet. The observed changes in the importance of the constraints (feeding time or digestive capacity) on monocot versus dicot ingestion may arise from the impact of body geometry on mouth size, speed of search for food, energy metabolism, digestive organ capacity and digestive turnover (Belovsky, in prep.).

From the above pattern of diet choice and body mass, we might be tempted to generalize about the defensibility of monocots versus dicots. We might conclude that monocots (primarily graminoids) are better defended against herbivores (less acceptable) than dicots, since a smaller range of herbivore sizes can utilize large quantities of monocots (2 vs. 4 orders of magnitude of body sizes). "Defense" is used here in reference to the acceptability of the food plant to the herbivore whether acceptability is determined by toxicity, low nutrient content, or low digestive capacity due to bulk or slow turnover. This illustrates the difficulty in trying to define plant defenses against herbivores based on the study of a single herbivore species or a single factor,

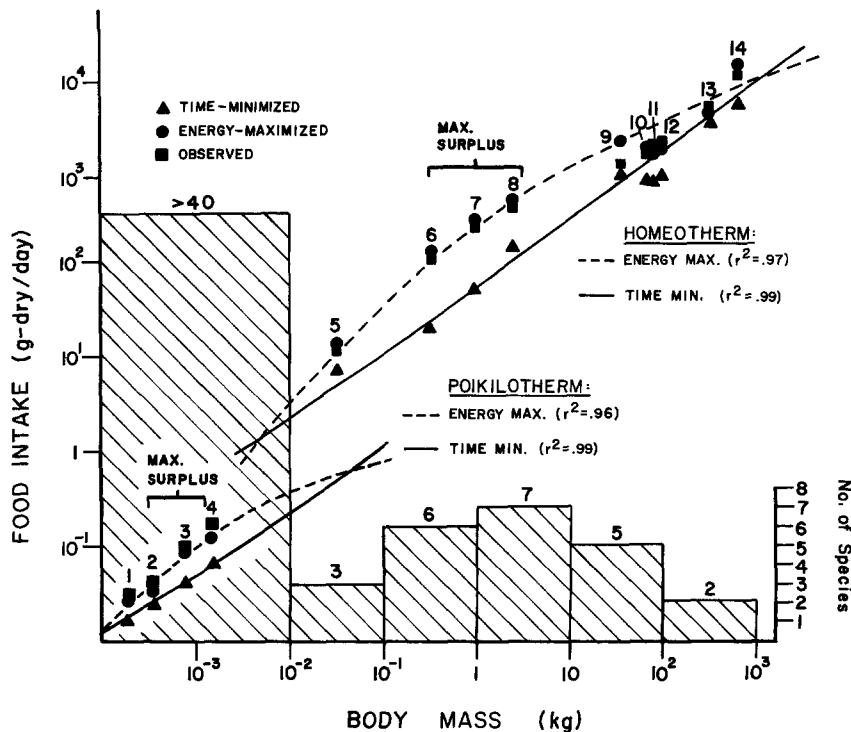


Fig. 6. The absolute food intake (g-dry wt/day) during summer predicted by the time-minimized ( $\blacktriangle$ ) and energy-maximized ( $\bullet$ ) solutions are plotted with the observed intake ( $\blacksquare$ : this study; Peden 1972; Short 1981; Alldredge et al. 1974; Wesley et al. 1973; Severson et al. 1968; Chappel and Hudson 1978b; Halls 1978; Hosley 1956; Hill 1956; Milne et al. 1976; Dean et al. 1980; Van Wormer 1969; Nelson and Leege 1982; Stelfox 1974; Armitage 1979) against body mass. The solid lines represent the curve fit to the predicted time-minimized intakes for endothermic and ectothermic herbivores; the dashed line is the curve fit to the predicted energy-maximized diets. The maximum difference between the dashed and solid curves represents body sizes which have more energy available to individuals and the intersection of the lines indicates either minimum or maximum body sizes for foraging (see text). The numbered points represent the species named in Fig. 3. The histogram presented illustrates the number of Bison Range herbivore species (right y-axis) of different body masses ( $< 10^{-2}$  kg: Orthoptera;  $10^{-2}$ – $10^{-1}$  kg: *Microtus pennsylvanicus*, *M. longicaudus*, *M. montanus*;  $10^{-1}$ – $10^0$  g: *Canachetes canadensis*, *Bonasa umbellus*, *Dendragapus obscurus*, *Thomomys talpoides*, *Spermophilus columbianus*, *Neotoma cineria*;  $10^0$ – $10$  kg: *Sylvilagus nuttalli*, *Lepus townsendi*, *L. americanus*, *Erethizon dorsatum*, *Ondatra zibethica*, *Marmota flaviventris*, *Castor canadensis*;  $10$ – $10^2$  kg: *Antilocapra americana*, *Oreamnos americanus*, *Ovis canadensis*, *Odocoileus hemionus*, *O. virginianus*;  $10^2$ – $10^3$ : *Cervus elaphus*, *Bison bison*)

