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HERBIVORE OPTIMAL FORAGING: A COMPARATIVE TEST OF THREE MODELS

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Explanations of herbivore food choice have followed two general theoretical pathways: (1) foraging for nutritional requirements or dietary diversity and (2) optimal foraging. The first and older approach suggests that herbivores consume plants to balance nutritional needs and avoid overingestion of toxic plant secondary compounds. A very detailed analysis of the nutritional characteristics of each potential food of herbivorous mammals is represented by the work of Freeland and Janzen (1974). The second approach employs various theories of optimal foraging (Pyke et al. 1977) in attempting to construct predictive mathematical models of food choice. Although the two approaches have overlapping perspectives, the optimization approach must be naive in comparison with the nutritional requirement/diversity approach because of the necessity of framing the constituent concepts in simple mathematical terms. In this paper I examine several optimization approaches to assess their levels of success in predicting herbivore diets.

Development of herbivore optimal foraging models has followed three different mathematical formulations: contingency models (Owen-Smith and Novellie 1982), models of food abundance weighted by net energy content (Stenseth et al. 1977; Stenseth and Hansson 1979; Stenseth 1981), and linear programming models (Westoby 1974, 1978; Belovsky 1978, 1984*a*, 1984*b*). Here I evaluate these different models by attempting to answer several questions. Does one of the models predict herbivore diets better? What herbivore and food plant characteristics appear to be important in modeling diet choice? How well does the optimization approach represent actual foraging behavior, given the models' naive approaches?

To compare the three different types of models, each type of model was applied (*a*) either to a data set presented by the model's originators, or to a new data set for the organism for which the model was designed if data collected by the originators was unavailable; and (*b*) to the data sets collected for the other two models. By using data that are appropriate to the model's intent, one can determine if a single best model exists or whether different herbivores might forage in fundamentally different manners that require distinct types of models. If there are differences between the models' predictions and the data, the models can be examined from a theoretical perspective to find an explanation.

METHODS AND EMPIRICAL DATA

Models

Contingency model.—Owen-Smith and Novellie (1982) used the standard contingency model of optimal foraging, CLUE, to ask, “What should a clever ungulate eat?” To analyze optimal diet choice, CLUE can be written as:

$$\frac{e}{t} \geq \frac{s \sum e_i a_i}{1 + s \sum a_i t_i} \quad (1)$$

where s is the animal's horizontal search capability (m^2/min), e_i is the net nutritional content of food i (usually measured in energy [kcal/g; Pyke et al. 1977], although Owen-Smith and Novellie [1982] also use protein content and dry weight for e_i); a_i is the encounter rate with items of food i included in the diet; because herbivores have stationary prey, a_i equals environmental abundance (g/m^2); t_i is handling time for food i (min/g); and e/t is the net nutritional content per unit handling time for a food class. To be included in the diet, the e/t must be greater than the right-hand side of the expression. Equation (1) is solved by starting with food items of the highest e/t and adding items of successively lower e/t until the right-hand side is maximized. CLUE employs Pulliam's (1974) version of the contingency model which, if search energy is unimportant, is identical to all other forms of the contingency model (Schoener 1974) as developed by Schoener (1969, 1971), Charnov (1976a), and MacArthur and Pianka (1966).

Owen-Smith and Novellie (1982) multiply the right-hand side of equation (1) by the term $(1 - f)$, where f is the proportion of the day spent feeding. They employ this modification to account for the inability of animals to feed all day. This modification of equation (1), however, is not used here since its use prevents equation (1) from being a marginal value (marginal values are a requirement for optimization) and consideration of the proportion of feeding time is not necessary when dealing with rates as equation (1) does.

CLUE is the most frequently used optimal foraging model; it has been shown to work for a number of nonherbivores (e.g., bluegill sunfish, Werner and Hall [1974]; great tits, Krebs et al. [1977]; redshanks, Goss-Custard [1977]; shore crabs, Elner and Hughes [1978]). The model's assumptions include: (1) the forager's ability to discriminate between foods on the basis of net energy content or some other nutritional component; (2) the forager's complete knowledge of food abundances (i.e., food is not changing in the short term); and (3) the forager's ability to simultaneously search for all food types (i.e., foods are randomly and independently distributed). Since individual plants within a given plant class i may vary in size and digestibility, Belovsky (1981a) modified equation (1):

$$\frac{e}{t} \geq \frac{s \sum_i \sum_j \sum_k e_{ijk} a_{ijk}}{1 + s \sum_i \sum_j \sum_k a_{ijk} t_i} \quad (2)$$

for food species i ; digestibility j ; items of size k ; and where e_{ijk} is energy/item of i , j , k traits; a_{ijk} is items/ m^2 of foods included in the diet of i , j , k traits; and handling

time, t_i , is assumed constant for all items of plant species i . Although the modification of the CLUE model in equation (2) may be more appropriate to herbivores because of high within-plant species variability (Belovsky 1981a), the standard contingency model was employed in this paper because in most instances within-plant species variability was not known for the model's parameters. Owen-Smith and Novellie (1982) did not utilize this modification in their original analysis for kudu (*Tragelaphus strepsiceros*) foraging. The data on kudu foraging is reported by Owen-Smith (1979) and Owen-Smith and Novellie (1982).

Linear program models.—Belovsky (1978, 1984a, 1984b) used a linear program model, LP, to assess diet selection by moose (*Alces alces*), beaver (*Castor canadensis*), and snowshoe hare (*Lepus americanus*). LP models are optimization models employing constraints to actions which are linear:

$$C \geq \text{ or } \leq \sum c_i x_i \quad (3)$$

where C is a constraint value which cannot be exceeded or must be surpassed; x_i is the quantity of food i consumed; and c_i is a constant that converts x_i into the same units as C . The optimal diet occurs at the intersection of constraint equations or their intersection with the axes. A number of ecologists have examined LP approaches to foraging (Westoby 1974, 1978; Pulliam 1975; Covich 1976; Belovsky 1978) and there exists a well-developed mathematical treatment of this technique (Strum 1972).

