Generalist Herbivore Foraging and Its Role in Competitive Interactions[1]

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Synopsis. Whether herbivores are food limited and compete interspecifically for food has been debated by population/community ecologists. To examine this proposition, a mechanistic approach based upon autecological observations is employed:

1) 45 foraging studies of 20 species of generalist herbivores indicate that the herbivores behave as energy maximizers in their diet selection, as determined by a linear programming model.

2) The constraints that determine the forager's energy maximizing diet can be used to determine whether a food item should be consumed, based upon a minimum digestibility that determines energy value and a minimum item size or abundance that determines cropping rate.

3) Population densities of a number of herbivore species depend upon the biomass of plants in the environment that satisfy the minimum characteristics sought by the herbivore.

4) Using experimental populations for several herbivore species that are known to be food limited, it can be demonstrated that these species compete with each other. The competitive isoclines are non-linear and arise from the fractions of each forager's food resources that it shares and exclusively uses, which depend upon each species' minimum food characteristics.

The results indicate that a mechanistic approach can provide considerable insights into herbivore community structure. The foraging constraints underlying the entire analysis may be body size dependent, providing a more general view.

Introduction

Community ecologists strive to understand the reasons that plant and animal species vary in their distributions and abundances, and how they are assembled into biological communities. This quest has ranged from "holistic-supraorganismic" views (*e.g.*, Odum, 1969; Patten, 1982) to reductionist autecological explanations (*e.g.*, Hutchinson, 1959; Brown, 1981) to the invocation of chance (*e.g.*, Strong *et al.*, 1979; Simberloff, 1983). Interest in this question and the various explanations continues. The evolutionary ecology approach as formulated by G. E. Hutchinson (1959) in his "Homage to Santa Rosalia" is a reductionist community ecology protocol that is based upon "building blocks" arising from species autecology and interactions, as presumably formed by natural selection (Brown, 1981). Although not beyond criticism (Brown, 1981; Lewin,

1983*a*, *b*), this latter approach has had some success and is attractive in its explanations.

Attempts to define sets of "building blocks" from autecology and species interactions that determine the assembly rules for species in a community should be concerned with two qualities. A wider range of species than congeners should be studied and these species should account for a substantial portion of energy/matter transfers in the ecosystem, if we are to claim that the "building blocks" are of general importance to ecological systems. With these qualities in mind, the guild of generalist herbivores, those herbivores that consume a wide range of plant parts and species, in various communities was studied using the "building block" approach for the following reasons. First, the natural history, physiology and anatomy of the taxonomically diverse generalist herbivores have received considerable attention from both theoretical and applied ecologists. This information provides an initial data base, even though disagreements exist on such basic matters as the details of digestion of plant tissue in ruminant and caecal digestive tracts (*e.g.*, McBee, 1971; Baile

and Forbes, 1974; Belovsky, 1984a). Second, generalist herbivores are the major consumers of primary production in many ecosystems (e.g., Lock, 1972; Chew, 1974; Mattson and Addy, 1975; French et al., 1979; McNaughton, 1979; Norton-Griffiths, 1979; Scott et al., 1979), making them an important component of energy/matter transfers.

Background

Two alternative hypotheses for the structure of generalist herbivore communities can be found in the ecological literature. Hairston et al. (1960) and Slobodkin et al. (1967) proposed that the distributions and abundances of herbivores are limited by predation, not food plant abundance. This hypothesis was derived from the simple observation that the world would not be green if herbivores were food limited, because massive defoliation would otherwise occur. In contrast, other ecologists suggest that herbivores are food limited and the reason that the world is green is because all plants are not edible, due to either nutritional unacceptability or toxicity from secondary compounds (Van Valen, 1973; Fretwell, 1977). Therefore, to study the assembly rules of generalist herbivore guilds (hereafter called "herbivores"), we are faced with the alternatives of studying either their predators or their foraging behavior, if we subscribe to simple alternative explanations.

There is increasing evidence that some populations of herbivores, especially vertebrates, may be food limited (e.g., Sinclair, 1975, 1979; White, 1976, 1978; Hansson, 1979; Hilborn and Sinclair, 1979; Belovsky, 1981; Caughley and Lawton, 1981). One might argue that many of these studies deal with larger mammalian species, whose predators have either been exterminated or seriously reduced in number by man; however, some of the studies indicate food limitation at sites known for their predator–prey interactions (e.g., Serengeti, East Africa, and Isle Royle National Park, Michigan). Furthermore, some cases of accepted predator limitation for herbivores have been questioned and food limitation has been offered as an equally plausible explanation (e.g., Kaibab deer herd, Caughley [1970]).

A search of the literature provides a compilation of biomass and species number values for large (> 1 kg) non-arboreal mammalian herbivores from different sites in the world. Non-arboreal herbivores were selected because they afforded the larger sample size. There is a positive correlation between an area's primary production and herbivore biomass/species number (Fig. 1A, B). In forested areas, primary productivity is restricted to the shrub/sapling/herb layer excluding the canopy which is beyond reach of the herbivores. This was accomplished using values reported in the literature for comparable plant communities (Ovington, 1962; Bray and Dudkiewicz, 1963; Odum, 1969; Whittaker, 1970; Garg and Vyas, 1975; Klinge et al., 1975; Malaisse et al., 1975). Even though large predator abundance and diversity are also correlated with primary productivity, this global comparison suggests that herbivores are food limited, and their diversity (species number) is associated in some unknown fashion with food abundance.