such as toxins. Also, this leads one to question the idea that monocots have coevolved in a mutualistic fashion with herbivores and are less defended while dicots are more defended (Owen and Wiegert 1976, 1981; Owen 1980; McNaughton 1979a, b).

The findings presented here are consistent with Feeny's (1976) and Rhoades and Cates' (1976) arguments that plants which are abundant and not patchily distributed in either space or time (monocots) will be heavily defended. This defense should be provided by quantitative defenses, which impact on most herbivores. Although little evidence exists for toxins in graminoids, an ultimate quantitative defense in plants is low nutrient or energy content which is the case for monocots. Plants that are not abundant and are very patchily distributed will be less well defended and their defenses will be qualitative, which impact on specific herbivores (dicots). Although it must be stressed that sweeping comparisons must be made with caution (Silvertown 1982), these results illustrate the need to examine plant defenses using a suite of herbivores in an environment and a range of factors that determine plant acceptability to the herbivore.

*Community effects of foraging.* Thus far in this analysis, we have examined the percentage of monocot and dicot comprising the diet, not absolute food intake. Figure 6 pres-

ents the predicted intake of food per day for energy-maximizing and time-minimizing strategies which can be compared with the observed intake for captive individuals in this study or others reported in the literature. The limits imposed by the energy-maximizing and the time-minimizing food-intake values bound the intake values an herbivore can achieve and still survive and reproduce in the environment. Contrasting the above two intake levels with the observed intake, the energy-maximized intake is found to be slightly better correlated with the observed intake ( $r^2 = 0.99$ ,  $n = 14$ ,  $P < 0.001$ , vs.  $r^2 = 0.92$  for time minimization). This is consistent with the conclusion that herbivores are energy maximizers, though without the diet comparisons above it would be weak support.

Using absolute food intake values, we can make some predictions of community structure on the basis of trophic dynamics. If the time-minimizing intake is greater than the energy-maximizing intake (Fig. 6), then the herbivore cannot satisfy its energy demands and will not persist in the environment. The minimum sizes for herbivores that are still able to satisfy their energy demands (Fig. 6) are  $10^{-5}$ – $10^{-4}$  kg and  $10^{-3}$ – $10^{-2}$  kg, for ectotherms and endotherms, respectively. As might be expected, the smallest ectotherms will be smaller than the smallest endotherms. This can be envisioned if we consider a similar ability to ingest energy for ectotherms and endotherms at a given

small size which arises from their similar digestive capacity and feeding time constraints. Consequently, the ectotherms should be able to survive at lower body sizes because of their lower absolute energy requirements at a given size than those for endotherms.

The smallest chewing ectothermic herbivores, first instar grasshoppers, fall into the  $10^{-5}$  to  $10^{-4}$  kg size class at the Bison Range and the smallest endothermic herbivores, recently weaned microtines, approximately 8 g, fall into the  $10^{-3}$ – $10^{-2}$  kg size class. Therefore, it appears that minimum herbivore sizes at the Bison Range may be consistent with the sizes set by foraging energetics.

A maximum size at which energy demands are not satisfied may also be found. For ectothermic herbivores the predicted maximum (approx. 50 g) is much larger than the observed maximum (approx. 1.5 g) indicating that foraging energetics may not explain the largest observed sizes. A maximum size, however, does emerge for endotherms at a size slightly greater than  $10^3$  kg (Fig. 6), corresponding with the largest mammal at the Bison Range, a large bull bison at 1,250 kg.