LP models have been applied so far only to herbivorous mammals (moose, Belovsky [1978]; snowshoe hare, Belovsky [1984a]; beaver, Belovsky [1984b]; mule deer, Spalinger [1980]). The models assume that: (1) the forager is able to discriminate between foods on the basis of nutritional content (most often energy) and other constraint parameters; (2) the animal has complete knowledge of food abundances and distributions; (3) nonequivalent foods are linearly substitutable by the forager; and (4) the forager may search for food classes either simultaneously (random and independent food distribution) or nonsimultaneously (food patchily distributed). Belovsky (1978, 1984a, 1984b) finds that four constraints are potentially operating: (1) daily energy requirements as satisfied by food energy content; (2) daily feeding time set by thermal physiology as utilized by food cropping rate; (3) daily digestive capacity in wet weight as utilized by food bulk (wet/dry weight); and (4) daily nutrient requirements as satisfied by food nutrient content. To date only sodium has been found to act as a nutrient constraint on herbivore diet choice (Belovsky 1978, 1984a). LP in this paper will be represented by moose (*Alces alces*) foraging (Belovsky 1978), the original test of linear programming. The data for moose foraging is reported by Belovsky (1978, 1981a, 1981b, 1981c) and Belovsky and Jordan (1978, 1981).

Food abundance weighted by net energy content.—Stenseth et al. (1977), Stenseth and Hansson (1979), and Stenseth (1981) used a model of herbivore foraging, SH, based upon the net energy of a food weighted by its abundance. The SH model states that herbivores should select the single food characteristic providing the greatest net energy value weighted by abundance ($\sum G_i$):

$$\sum_i G_i(x, y) = \sum_i d_i(y) F_i(x) x - m(y) \quad (4)$$

where $d_i(y)$ is the inverse of cost of acquisition in terms of time at a given food abundance (y) for food class i (m^2/min); $F_i(x)$ is the abundance of food type i of energy value x (g/m^2); x is the digestible energy value (kcal/g); $m(y)$ is the metabolic rate at food abundance y (kcal/min); and $G_i(x,y)$ is the net energy/ min for food class i of energy content x and abundance y . The algebraic expression of $d_i(y)$ and $m(y)$ follows the CLUE model (see below: Energy intake).

SH employs a model first proposed by Griffiths (1975) for fish feeding on invertebrates. SH models assume: (1) the forager has an ability to discriminate between foods of different energy content; (2) the forager is knowledgeable of food class abundances; and (3) foragers search simultaneously for foods (food is randomly and independently distributed) of different classes i and of the same quality x . The SH model (Stenseth et al. 1977; Stenseth and Hansson 1979; Stenseth 1981) was proposed for foraging by microtine rodents. A complete set of microtine feeding data to test the SH, LP, or CLUE models has not been provided in the literature; therefore, data on *Microtus pennsylvanicus* foraging in Montana was collected as presented in the Appendix.

Model goals.—All three foraging models have two dichotomous goals potentially sought by a forager (Schoener 1971; Pyke et al. 1977; Hixon 1982): (1) *time-minimizer*—the forager attempts to attain some minimum needed intake of the most limiting nutrient in the least amount of foraging time; and (2) *nutrient-maximizer*—the forager attempts to ingest the greatest intake of some nutrient in the available foraging time.

These goals are generally posed with energy as the currency (Pyke et al. 1977; Schoener 1971). Stenseth (1981) proposes a third goal which maximizes nutrient intake in the minimum feeding time, since an animal will often seek the greatest total currency ingested given limited feeding time. This goal, however, is identical with the nutrient-maximizer (Hixon 1982) provided by all three models if feeding time is limited and, therefore, is not a special case.

Each of the two goals has a basis in natural selection (Schoener 1971; Hixon 1982). The time-minimizer, by achieving its minimum nutrient requirements in the least foraging time, presumably will limit exposure to deleterious factors (predators, dehydration, hypothermia, etc.) encountered while foraging and will have more time to devote to advantageous nonforaging behavior (grooming, care of young, mating, etc.). On the other hand, if the nutrient incrementally determines survival and reproductive output, the nutrient maximizer will have greater fitness the more nutrient it ingests. These dichotomous strategies are endpoints along a continuum, and the ecologist's goal is to determine to what extent one of the two endpoints is approached by foraging animals.

DATA

For use in these models, foraging and food availability data for kudu, moose, and *Microtus pennsylvanicus* appear in table 1 and figure 1. All data are presented for major food plant classes (i.e., leaves of shrubs, grasses, herbs, aquatic macrophytes, etc.), which is the simplified approach employed by all three models, rather than for species composition of the diet. Because the *M. pennsylvanicus*

TABLE 1
SUMMARY OF THE DATA USED TO SOLVE THE SH, CLUE, AND LP MODELS
FOR THE FOUR HERBIVORE DATA SETS

| | <i>Microtus</i> ^a Dry Site | <i>Microtus</i> ^a Wet Site | Kudu ^b | Moose ^c |
|---|--|--|---------------------|--------------------|
| Digestible energy (kcal) | 0.07x + 0.65 | 0.07x + 0.65 | 0.08x + 2.16 | ...* |
| <i>t_i</i> (min/g) | | | | |
| Grass | 5.77 | 5.77 | ... | ... |
| Forbs | 2.99 | 2.99 | ... | ... |
| Herbs (grass + forbs) ... | ... | ... | .1 | .09 |
| Shrub leaves | ... | ... | .1 | ... |
| Aquatics | ... | ... | ... | .04 |
| Terrestrial (herbs + shrub leaves) | ... | ... | ... | .054 |
| <i>s</i> (m ² /min) | .04 | .04 | 10.0 | 16.6 |
| Digestive capacity (g-wet/day) | 31.2 | 31.2 | 8296.0 ^d | 32900.0 |
| Food bulk (g-wet/g-dry) | | | | |
| Grass | 1.64 | 1.64 | ... | ... |
| Forb | 2.67 | 2.67 | ... | ... |
| Herbs (grass + forbs) ... | ... | ... | 2.04 ^e | 4.4 |
| Shrub leaves | ... | ... | 2.63 ^e | ... |
| Aquatics | ... | ... | ... | 20.0 |
| Terrestrial (herbs + shrub leaves) | ... | ... | ... | 4.04 |
| Foraging time (min/day) | | | | |
| Predicted | 440.0 | 419.0 | ... | 299.0 |
| Observed | 430.0 | 427.0 | 378.0 | 307.0 |
| terrestrial, 256.0 aquatic, 150.0 ^g | | | | |
| Cropping rate (min/g) | | | | |
| Grass | 45.55 | 38.4 | ... | ... |
| Forb | 21.87 | 19.9 | ... | ... |
| Herb (grass + forbs) ... | ... | ... | .1 | .12 |
| Shrub leaves | ... | ... | .1 | ... |
| Aquatics | ... | ... | ... | .05 |
| Terrestrial (herbs + shrub leaves) | ... | ... | ... | .065 |
| Energy requirements (kcal/day) | 13.9 ^f | 16.9 ^f | 5389.0 ^f | 14000.0 |
| Energy content (kcal/g) | | | | |
| Grass | 2.11 | 2.11 | ... | ... |
| Forb | 2.30 | 2.30 | ... | ... |
| Herbs (grass + forbs) ... | ... | ... | 3.2 ^e | 4.1 |
| Shrub leaves | ... | ... | 3.5 ^e | ... |
| Aquatics | ... | ... | ... | 3.8 |
| Terrestrial (herbs + shrub leaves) | ... | ... | ... | 4.25 |

* Nonapplicable values.