If food does limit herbivore populations and guild organization, we must understand herbivore food choices. This leads to an additional set of simple alternative hypotheses: food choice based upon energy/nutrition or upon food plant toxicity/herbivore detoxification ability. These are not strictly alternatives; however, different researchers tend to emphasize one over the other (e.g., Freeland and Janzen, 1974; Westoby, 1974, 1978; Gilbert and Raven, 1975; Feeny, 1976; Rhoades and Cates, 1976; Rosenthal and Janzen, 1979; Owen-Smith and Novellie, 1982; Belovsky, 1984a). Because of these different emphases, I have limited the analysis to herbivores that select a general rather than a specialized diet. Specialists such as many lepidoptera appear more likely to select diets primarily on the basis of plant toxicity and detoxifying abilities; while generalists, although their food choice is potentially limited by toxins (Freeland and Janzen, 1974), may be more strongly influenced by energy/nutrition considerations (Belovsky, 1984a). The
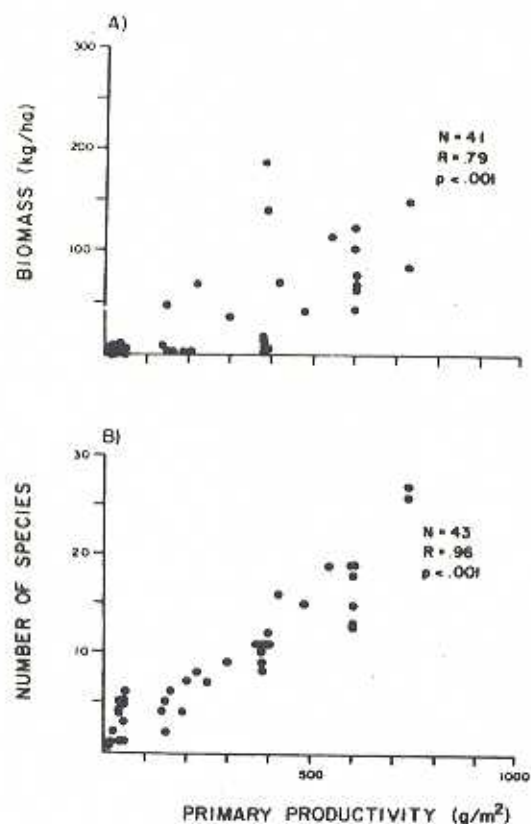
FIG. 1. A) Biomass density of non-arboreal herbivores weighing more than 1 kg *versus* primary productivity in the shrub/sapling/herb layer of plant communities. B) Species number of non-arboreal herbivores weighing more than 1 kg *versus* primary productivity in the shrub/sapling/herb layer of plant communities. (References: 0–21.)
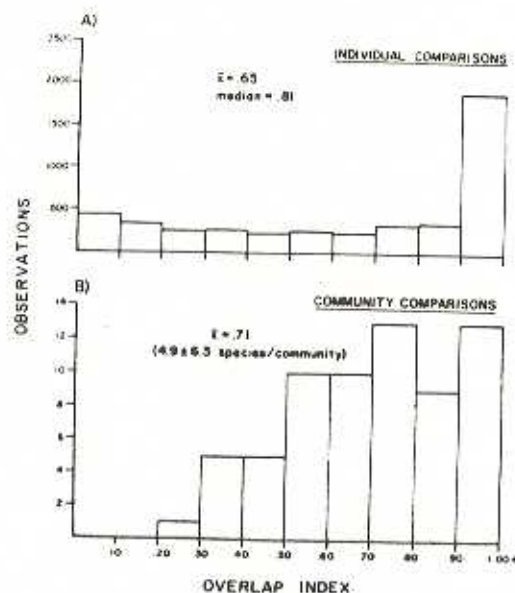

FIG. 2. A) Distribution of values of Levin's (1968) overlap index based on plant growth forms (*e.g.*, twigs, leaves, grass, etc.) for 4,454 pairs of generalist herbivore species. The mean and median overlap values are also presented. B) Distribution of average values of Levin's (1968) overlap index based on plant growth forms (*e.g.*, twigs, leaves, grass, etc.) for all the herbivores reported in a single community (a single study site). The mean overlap value and the average number of species for a community are also presented. (References: 1, 2, 7, 9, 13, 17, 22–108.)

more predictable nature of energy/nutrition considerations lends itself to a "building block" approach for generalists, in comparison to the specific detail required to understand toxicity characteristics (Belovsky, 1984a). If food is limiting to herbivore populations, a logical explanation for guild organization is competition for food.

From a compilation of 74 herbivore diet studies of two or more sympatric species (4,454 species-pair comparisons from 74 sites), we can use an index of diet similarity (*i.e.*, Levins, 1968) to indicate whether herbivores commonly feed upon the same food plants and might compete. These overlap measures were based upon plant growth

forms included in the diet (*e.g.*, grasses, forbs, deciduous leaves, and twigs). Growth form was used since not all studies examined the diet's species composition, and in many cases diet sample sizes did not justify a resolution to species composition. A very high degree of diet similarity is found for generalist herbivores on the basis of sympatric species pairs (Fig. 2A) and the average for all sympatric species (Fig. 2B).

The apparent common basis of food choice by herbivores may reflect the potential of competition to shape herbivore guilds. However, high overlap also may indicate the absence of competition (Vandermeer, 1972; Strong, 1983), permitting the sharing of common resources. Therefore, we cannot necessarily use these data with correlation analyses, as commonly employed in community ecology, to understand the structure of generalist herbivore guilds in an unambiguous fashion.

An approach involving the study of autecological and species interaction "building blocks" might provide explicit expressions for population dynamics and the interaction between populations (mechanistic models) to help understand the structure of herbivore guilds. To follow this approach, the answers to three questions may be useful:

1) Do herbivores have a common foraging goal?

2) Do herbivores select foods by a common set of criteria?, and

3) Can these foraging goals and criteria be used to understand competition between generalist herbivores, if they are food limited?

I hope to answer these questions and determine whether a general hypothesis of herbivore evolution and guild assembly can be constructed.

Answers to the questions

1) *Do generalist herbivores have a common foraging goal?*

Optimal foraging theory provides a potential starting point to address this question. Belovsky (1984a) points out a series of potential differences between herbivores and non-herbivores that must be evaluated in developing foraging models. These differences include constraints on herbivore foraging behavior and the distribution of food items in the environment.

Herbivores potentially may be confronted by four constraints on their foraging behavior: daily digestive capacity, daily feeding time, daily energy demands, and daily nutrient requirements. The first two constraints provide upper limits to an herbivore's actions, while the latter two define lower limits.