The maximum size for ectothermic herbivores may be set by considerations other than foraging, such as predation, the physiology of respiration, and climate. Competition with the smallest endothermic herbivores also may preclude larger ectotherms. The endotherms within these size ranges may be competitively superior as they appear to be able to acquire more energy in foraging relative to their requirements (greater deviation between time-minimized and energy-maximized lines in Fig. 6) than ectotherms. The cause of this observation is uncertain but it might arise from the endotherm's foraging constraints being less dependent upon climatic conditions (feeding time and digestive capacity are not temperature dependent).

If foraging also sets a maximum size for endothermic herbivores, we must question arguments that large mammalian herbivores went extinct at the end of the Pleistocene from human hunting (Martin 1973). Many of the extinct herbivorous species were larger than *Bison bison* and the above analysis indicates that larger herbivores are not energetically capable of surviving in this grassland which is one of the more productive regions in North America for herbivores. Therefore, the existence today of the larger extinct herbivores would be impossible; *i.e.*, no niche space exists for them. Perhaps, the environment changed at the end of the Pleistocene by becoming more xeric (Hester 1967) which might have made the foraging energetics of the larger species untenable.

From Fig. 6, one can see that certain body sizes of herbivores can obtain relatively more energy above their requirements (energy obtained/energy requirement) than other herbivore sizes, *i.e.*, they are more efficient. This ratio is measured as the distance between the energy-maximized and time-minimized intakes since Fig. 6 is plotted in a log-log fashion. Even though these body sizes are more efficient, this does not imply that they should be selected for over other body sizes in the environment, because different sizes of herbivores use different food resources and have different amounts of food available in the environment (Belovsky 1984a, 1986). Nonetheless, individuals of certain sizes will be more efficient in acquiring the food energy available to them. If food availability limits the population growth of the herbivores studied, then individuals of species with certain body sizes should be capable of acquiring more ener-

gy relative to their requirements than species with other body sizes. This might result in a more rapid population growth for species of these body sizes and a greater ability to withstand more intense competition for food. An ability to withstand intense competition might be reflected as the ability of more species of these sizes to coexist together.

To test whether more species coexist at body sizes with greater foraging efficiency, the number of species in a body size range can be compared with the body size's energy intake relative to metabolic requirements (feeding efficiency). Also, small body sizes may have greater numbers of species because small size permits greater specialization on microhabitats which are unavailable to larger species (Hutchinson and MacArthur 1959), *i.e.*, the environment is patchier for small species.

Using the data in Fig. 6, we find that body size is highly correlated with species number, if energy intake relative to metabolic requirements is held constant, (partial correlation coefficient;  $r=0.98$ ,  $P<0.001$ ,  $n=14$ ); and energy intake relative to requirements is highly correlated to species number, if body size is held constant (partial correlation coefficient;  $r=0.95$ ,  $P<0.001$ ,  $n=14$ ). Overall, these two variables explain 98% of the variance in species number, with body size accounting for 71% and energy intake relative to requirements accounting for an additional 27%.

Although body size is more important, the combination of body size and feeding efficiency to explain species number may be the reason for observed log-normal distributions of species number vs. body size (Hutchinson and MacArthur 1959; Schoener and Janzen 1968; May 1979). This species abundance distribution might arise from three distinct regions of body size and abundance characteristics. Small to intermediate-sized herbivores may be able to take advantage of greater microhabitat specialization and their greater foraging efficiency to have the greatest abundance, leading to a peak in the body size-abundance curve. Very small herbivores only have the advantage of greater microhabitat specialization because they have a low feeding efficiency; and larger herbivores have neither advantage. This leads to a left tail (very small sizes) of the size-abundance curve that is higher than the right tail (very large sizes). Therefore, a curve approximating a log-normal distribution might be produced.

The above statements on species number only bear on competition within a body size class, *i.e.*, competition between species that forage similarly. It does not pertain to competition between body size classes, since this depends upon how similar in feeding different size classes are. Belovsky (1984a, 1986) has shown experimentally how competition for food can explain the population dynamics of herbivores that are not taxonomically closely-related or have very different body sizes.