^a This study.

^b Owen-Smith 1979; Owen-Smith and Novellie 1982.

^c Belovsky 1978.

^d From similar-sized ruminants, Belovsky, MS.

^e Belovsky 1978.

^f 140W⁻⁷⁵, Moen 1973.

^g Only 43 min used because of digestive capacity limitations, Belovsky 1981b.

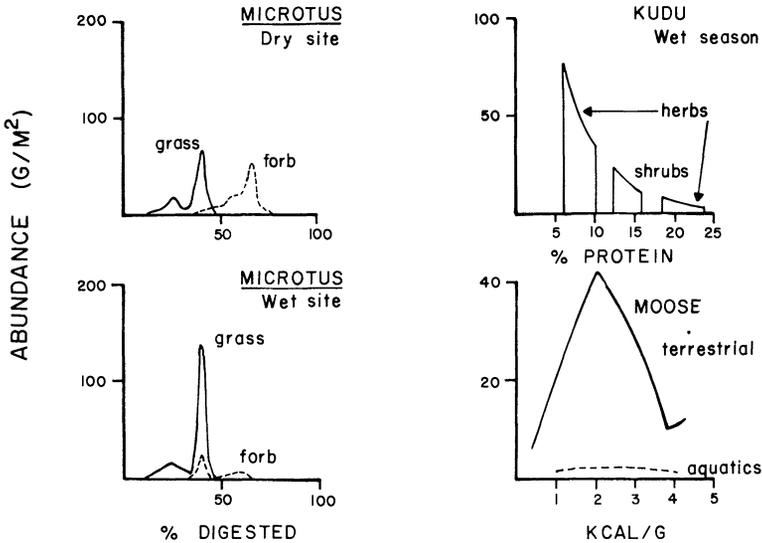


FIG. 1.—Plots of the abundance of vegetation (g/m^2) versus its quality for the four herbivore data sets. Quality is determined as % digestibility by pepsin and acid, % protein or net energy/g. These plots represent the ΣF_i functions of the SH model.

data has not been presented previously, a discussion of its collection appears in the Appendix.

RESULTS

Diet composition can be solved for *Microtus*, kudu, and moose using the data in table 1 and figure 1 for the three foraging models. Figure 2 contains the graphical solutions to the three models for visual comparison of the different approaches. The model for moose was graphically solved using two food classes or dimensions (terrestrial and aquatic vegetation) rather than three as originally presented (Belovsky 1978). This permits a graphical comparison with the other foragers that have two food classes for diet choice (*Microtus*, grass and forb; kudu, herbs and leaves of shrubs). The simplification for moose was achieved by combining two of the original categories, leaves of deciduous plants and herbs, into one terrestrial food class. When the models are compared visually (fig. 2), it is immediately apparent that each model predicts diet on different criteria as expected from each model's assumptions and construction.

1. In two of four cases (kudu and wet-site *Microtus*), the SH model solution is dominated by the plant characteristic that is most abundant (figs. 1 and 2 compared), while only for moose and dry-site *Microtus* does plant quality modify abundance sufficiently to shift the predicted diet to plant characteristics of slightly less than maximum abundance.