In many environments food plants within different growth forms (grasses, forbs, browse, etc.) are found to be contagiously (patchily) distributed. In addition, these patches of different growth forms are negatively associated with each other (Belovsky, manuscript) because each growth form tends to be better adapted to different microhabitats. This necessitates an herbivore foraging upon one growth form at a time because of their spatial separation into

patches. Therefore, an herbivore must make decisions to forage on one growth form (patch) or another in a given time period (non-simultaneous search) because it cannot be in two places at once. This type of time constraint is unlike that (simultaneous search) in most other foraging models (Schoener, 1971; Pyke *et al.*, 1977).

The foraging of an herbivore can be predicted for two alternative goals: feeding time minimization or energy/nutrient maximization (Schoener, 1971). A feeding time minimizer attempts to satisfy its energy/nutrient demands in the least amount of time; presumably because more time spent in other activities (*e.g.*, mating, grooming, offspring care, etc.), and less exposure to predators and deleterious environmental conditions, (*e.g.*, hypothermia, desiccation, etc.) increase fitness more than does greater ingestion of energy/nutrients. Alternately, an energy/nutrient maximizer has greater fitness by obtaining more of the nutritional requirements for reproduction and survival when food is in short supply than by spending time in nonforaging activities. Either foraging goal can be solved for using established optimization techniques. Linear programming is a commonly employed mathematical technique for finding the optimal solution to constrained problems where the constraints are linear (Strum, 1972). If the constraints are non-linear, the more complex technique of non-linear programming would be applied (Strum, 1972).

As an example of how to model herbivore foraging, a linear programming solution to the foraging constraints will be constructed for an adult Columbian ground squirrel (*Spermophilus columbianus*) in Montana during summer (Belovsky, 1985). This example will illustrate how the energy/nutrient-maximizing and time-minimizing solutions are obtained. The diet will be solved for the dry matter consumption (g-dry wt/day) of two plant growth forms: grasses and forbs in a prairie environment.

Time constraints depend upon the forager's daily feeding time (min/day) and its use in cropping different foods (min/g-dry wt). A ground squirrel's daily feeding time is dependent upon the thermal environ-

ment (Belovsky and Slade, 1985). Cropping rates are dependent upon food abundance and its spatial distribution. The time constraint is linear if search is non-simultaneous and will be composed of two linear segments in a convex arrangement if search is simultaneous.

Digestive constraints depend upon the forager's digestive capacity and its fill by different foods. Digestive capacity depends upon the digestive organ's (stomach and caecum for ground squirrels) ability to hold food (g-wet wt) and its turnover of food (X's filled/day). Different foods use different amounts of digestive capacity depending upon their bulk (g-wet wt/g-dry wt).

Energy/nutrient constraints depend upon the forager's energy/nutrient requirements (e.g., cal/day) and their satisfaction by different foods (e.g., cal/g-dry wt). The energy/nutrient requirement must be the quantity needed by the forager in the field to survive and replace itself by reproduction, including fat deposition for hibernation in ground squirrels (e.g., ecological energy requirements not basal values). Satisfaction of these demands by different foods depends upon each food's gross nutrient/energy content and the forager's ability to digest the food.

The constraints for a ground squirrel are presented in Figure 3 and are plotted to point out the range of diets (feasible) that satisfy the constraints. In a 2-dimensional problem, such as this, the energy/nutrient-maximizing and feeding time-minimizing goals must occur at corners of the region of feasible diets according to linear programming theorems. Obviously, the ground squirrels' observed diet is much closer to the predicted energy/nutrient-maximizing diet (Fig. 3) and is different from the availability of the foods (70% grass).

Over the past 11 years foraging data were acquired for 20 species of generalist herbivores in 45 species/season/location combinations. The herbivores range in body size from a 2.5×10^{-4} kg orthopteran to a 636 kg mammal. Linear program solutions for their foraging strategies were obtained from these data (Belovsky, 1978, 1981, 1984a, b, c, 1985, unpublished
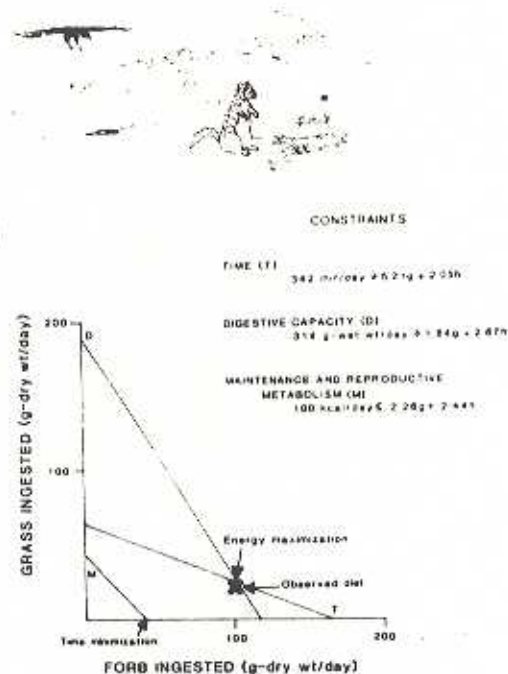

FIG. 3. An example of a linear program model for diet choice by Columbian ground squirrels (*Spermophilus columbianus*). The measured constraint equations are presented and plotted indicating the feasible diet combinations (shaded region), the time-minimizing diet, the energy/nutrient-maximizing diet and the observed diet. g and h in the constraint equations refer to the daily ingestion of grass and forb (g-dry wt/day), respectively. The ground squirrels appear to forage as energy maximizers.

data; Ritchie, 1983). When the time-minimizing and energy/nutrient-maximizing solutions are compared with the observed diets (Fig. 4A, B), the energy/nutrient-maximizing strategy provides a very close fit to the observed diet choices (energy/nutrient maximized: $r = 0.96$, n = 45, $P < 0.001$; vs. time minimized: $r = 0.05$, n = 45, n.s.). Furthermore, in all cases but one (*Cervus elaphus*), the energy/nutrient-maximizing diet is significantly different from food availability.