The relationship between diet and body size presented above indicates that if food is the object of competition, the competition probably is most intense for energy-rich foods, since all the herbivores appear to be energy maximizers. Also, herbivores with certain body sizes are more likely to exhibit competition. Insects between  $10^{-4}$  and  $10^{-3}$  kg will compete most intensely with mammals between  $10^{-1}$  and  $10^{-2}$  kg for dicots, while insects between  $10^{-3}$  and  $10^{-2}$  kg will compete most intensely with mammals between  $10^2$  and  $10^3$  kg for monocots. The separation of herbivores into body mass classes, which tend to compete more intensely with each other, arises from their similarities

in foraging constraints (*i.e.*, feeding time-cropping rate, digestive capacity-food fill) examined above.

## Conclusion

The optimal foraging analysis presented in this paper leads to a number of conclusions about herbivore foraging behavior. First, a single foraging model employing the same constraints (feeding time, digestive capacity and energy requirements), linear programming, appears to apply to all the herbivores studied. Second, all the herbivores in this study appear to be adopting a goal of energy maximization for all but very short periods (*e.g.*, pronghorn males in the mating season). Third, the model solved for energy maximization appears to predict diets that follow a pattern with forager body size. Whether or not the same patterns occur in other herbivore communities must still be investigated, although similar patterns have been observed in a forest environment for a less diverse herbivore assemblage [moose, *Alces alces*; beaver, *Castor canadensis* and snowshoe hare, *Lepus americanus* (Belovsky 1978, 1984b, c)].

The observed foraging behavior patterns probably occur because herbivores have common anatomical and physiological processes constraining their diet choice (Belovsky 1984d). These physiological processes are probably body-size dependent, which leads to the relationship between diet choice and body size (Belovsky unpublished work).

Why do herbivores behave as energy maximizers? Perhaps seasonal food shortages arising from low abundance and quality, such as occur in winter, necessitate a long-term goal of energy maximization. Food shortages are not unique to herbivores living in temperate climates, for periods of low food abundance and quality also exist in tropical areas (Sinclair 1975). One must, however, bear in mind that the analysis has been restricted to generalist herbivores, those consuming a range of plant species, not specialists, such as many Lepidoptera, that feed on only one or several plant species (Belovsky 1984d).

The foraging strategy analysis provides more than just a means of estimating a species' diet and insights into its rationale for diet choice in the context of behavioral ecology. It enables us to examine community ecology problems. For example, the herbivore foraging analysis presented here indicates: 1) how 'plastic' different herbivore species are to changing environments through diet variability, 2) whether the largest and smallest body sizes for herbivores in an environment are set by foraging limitations, 3) whether or not certain herbivore body size classes are able to acquire more energy relative to their requirements, which should influence their population dynamics, if food limited, and 4) how foraging may bear on questions of the number of herbivore species in the environment and the potential for competition (Belovsky 1984a, 1986).

The underlying assumption for inferring community patterns from the foraging strategy model is that food limits the population dynamics of the herbivores. This immediately raises the question of the HSS hypothesis (Hairston et al. 1960; Slobodkin et al. 1967): that predators limit herbivore numbers. A review of the literature on generalist herbivore abundances and a set of experiments conducted by me (Belovsky 1984a, 1986) indicate that generalist herbivores appear to be food limited. This is not to say that predation does not influence herbivore population dynamics, but food

availability and its apportionment between different species appears to be of principal importance (Belovsky 1984a).

Food limitation of herbivores, however, is by no means established and additional investigations on this matter must be undertaken. Whether differences should exist between specialist and generalist herbivores for food limitation is unknown and may be important for the relevance of HSS. Nonetheless, if this assumption continues to be borne out, the utility of foraging models for answering community structure questions can be seen and permits the linking of behavioral ecology with population biology (Belovsky 1986; Werner 1977).

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**Note added in proof.** Fig. 2b. The energy-maximized diet should appear at the intersection of the *x*-axis (Monocot Intake) and the Digestive Capacity constraint (*S*). Also, the confidence region represents  $\pm 1$  SE, not 95% confidence, for bison.