2. In all four cases, the CLUE-predicted diet is dominated by plants of the greatest quality rather than abundance.

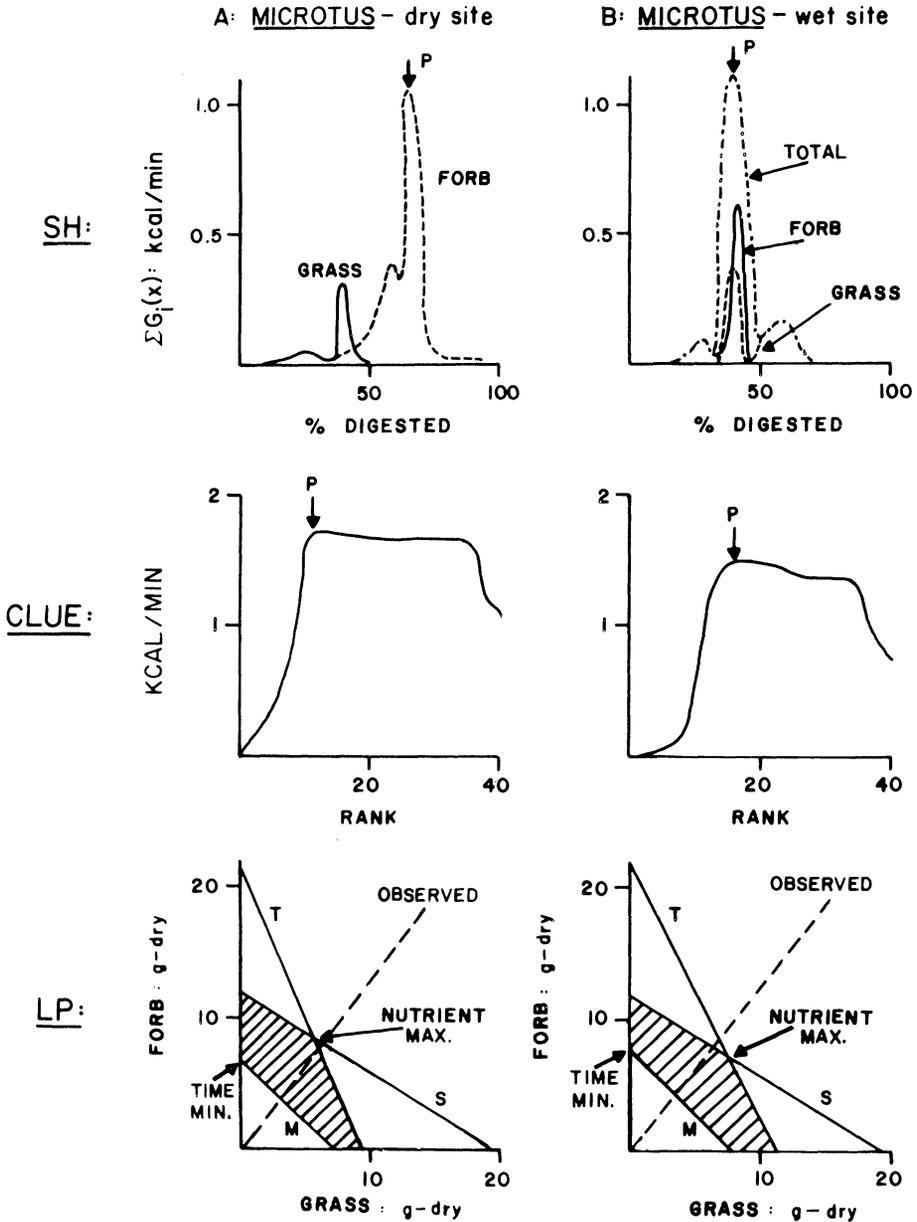


FIG. 2.—Graphical solutions to the SH, CLUE and LP models for the four herbivore data sets. SH model: P is predicted quality of food eaten if specialization occurs on a single food quality (greatest ΣG_i); CLUE model; P is lowest quality food included in the diet; LP model: T is time constraint (moose example: T_A is feeding time for aquatics and T_T , time for terrestrials) (Continued).

C: KUDU - wet season

D: MOOSE

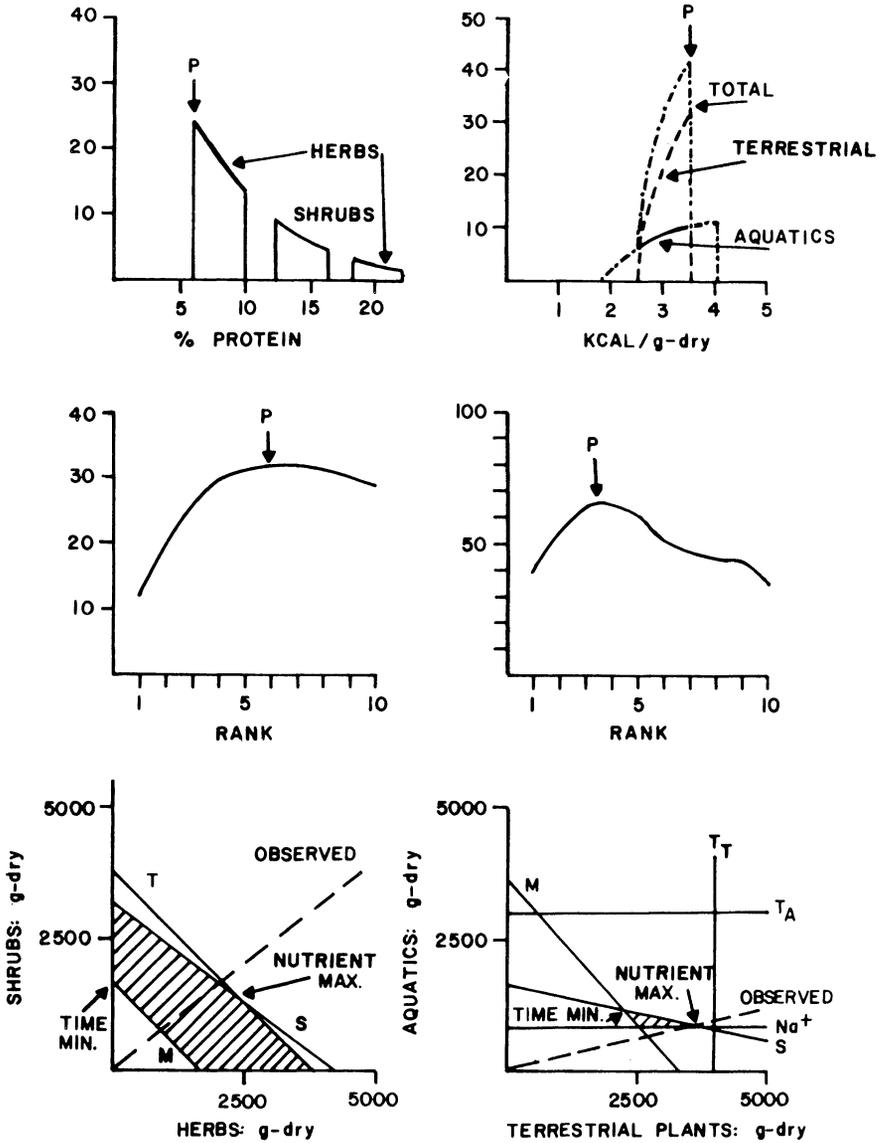


FIG. 2 (Continued).—S is digestive capacity constraint; Na⁺ is sodium requirement constraint; M is energy required for maintenance. Striped region = diets that satisfy the foraging constraints; the time-minimized and nutrient-maximized diets are indicated; dashed line = diet combinations that provide observed diet proportions.

3. In all four cases, the LP model solution that comes closest to the observed diet is that of the nutrient-maximizer, which is determined by the intersection of foraging time (T) and digestive capacity (S) constraints, with the exception that the moose solution also includes a sodium requirement constraint (Na^+).

Table 2 contains the quantitative diet predictions of each model and the observed diets. Using the two *Microtus* data sets, the SH model provides greater diet variability with changes in absolute food abundance than the CLUE or LP models. This occurs because the diets predicted by CLUE and LP are conservatively set by the foods with the highest e/t values or by the intersection of time and digestive constraints, while the SH diet is set primarily by food abundance. Indeed, the observed diets appear quite conservative.

Comparison of diet proportions predicted by each model with observed values indicates that the LP nutrient-maximizing model provides the most probable explanation ($n = 8$: LP nutrient-maximizer, $r^2 = 0.95$; SH, $r^2 = 0.29$; CLUE, $r^2 = 0.11$; LP time minimizer, $r^2 = 0.02$) and the only one which is statistically significant ($P < .05$). Furthermore, it provides a significant correlation with the observed diet of 0.98 for 16 additional herbivore species for which CLUE and SH data are unavailable (Belovsky 1984a, 1984b, MS).

Energy intake is one reason, perhaps the most important, for foraging and one might argue that even if the SH and CLUE models do not predict diet composition very well, they might provide good approximations of energy intake. Table 3 contains the predicted and observed energy intakes. To estimate intake for the SH and CLUE models, the feeding time or digestive capacity constraint was applied depending upon which led to the lower intake, i.e., the herbivore was only allowed to ingest enough food of the model's predicted e/t to utilize either all the amount of time or digestive capacity available, whichever led to less energy ingested.