These results suggest that the generalist herbivores examined employ a single foraging goal, energy/nutrient maximization. Why should a single goal of energy/nutrient maximization exist? Perhaps, because herbivores use a food source that is nutritionally of low quality relative to its
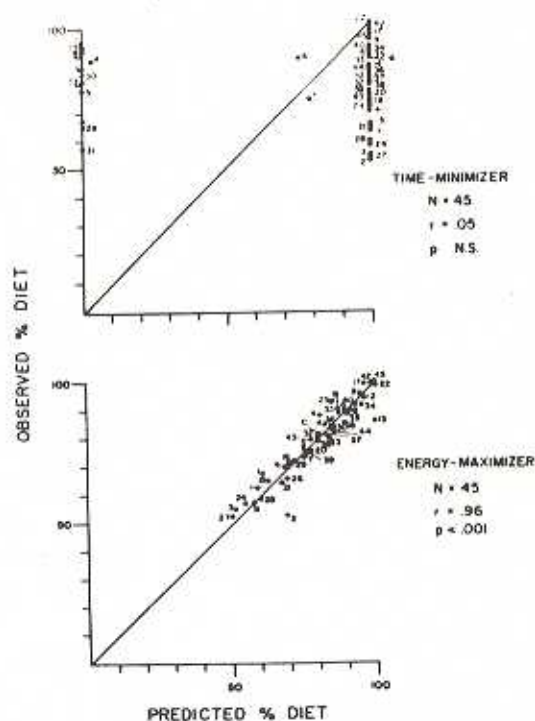
FIG. 4. A) The proportions of the time-minimized diet predicted by the linear program model compared with the observed diet proportions. B) The proportions of the energy-maximized diet predicted by the linear program model compared with the observed diet proportions. For each species of forager, the diet was composed of two plant growth forms (forb vs. grass, aquatic vs. deciduous leaves, etc.) and the observed larger of the pair were plotted. For both plots, the numbers represent the following species: 1) kudu, Tragelaphus strepsiceros; 2–3) meadow vole, Microtus pennsylvanicus; 4–5) snowshoe hare, Lepus americanus; 6) beaver, Castor canadensis; 7–8) moose, Alces alces; 9) grasshopper, Chorthippus parallelus; 10) grasshopper, Melanoplus femur-rubrum; 11) grasshopper, Melanoplus sanguinipes; 12) grasshopper, Circotettix undulatus; 13) grasshopper, Dissosteira carolina; 14, 30–43) Columbian ground squirrel, Spermophilus columbianus; 15, 23) cottontail, Sylvilagus nuttalli; 16, 24–29, 44) yellow-bellied marmot, Marmota flaviventris; 17) pronghorn antelope, Antilocapra americana; 18) white-tailed deer, Odocoileus virginiana; 19) mule deer, Odocoileus hemionus; 20) bighorn sheep, Ovis canadensis; 21) elk, Cervus elaphus; 22) buffalo, Bison bison; 45) horse, Equus caballus. (References: Belovsky, 1978, 1981, 1984a, b, c, 1985, manuscript; Ritchie, 1983.)

displacement of digestive tract capacity and because they may often encounter a seasonal short supply of nutritionally high quality plants, herbivores may have to seek

the greatest energy/nutrient ingestion to survive and reproduce (Belovsky, 1984a).

2) Do herbivores select foods by a common set of criteria?

The diet predicted by the linear program model deals with the selection of plant growth forms, which is synonymous with patch choice, since in the cases examined above, the growth forms (patches) are negatively associated with each other (Belovsky, manuscript). The solution to the linear program model that maximizes energy/nutrient intake depends primarily upon two of the three constraints: daily digestive capacity and daily feeding time. In combining these two constraints, we can define a set of criteria that an herbivore might adopt to decide whether or not an item of a plant growth form (e.g., blade of grass, leaf or twig of browse, plant or leaf of forb, etc.) is acceptable: minimum digestible energy/nutrient content (D) and cropping rate (C) necessary to satisfy daily energy/nutrient requirements (Belovsky, 1981, 1984b, c). Furthermore, D should be a function of some measure of plant chemical quality (Q) and C should be a function of the abundance of food items (A) and their size (mass/item: L).

While the plant growth forms are distributed in patches that are negatively associated with each other, the food items of a certain growth form are within the same patches, so they can be searched for simultaneously. This means that the search time spent between patches does not need to be considered in defining the choice of items within a growth form. The minimum digestibility (D: fraction of energy/nutrient digestible) can be defined as (Belovsky, 1981):

$$Q \geq \frac{MB}{SFK\gamma}. \qquad (1)$$

Q is the minimum plant chemical quality related to digestibility (e.g., % mineral plus protein content), γ is a constant converting Q into D (e.g., fraction digestible/% mineral + protein), M is the herbivore's daily requirements for energy/nutrients (e.g., cal/day), B is the food bulk (g-wet wt/g-dry wt), K is the energy/nutrient content

of the plant growth form (*e.g.*, cal/g-dry wt), F is the digestive organ's turnover (X's/day) and S is the herbivore's digestive organ capacity. The minimum item size (L: dry wt/item) selected by an herbivore can be defined as (Belovsky, 1981):

$$L \geq \frac{M}{T_c CK\gamma Q} = \frac{M}{T_c K\gamma Q\epsilon A}. \quad (2)$$

A is the abundance of items (items/area), C is the cropping rate (items/min), ϵ is a constant converting A into C (area/min), assuming a linear (Type 1) functional response as suggested by Holling (1965) for herbivores, and T_c is the herbivore's daily feeding time (min/day).

I have measured Q as either the mineral plus protein content of the vegetation or its solubility in HCl and pepsin which is correlated with D (Belovsky, 1981, 1984*a*, *b*). L can be measured as the size of an item or portion of it consumed by herbivores (g-dry wt/item), while A is a measure of food plant item density (leaves, twigs, etc./area). Knowing the availability of Q and L values for items of each plant species composing a growth form, the species composition of an herbivore's diet can be predicted by computing the fraction of items of each plant species that satisfies the herbivore's minimum D and L values (Belovsky, 1981, 1984*b*, *c*). In addition, the minimum Q and L values can be measured as the smallest 10% of all Q and L values selected by an herbivore. The predicted and observed minimum Q and L values can be compared (Fig. 5), indicating very close agreement.

If herbivores select food items according to minimum Q and L values (eqs. 1 and 2), they will be consuming, on average, items of lower Q and L values than will a forager that selects items to maximize energy/nutrient intake. Minimum Q and L values are set by energy/nutrient requirements and feeding time, while the energy/nutrient-maximizing forager will select items based on the availability of the highest energy/nutrient items and their cropping rates. A diet that maximizes energy/nutrient intake with simultaneous search, as is the case for the selection of items within

a growth form (contingency model [Schoener, 1971; Pyke *et al.*, 1977]), provides a much poorer fit with the observed species composition of the diet and observed minimum Q and L values for moose and snowshoe hare (Belovsky, 1981, 1984*b*) than eqs. 1 and 2. Even though eqs. 1 and 2 may represent sub-optimal decision rules, these rules may minimize the herbivore's chances of making a dietary mistake, especially given the large number of items an herbivore will encounter and choose in a day (*e.g.*, a moose in summer selects over 20,000 items/day: Belovsky, 1981). If the herbivore is unable to integrate the information on this large number of potential food items, the observed decision rules (eqs. 1 and 2) may be a form of "risk averse" strategy (Caraco, 1980) that minimizes mistakes.

The answer to the second question seems to be related to a set of food choice criteria for each plant growth form based on a minimum plant quality and item size arising from the herbivore's digestive capacity, feeding time and energy/nutrient requirements. With the answers to the first two questions, we have a foundation for defining how much food is usable by an herbivore and what proportion of this food is usable by a potential competitor; this leads to the third question.

3) Can these foraging goals and criteria be used to understand competition for food between generalist herbivores?

To address this question, a situation in which herbivores appear to be food limited must be studied. Two such systems have been examined: moose and snowshoe hare at Isle Royale National Park, Michigan (Belovsky, 1984*d*) and two species of orthopterans at the National Bison Range, Montana (Belovsky, manuscript). For each of the four species' populations in allopatry, the foraging criteria for minimum food item size and quality (eqs. 1 and 2) can be used to predict the quantity of vegetation usable by each species. If the usable food is positively correlated with observed consumption, food limitation may be indicated and such a relationship is found (Fig. 6).

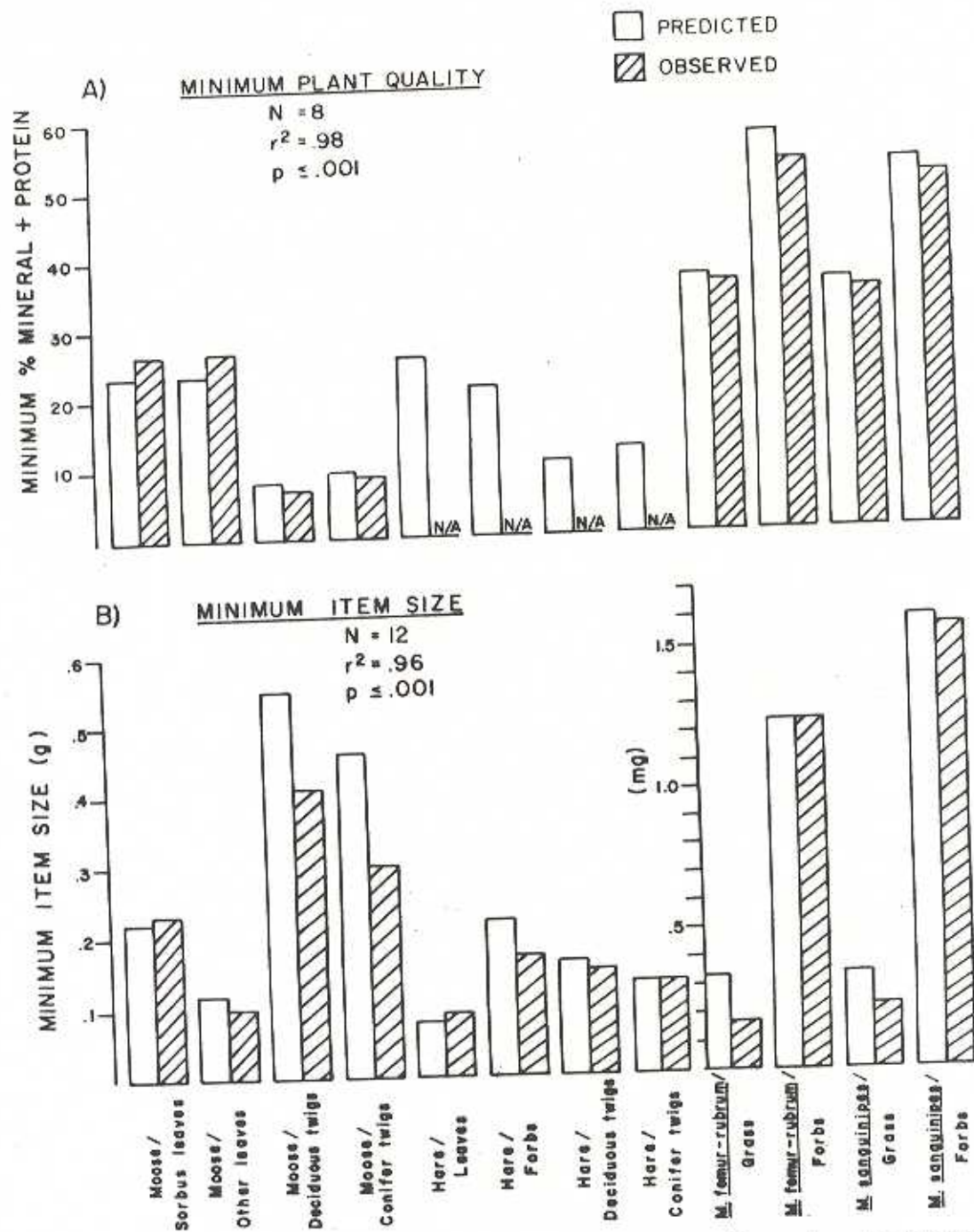For field observational data (Isle Roy-

FIG. 5. A) A comparison of the predicted (eq. 1) and observed minimum plant quality selected by four herbivore species (Belovsky, 1984d, manuscript). Quality is based on % mineral plus protein content which is closely correlated with digestibility measures for these species. N/A means not measured. B) A comparison of the predicted (eq. 2) and observed minimum plant item sizes selected by four herbivore species (Belovsky, 1984d, manuscript).