Owen-Smith and Novellie (1982) entered a digestive constraint into CLUE before diet choice by equating digestive rate with ingestion rate. They argue that e/t values included in the diet in the unconstrained CLUE model will either be restricted to higher e/t values when the unconstrained diet provides more food in available feeding time than the digestive system can process, or expanded to include lower e/t values if the unconstrained diet does not provide sufficient food in available feeding time to fill the digestive capacity. This modification leads to diets that are no longer optimal because the approach does not compare marginal values (g/min), the criteria of mathematical optimization.

Maximum energy intake does not occur when the digestive rate equals ingestion, but at the smaller of the two maximum e/t values provided by the expressions:

$$elt = \begin{cases} (\sum a_i e_i)(\sum a_i d_i) \\ \text{or} \\ s \sum a_i e_i / (1 + s \sum a_i t_i) \end{cases}$$

where d_i is the digestive rate for food i (g/min). The first expression reflects diet choice if digestive capacity is limiting and the second expression reflects diet

TABLE 2

PERCENTAGE OF DIFFERENT FOOD CLASSES IN THE DIET PREDICTED BY THE CLUE, SH, AND LP MODELS FOR THE FOUR HERBIVORE DATA SETS AND COMPARED WITH OBSERVED DIETS. (Values in parentheses for the SH model indicate the diet if the herbivore specializes on only one food class's quality with the highest G_i value, rather than all food classes with the quality providing the greatest ΣG_i .)

| | % OF DIET | | | | Observed |
|---------------------------|-----------|----------|-------------------------|-----------------------------|-----------------|
| | CLUE | SH | LP Time Minimizer | LP Nutrient Maximizer | |
| <i>Microtus</i> —dry site | | | | | |
| Grass | 0 | 0(0) | 0 | 41 | 47 ^a |
| Forb | 100 | 100(100) | 100 | 59 | 53 |
| <i>Microtus</i> —wet site | | | | | |
| Grass | 0 | 85(0) | 0 | 49 | 45 ^a |
| Forb | 100 | 15(100) | 100 | 51 | 55 |
| Kudu—wet season | | | | | |
| Herbs | 41 | 100(100) | 0 | 61 | 67 ^b |
| Shrub | 59 | 0(0) | 100 | 39 | 33 |
| Moose | | | | | |
| Terrestrial | 71 | 75(100) | 78 | 82 | 82 ^c |
| Aquatics | 29 | 25(0) | 22 | 18 | 18 |

^a This study.

^b Owen-Smith 1979; Owen-Smith and Novellie 1982.

^c Belovsky 1978.

TABLE 3

ENERGY INTAKES PREDICTED BY THE CLUE, SH, AND LP MODELS AND OBSERVED ENERGY INTAKES FOR THE FOUR HERBIVORE DATA SETS

| | kcal/day INGESTED | | | | Observed |
|---------------------------------|-------------------|---------|-------------------------|-----------------------------|-----------------------|
| | CLUE | SH | LP Time Minimizer | Lp Nutrient Maximizer | |
| <i>Microtus</i> —dry site | 26.9 | 16.5 | 13.9 | 30.9 | 29.8 ^a |
| <i>Microtus</i> —wet site | 23.0 | 17.3 | 16.9 | 31.8 | 29.8 ^a |
| Kudu—wet season | 11732.0 | 10832.0 | 5389.0 | 12121.0 | ~13000.0 ^b |
| Moose | 13366.0 | 14044.0 | 14000.0 | 15458.0 | 15861.0 ^c |

^a This study.

^b Owen-Smith 1979; Owen-Smith and Novellie 1982.

^c Belovsky 1978.

choice if the feeding time constraint is encountered before the digestive constraint. Figure 3 contains the solution for the maximum elt and Owen-Smith and Novellie's (1982) solution for the kudu, showing that the true maximum can lead to broader or more restricted diets than predicted by Owen-Smith and Novellie (1982).

Energy intake for generalist herbivores was always most closely predicted by

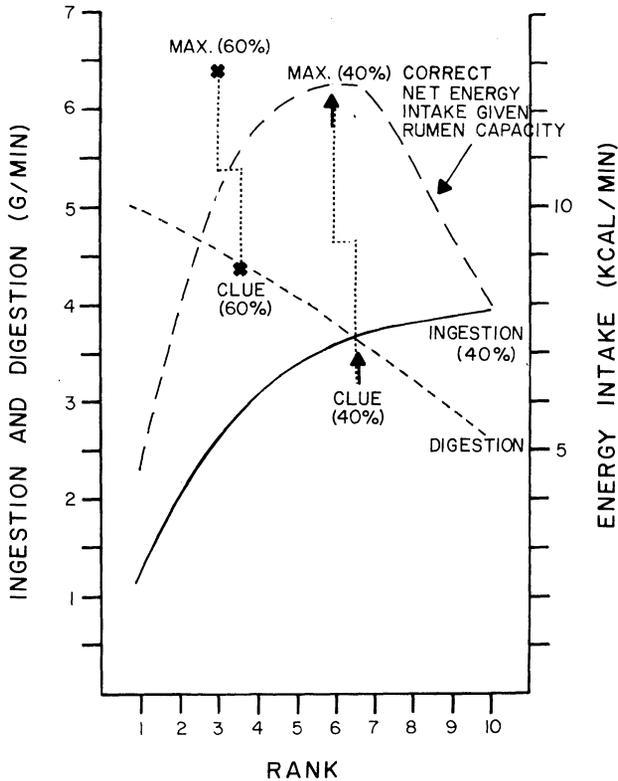


FIG. 3.—Owen-Smith and Novellie (1982) include a digestive capacity constraint for kudu in the CLUE model. Their solution occurs at the intersection of ingestion (—) and digestive turnover rates (---). The graphical solution is presented only for feeding time equal to 40% of a day. Also plotted is net energy intake for different diet breadths, given the correct inclusion of a digestive capacity constraint (—) (see text). Correct maximum energy intake is compared with predicted values for other percentages of feeding time (deviations: ····, with vertical and horizontal distances reflecting errors in elt and diet breadth, respectively).

the LP nutrient-maximizing model (\bar{x} deviation from observed = +0.3%, mean overall deviation regardless of sign = 5%). Also, the CLUE model does considerably better than the SH model (\bar{x} and overall deviation = -14% vs. -33%). The SH model does the worst in three of the four cases (moose and both microtines), with these herbivores barely obtaining maintenance and reproductive energy requirements.