ale), unlike the situation in experimental populations (Bison Range), one also might expect a positive correlation if other factors (*e.g.*, predation, weather) are limiting because foragers should feed where the most food is located. First, this may not be observed if predators are more likely to kill their prey or weather is more severe where food is abundant (Moen, 1973; Edwards, 1983). Second, even if foragers did seek sites with the most food, but are not food limited, one should observe greater proportional use of areas with high food abundance, because the foragers are not forced to feed in all areas. Rather, an approximately constant proportional use is observed in my studies, suggesting food limitation. Finally, because usable food is not found to be correlated with total plant biomass (Fig. 6), we may have a reason why some past studies have not found herbivores to be food limited.

To test for competition an experiment must be conducted which compares the densities attained by each species in allopatry and in sympatry. If the sympatric populations attain a lower density than the allopatric, competition is indicated. The Isle Royale system is a naturally occurring manipulation of populations arising from island distributions, while the Bison Range system is a set of caged populations in the field. Both experimental systems indicated competition (Fig. 7).

To determine whether the sympatric populations compete for food, we need two pieces of information: 1) what portion of each species' usable food is shared with the other species, and 2) how would food competition affect population growth trajectories and equilibrium densities. The first problem requires a comparison of each competitor's minimum food quality and minimum item size with the other species' values to determine overlapping food use. Depending upon the overlap in food use, the second problem involves the mathematical representation of the competitive dynamics through the use of simultaneous differential equations.

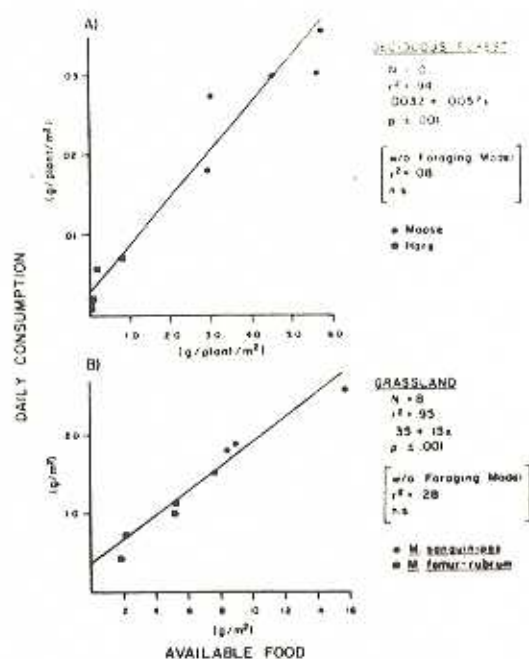Food utilization by the different herbivores is represented in Figure 8, indicating

FIG. 6. A plot of daily food consumption by herbivores *versus* available food is presented. A) contains data for two forest herbivores: moose and snowshoe hare on different islands (Belovsky, 1981, 1984*b*); and B) contains data for two prairie herbivores—grasshoppers: *M. sanguinipes* and *M. femur-rubrum* in population cages in the field (Belovsky, manuscript). Available food is determined using the minimum food quality (eq. 1) and item size (eq. 2) with the distribution of item quality and size in the environment to convert total plant biomass into an estimate of usable food. This measure of usable food is correlated with actual food consumption; the regression between food consumption and total plant biomass is provided and shown not to be correlated.

regions of shared and exclusively-used foods for each herbivore, based upon their different minimum food item qualities and item sizes selected. For the use of twigs by moose and hare, there also exists a maximum twig size that each can handle (Fig. 8A); this value was empirically determined since at present no *a priori* means of estimation exists. The maximum size is probably related to the herbivore's ability to break off items of different sizes. Note that the quantity of each herbivore's food resources and their allocation between shared and exclusively-used portions var-
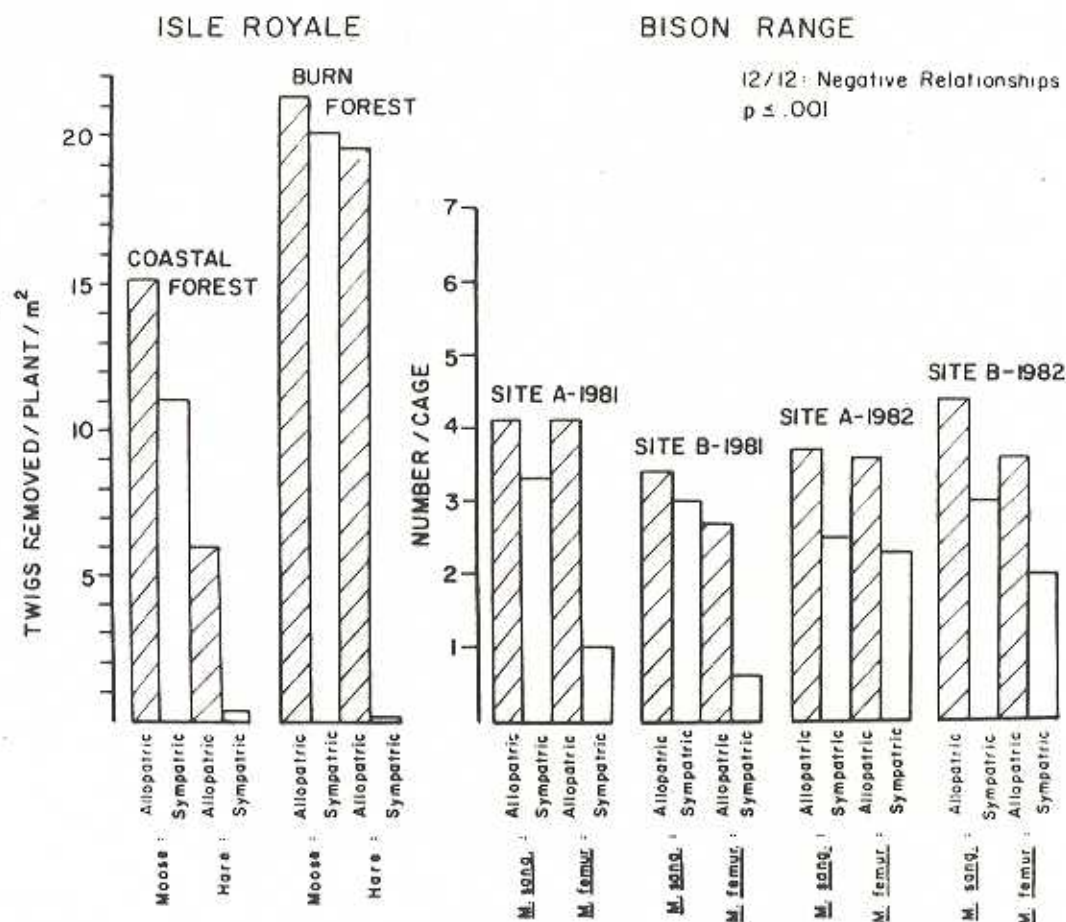
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FIG. 7. Densities for two pairs of herbivore species when they are alone (allopatry) are compared with densities when both are together (sympatry) (Belovsky, 1984d, manuscript). Because allopatric densities are greater than sympatric values, competition is indicated.