What is the sensitivity of the models to errors in parameter estimation? The parameters of the LP model can be varied to determine the sensitivity of the predicted diet. In the cases examined here and elsewhere (Belovsky 1978, 1984a, 1984b), the variation in parameters would have to be very large (variation greater than 20%) for the predicted diet to deviate more than 10% from the observed diet.

The CLUE and SH models are even less sensitive because their determinations are based more on relative rankings of food rather than absolute food values (MacArthur and Pianka 1966).

DISCUSSION

A number of reasons for the observed predictive qualities of the three models arise from biological considerations.

Foraging constraints (digestion, foraging time, and nutrition) are the major differences between the LP model and the SH-CLUE models. Belovsky (1978) and Westoby (1974, 1978) indicate that herbivorous mammals are faced with some foraging difficulties arising from their physiology. Foremost among these problems is their need to digestively process plant foods within a limited organ capacity for greater time periods than required for animal tissue, fruit, etc. This arises from the structural components (e.g., cellulose) in plant tissue and leads to a digestive capacity constraint, because the food is of low nutritional value per unit of bulk.

The digestive constraint also influences foraging time limits (Belovsky 1981*a*) because the herbivore cannot forage if its digestive organ is full. This processing limit to foraging time must be incorporated into other limitations on feeding time such as the thermal environment (Belovsky 1981*a*). In fact, the microtine examples in this paper (table 2) and the moose feeding times (Belovsky 1981*a*) appear to be predominantly determined by thermal physiology and environment; Owen-Smith and Novellie (1982) also suggest thermal limits to feeding time for the kudu.

Nutritional constraints may arise for herbivores since plants often are nutritionally inadequate, i.e., the relative abundance of components in plant tissue is not the same as in the forager's tissues (Westoby 1974, 1978; Freeland and Janzen 1974; Belovsky 1978; Belovsky and Jordan 1981). The authors of both the SH and CLUE models suggest that their models can be used with currency other than energy (e.g., protein: Owen-Smith and Novellie 1982), but then energy must be eliminated from the solution to the model. Only the LP model permits simultaneous treatment of energy and other nutrients and/or toxins.

Nonsimultaneous search is assumed in the LP model, as developed here. McNair (1979) points out that relaxation of the simultaneous search assumptions in the CLUE model can lead to radically different optimal diets, especially if the foods are clumped. This may account for the success of the LP nutrient-maximizing model and failure of the CLUE model to predict diets for herbivorous mammals. Plants in the various food plant classes should grow under different microenvironmental conditions leading to one plant class dominating in an area, i.e., patches of grass versus forb, aquatic plants versus terrestrial plants, woody vegetation versus meadows, etc. The moose example (Belovsky 1978) is most obvious in this respect since aquatic vegetation occurs in ponds, and for the most part, deciduous leaves occur in forests and herbaceous plants in distinctly isolated forest openings. Indeed, Owen-Smith and Novellie (1982) state that spatial heterogeneity in plant distributions may explain why their CLUE model does not predict kudu diets very well.

The foraging goal of the three herbivores considered here appears to be nutrient maximization with energy as the currency, since this LP solution predicts observed values best. These herbivores may maximize their nutrient intake to survive either long- or short-term energetic deficiencies. The deficiencies may arise from low energy content per unit of stomach fill or low food abundance and may account for the low body fat content of wild herbivores.

To characterize foragers as time minimizers and nutrient maximizers is not trivial, as Hixon (1982) recently pointed out. If an animal achieves a nutrient steady state (no net body weight change) over a year, it might be a nutrient maximizer or a time minimizer under two different circumstances. (1) For the nutrient maximizer, periods of nutrient intake above requirements are followed by periods during which maximum possible nutrient intake equals or is surpassed by requirements. (2) For the time minimizer, nutrient intake in each period equals requirements for that period. A mix of the two strategies, and perhaps the most realistic case, could occur if an animal maximizes nutrients during some periods so it can behave as a time minimizer in other periods (e.g., breeding season).

Each of the studies reported here was carried out in the season of greatest food abundance and nutritional quality. Therefore, because the herbivores' diets are predicted best by nutrient maximization, they appear to follow either a nutrient-maximizing strategy or a mixed strategy to survive times of lower food availability.

Optimality criteria are mathematically satisfied by the CLUE and LP models (von Neuman and Morgenstern 1944) given their assumptions (Schoener 1971; McNair 1979; E. Charnov, MS). On the other hand, the SH model has the same assumptions as the CLUE model but it also assumes that only one food value is consumed. If and only if, the term $d_i(y)$ of the SH model equals $s/(1 + s\sum a_i t_i)$ of the CLUE model and $m(y)$ equals $s\sum a_i C_s/(1 + s\sum a_i t_i)$, where C_s is the energetic cost of search added to the CLUE model, will the SH model equal the CLUE model based on the inclusion of a single food. The problem with the SH model is that the inclusion of only the single food class with the highest product of energy content and abundance may only on occasion be the optimal diet and generally is not optimal, since a variety of foods may produce a higher e/t . Therefore, the SH model when analyzed mathematically does not satisfy the criteria of mathematical optimization. This may explain SH's poor predictive capabilities. Furthermore, abundant foods will tend to be included in the diet, no matter what optimization criteria are employed, and SH simply reflects diet selection based on abundance.

Under what circumstances might the SH model be appropriate? If the animal were to feed on only one food quality as assumed in the SH model, a conspecific that took a diet as predicted by the CLUE model would choose a diet with the highest nutrient content/handling time providing the highest relative fitness, i.e., ingest more of a nutrient or attain minimum nutrient requirements in the least time. The SH diet would lead to equal fitness only if the CLUE diet happens to include the single food which has the highest product of nutrient content and abundance (nutrient/handling time). The SH model often leads to the exclusion of the highest quality foods from the diet since they tend to be of lower environmental abundance, while the CLUE model often includes foods of the highest quality.

Therefore, it seems likely that the exclusion of high quality foods can only be evolutionarily maintained by group selection, violating the Darwinian concept of individual selection, or by risk factors (Caracao 1980; Levins and MacArthur 1969) which are not considered in the SH or CLUE models.

General characteristics of herbivore diet selection emerge from the above analysis. First, foraging time and digestive capacity constraints appear to be the most important factors influencing diet choice. Spalinger (1980) had only limited success in applying the LP model to mule deer (*Odocoileus hemionus*) foraging. Spalinger's (1980) difficulties may have arisen for a number of reasons: he attempted to describe the plant species composition of the diet rather than plant classes; he did not include a feeding time constraint; and he used a digestive capacity constraint based upon dry rather than wet weight. In each of the LP solutions presented here, a time constraint was used and the digestive capacity constraint was constructed in terms of wet weight versus food bulk. Hanley (1980) argues that digestive capacity constraints should be presented in terms of dry weight and differing food class passage rates; indeed Owen-Smith and Novellie (1982) take this approach. This question is in no way resolved because the physiology of this process is still in debate (Baile and Forbes 1974; Belovsky 1978; Hanley 1980). A pragmatic view can be taken here by stressing that the use of a constraint based on wet-weight digestive capacity, as filled by food bulk, successfully predicts diet, while that based on dry-weight capacity, as made available by variable digestive rates, does not work (i.e., the kudu case).

Another question remains concerning the species composition of each plant class included in the diet. Belovsky (1981*a*, 1984*a*, 1984*b*) has shown that the foraging for the constituent species composing each food class meets the assumptions of simultaneous search, but diet selection does not maximize elt as proposed by the CLUE model. Rather, the herbivores appear to select all plants within a species that possess digestibility and item size characteristics (i.e., leaf weight, twig weight, etc.) greater than minimum digestibility and item size values needed by the forager to supply energy or other nutritional requirements. The available foraging time and digestive capacity values are allocated to each food class by the LP model's energy-maximizing solution.

This level of herbivore foraging is not optimal, but is "risk averse" (*sensu* Caracao 1980). "Risk-aversion" may arise when an herbivore does not have the behavioral ability to synthesize all the information necessary to solve an optimality problem and therefore will have a fairly large probability of making mistakes. Therefore, attempting to avoid mistakes, although not as good as an optimal diet if no mistakes are possible, may provide a better diet than the optimal diet given the likelihood of mistakes. For example, a moose (Belovsky 1981*a*) would have to integrate information on leaf weight and quality for over 20,000 leaf items or more than 2,000 mouthfuls of food per day. The *Microtus* in this paper would have to synthesize information on over 310 items or over 3,000 mouthfuls. This level of information synthesis may simply be too great.

The distinction between the above two levels of herbivore foraging (quantity of each food class in the diet versus its species composition) is important. The quantity of each food class in the diet appears to follow an optimal foraging model

(LP) which in many respects is similar to patch selection models (Charnov 1976*b*), since nonsimultaneous search is required for plants that are clumped in their distribution. The species composition of each diet class, however, poses a problem more similar to the traditional diet models of optimal foraging (CLUE), but the herbivores appear to forgo optimization at this level for "risk aversion."

Stenseth (1981) used the SH model to make general feeding predictions for herbivores and to show why he believed the SH model was more appropriate for herbivores than the CLUE model. Since the SH model not only does not reliably predict herbivore diets but also is theoretically implausible, general statements based on the SH model are not tenable. Two major generalizations arising from LP are: (1) Both the relative and absolute abundances of each food class are important in determining the LP model diet. Relative abundance of each food class is far more important in the CLUE than LP model because of simultaneous search in CLUE, while the LP diet depends heavily on the absolute abundance of each food as related to their cropping rates under nonsimultaneous search. The SH diet trivially has to be a function of absolute abundance because it is the weighting value used to predict diet.

2) Herbivores will specialize and take only one food class, assuming two food classes in the LP model, if one food is prohibitively costly in terms of either foraging time or its filling of the digestive organ. Stenseth (1981) maintains that specialization arises with high food abundances since the cost of food acquisition in terms of time should be reduced. This is but one of several ways that specialization might emerge in the LP model; indeed, food abundance can lead to specialization or a broadening of diet depending on relative constraint values for the two food classes. Therefore, simple predictions concerning specialization with changes in food class constraint parameters cannot be made, and the necessary conditions for specialization can emerge from factors other than increases in abundance (e.g., plant growth forms which influence the herbivore's ability to crop food). Finally, Stenseth and Hansson's (1979) claim that microtine stomachs dominated either by forbs or grasses indicate phenotypic specialization is not valid since a single stomach can be filled in a meal which easily could be a single forb plant or grass clump encountered (approximately 2 g wet wt).

Last, we must ask how general are the models for all herbivore taxa? Sufficient data to test all three models was available for only three mammal species. Perhaps the foraging of other species does not agree with these results; however, sufficient data to test the LP model is available for an additional 16 species of generalist herbivores, indicating a high degree of predictive success using the LP-nutrient maximizing model as found here (Belovsky, 1984*a*, 1984*b*, MS). Of other terrestrial herbivores, insects are most important and their feeding is questionably explained by the models presented in this paper; however, the diets for four species of orthopterans appear to fit LP model predictions (Belovsky, MS). Orthopterans, however, are generalist feeders, while many insects are specialists (i.e., most Lepidoptera). Perhaps the LP model only applies to generalists and a model that examines the costs of making foraging mistakes (i.e., deviating from a specialized diet) is more appropriate for specialists such as Lepidoptera (Levins and MacArthur 1969).

SUMMARY

Three models of herbivore foraging are tested in this paper: contingency models (Owen-Smith and Novellie 1982), nutrient content weighted by food abundance (Stenseth and Hansson 1979), and linear programming (Belovsky 1978). The models are tested using data from two microtine populations, kudu, and moose. In all four cases, the linear programming model solved for nutrient maximization best predicted the diet composition by food classes (grass, forb, etc.) and energy intake. Foraging time and digestive capacity are the two most important constraints in the linear programming model.

Contingency models do not appear to predict herbivore diets for several reasons. First, either they often do not contain constraints or the constraints are incorrectly applied. Second, simultaneous search is assumed which may not hold for plant foods. The results presented here contradict Owen-Smith and Novellie's (1982) claim that linear programming is a special case and the contingency model is a representation of herbivore diet choice. Finally, the model of food energy content weighted by abundance might not be expected to work a priori, because it is not an optimal foraging model. In addition, this model's diet predictions are dominated by food abundance. Furthermore, Stenseth's (1981) claim that linear programming is similar to this model is shown to be incorrect.