ied between habitats and years (Fig. 8); this must arise from different conditions for plant growth.

The observed allocation of food between a shared and exclusive component leads to a form of competition which can be mathematically represented for two species as:

$$\frac{dN_1}{dt} = R_1 N_1 \left(\frac{I_{E1}}{N_1} + \frac{I_{01}}{N_1 + \alpha N_2} - C_1 \right),$$

$$\frac{dN_2}{dt} = R_2 N_2 \left(\frac{I_{E2}}{N_2} + \frac{I_{02}}{N_2 + \beta N_1} - C_2 \right). \quad (3)$$

N_1 is the number of individuals of species 1; N_2 is the number of individuals of species 2; R_1 is the conversion of resources for species 1 into births and deaths; R_2 is the conversion of resources for species 2 into births and deaths; I_{E1} is the quantity of resources that can be exclusively used by species 1; I_{E2} is the quantity of exclusive resources for species 2; I_{01} is the quantity of resources for species 1 shared with species 2; I_{02} is the quantity of species 2's resources shared with species 1; α is the competition parameter equating resource use by an individual of species 2 into equivalent resource use by a number of individuals of species 1; β is the competition parameter converting resource use by an individual of species 1 into equivalent
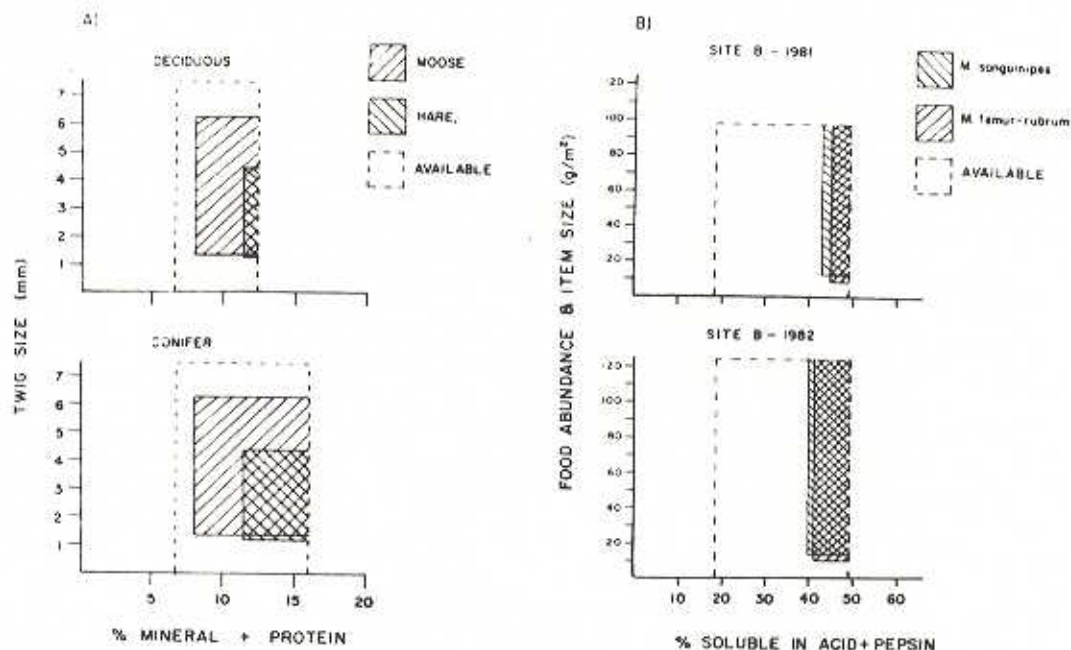
FIG. 8. A) The observed use of different plant quality and item sizes by moose and snowshoe hare in two different forest types at Isle Royale National Park, indicating differential amounts of shared and exclusive food resources for each species. B) The observed use of different plant quality and item sizes by two grasshopper species in two different years at the National Bison Range, indicating differential amounts of exclusive and shared food resources for each species. The minimum values sought by the grasshoppers for grasses and forbs are the same in different years but the proportions of grass and forb in the environment change between years modifying the average minimum sought by the grasshoppers.

resource use by a number of individuals of species 2; C_1 is the quantity of resources required per capita by species 1 if an individual is to survive and have replacement reproduction; and C_2 is the per capita requirements for species 2 (Schoener, 1974).