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APPENDIX
MICROTINE DATA

Study sites.—*Microtus pennsylvanicus* foraging was studied at two sites at the National Bison Range, Montana. One study site (820 m elevation) is bordered by a creek and pond, maintaining wet conditions, and was studied from June–September 1979. This site is dominated by grasses (84%) and has a very large standing crop biomass of green vegetation ($635 \text{ g/m}^2 \pm 299$). *Poa pratensis* (67%) is the dominant grass with *Agropyron spicatum*, *Agrostis alba*, *Agropyron repens*, and *Carex* sp. also relatively abundant (>5%). The most abundant forbs are *Solidago* sp. (67%) and *Cirsium arvense* (31%).

The other study site is located on a tableland (850 m elevation) above the wet site, and is far drier. It was studied from June–September 1981. The vegetation is about equally divided between grass (52%) and forbs, with a lower standing crop of green vegetation ($460 \text{ g/m}^2 \pm 186$) than the wet site. The grasses are dominated by *Poa pratensis* (62%) and *Agropyron smithii* (37%), while forbs are dominated by *Cirsium arvense* (51%), *Aster falcatus* (35%), and seedling *Symphoricarpos occidentalis* (10%).

Each site covers approximately 0.1 ha; this area was chosen as large enough to contain a representative *Microtus* population and small enough to ensure a relatively homogeneous plant community. Within each area during August, 10 0.25-m² plots were set out along a

transect running the length of the study site (50 m) and the vegetation within each plot was clipped, separated by species, oven-dried, and weighed. This provided the vegetation analysis.

Microtus diet.—During July and August, 1979, 22 *Microtus* were snap-trapped (minimum of 10/mo) in the wet site and from June through August, 1981, 50 were trapped at the dry site (minimum of 14/mo). The animals were weighed and sexed, their stomachs and caeca were removed and weighed, and the stomachs were saved for diet analysis. Stomach contents were dried and ground through a 20-mesh Wiley mill. Five slides of the contents from each stomach were made according to the procedures reported by Hansen et al. (1977). The same procedures were followed in preparing reference slides of the available plants. On each slide, 25 fragments were identified to plant species if possible (22% identifiable to species) and almost always to grass versus forb. Our success in identifying fragments to species was similar to Hansson's findings (1970).

Microtus behavior and physiology.—Microtines are difficult to observe in the wild because they are small and secretive, especially in dense vegetative cover. Therefore, to make behavioral and physiological measurements, captive *Microtus* were maintained in glass terraria (38 liters with a floor of 0.2m²). To measure daily feeding time and cropping rates on different plants, *Microtus* (1 *Microtus*/terraria, 2 terraria) were allowed to feed for 4 h on a 0.2m² piece of sod with vegetation from the respective study sites which was placed in the terraria. The sod samples were chosen at random from within the study sites in an attempt to insure that the microtines encountered all plant classes in the frequency of their occurrence in the environment over all trials. The *Microtus* can be observed in the terraria during the day and at night with subdued light or red light.

The LP model requires a measure of total daily feeding time. This was determined by watching the microtines in the terraria over extended periods (>4 h). These periods were chosen so that every 4-h period during a complete day was sampled twice; the time spent feeding per day was based on the total time of observation (48 h: 24 h with sod from each study site.) Belovsky (1981a) pointed out that a measure of maximum daily feeding time arrived at independently of the forager's observed feeding time is necessary, if one is to argue that the forager is a nutrient maximizer. To provide such an independent estimate, Belovsky (1981b) developed a model in which the forager's thermal physiology is used in a thermodynamic model (Porter and Gates 1969) to measure heat fluxes, which are then used in a dynamic programming optimization model (Bellman and Dreyfus 1962) to predict where and what an animal should do at each hour. A preliminary analysis of such a model for the microtines indicates that they forage for the maximum time allowed by thermal considerations (observed time = 430 and 427 min/day for the two sites, while predicted time = 440 and 419 min/day; G. Belovsky, unpubl. data).

During the observations of daily feeding time, cropping rates were measured by recording the number of items consumed within a 2-min period. Observations were restricted to those 2-min periods in which either only grasses or only forbs were consumed, thereby providing intake rates for grasses and forbs separately (samples of 2-min observation periods for the wet site: $n = 30$ for grasses and $n = 8$ for forbs; for the dry site: $n = 20$ for grasses, $n = 10$ for forbs). Multiplying the item ingestion rates by the average weights of items observed to be eaten provided the cropping rate in g-dry wt/min, as required by the LP model. Pieces of sod containing only grasses or forbs were not selected for these trials since it was desirable to provide the microtines with dietary choices and this was satisfied by the random choice of sod pieces. Also, during the 68 2-min observation periods the horizontal search ability of the microtines, s (m²/min), was computed as distance traveled times the width of the animal divided by the time to move the distance. Distance was measured using a 2-cm grid system.

The minimum cropping time or handling time for the SH and CLUE models was measured by providing microtines with either only cut grasses or only cut forbs ad libitum. A mixture of the species of grasses or forbs present in the study areas was included in the ad libitum food supplies. This minimum cropping rate was measured during 2-min periods of uninterrupted feeding, as above (samples of 2-min periods, $n = 40$ for grasses and $n = 10$ for forbs).

Digestive physiology parameters were measured using captive *Microtus*. Dry matter digestibility (1 - g dry feces/g dry ingested food) of food plants was determined by feeding captives four plant species, each separately: *Tragopogon dubius*, *Melilotus* sp., *Poa pratensis*, and *Agropyron smithii*. These digestibility values are correlated with the chemical digestion of the plants in 0.1 N HCl and pepsin (Terry and Tilley 1964), a simulated digestive process:

$$DM = 0.015P + 0.135 \quad (n = 12, r^2 = 0.85, P < .01) \quad (5)$$

where *DM* is the fraction of dry matter digested by the microtines and *P* is the fraction of dry matter digested by acid-pepsin. The clipping plot plant samples (see above) were digested by the acid-pepsin technique (5 samples/species), and because of the measured correlation between actual digestion and the acid-pepsin digestion, these values were used to rank the foods by quality (figs. 1a, 1b).

The LP model required knowledge of microtine digestive capacity. Static digestive capacity was measured as the weights of stomach and caecal contents (see above), the digestive organs of caecal digestors (McBee 1971), multiplied by the daily turnover of contents. Turnover rate was obtained using Storr's (1963) technique: captive animals are fed until satiated, the food is removed, the captives are sacrificed over a period of time (5 h) at regular intervals (30 min), and the stomach-caecal contents are weighed to obtain changes in contents from a condition of satiation. Fifty animals were used (5/period), providing a turnover rate of 8.1 times/day, similar to the 7.8 times reported by Lee and Horvath (1969).

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