Using non-linear regression techniques (Marquardt, 1963), Schoener (1974) demonstrated how equilibrium population densities could be used with carrying capacity values to determine if competition might explain observed population densities and the type of competitive interactions (interference, exploitative with shared and exclusive resources, etc.). Employing these techniques, Belovsky (1984*d*) found that moose and hare densities at different locations where food resources for each species were known appeared to be predicted by the above set of differential equations (eq. 3), indicating competition for food by the suggested mechanisms. Other competition models (Schoener, 1974) were

fit to these data and were found to be statistically less predictive. The same was done for the grasshopper population cages, also indicating exploitative competition with shared and exclusive resources.

A more robust test of the applicability of the model for exploitative competition with shared and exclusive resources arises if the competitive isoclines ($dN_1/dt = 0$, $dN_2/dt = 0$) and/or the trajectories of population decline (dN_1/dt, dN_2/dt) are compared with eq. 3. This was possible with the grasshopper population cages at the Bison Range (Fig. 9). The trajectory data are obtained by periodically censusing the cages, but the isoclines must be measured in separate experiments where one species is maintained at a constant density by replacing losses, while the other species is started at a given density and allowed to decline to an equilibrium value. Both the trajectories and isoclines fit eq. 3 better than other competition models.

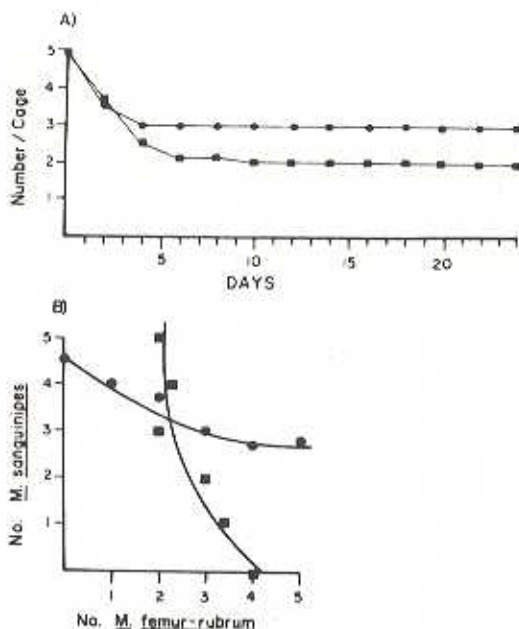These results suggest that competition

FIG. 9. A) An example of the results over the duration of the experiment in 1982 from grasshopper population cages (mean of six cages) containing both species. The data depict the declines in both species' numbers to equilibria (Belovsky, manuscript). B) The results from grasshopper population cages (mean of five cages) in which one species is allowed to vary (■ *M. femur-rubrum*, ● *M. sanguinipes*), while the other species is kept at a constant density by the replacement of grasshoppers lost by mortality. The lines represent the best fit nonlinear regressions to eq. 3 and can be considered competitive isoclines.

occurs for food that is apportioned between shared and exclusive classes. Very convincing support for this conclusion would be if the α and β terms, and the proportions of exclusive resources predicted by the nonlinear regression for eq. 3, agreed with values arising from each species' minimum quality and item size characteristics for food plants. Algebraically, the α and β relationships can be shown to arise from the probability of encountering a food item already consumed by an individual of the other species and the importance of a lost food item (Belovsky, 1984d), *i.e.*:

$$\alpha = (q_2/q_1)/\theta,$$
$$\beta = (q_1/q_2)/\theta. \qquad (4)$$

q_2 is the proportion of species 2's resources that is shared with species 1 ($I_{02}/I_{E2} + I_{02}$), q_1 is the proportion of species 1's resources that is shared with species 2 ($I_{01}/I_{E1} + I_{01}$) and θ is the ratio of the total resources for species 1 to those for species 2 ($I_{E1} + I_{01}/I_{E2} + I_{02}$) or vice versa ($I_{E2} + I_{02}/I_{E1} + I_{01}$), whichever ratio is larger. The proportion of exclusive resources predicted by the foraging strategy and the α and β values can be compared with the regression estimates of these values (Table 1), indicating very good agreement (exclusive resource: $r^2 = 0.98$, n = 6, $P < 0.001$; α and β: $r^2 = 0.99$, n = 6, $P \leq 0.001$). Therefore, there appears to be an *a priori* way of estimating potential competition parameters for herbivores through foraging theory, as found for sunfish by Werner (1977).

TABLE 1. *Observed competition model parameters (eq. 3) as determined by the non-linear regression of population data are compared with competition parameters predicted from foraging data in Figure 8.*

	% Exclusive		Competition parameter	
	Predicted	Observed	Predicted	Observed
Isle Royale				
Moose				
Deciduous forest	75.6	88.9	32.9	28.6
Coniferous forest	60.3	68.9	12.4	10.5
Hare				
Deciduous forest	1.0	0.2	2.0	2.2
Coniferous forest	1.0	4.2	2.0	1.6
Bison range				
M. femur-rubrum	2.5	4.4	2.48	2.87
M. sanguinipes	39.3	34.1	0.95	0.91

TABLE 2. *The linear program model's constraints written as functions of body mass (W; kg), grass biomass (P_g; g-dry / m^2), forb biomass (P_f; g-dry / m^2), and total plant biomass for a given season (P_t; g / m^2) (Belovsky, manuscript). g and f are the daily consumption of grass and forb (g-dry at / day), respectively.*

Time constraint:

denominator multiplier choices

$$\frac{856 - 15.6W^{.42}}{P_t^{.25}}\left(\frac{(P_g + P_f)^{.25}}{P_t^{.25}}\frac{\min}{\text{day}}\right) \geq \left\{ \begin{array}{l} 1/0.16P_g^{-.25}W \left\{ \begin{array}{l} \times 1, \\ \text{if: } 3.25P_g^{-.25}W^{-.67} \geq 1 \\ \times (3.25P_g^{-.25}W^{-.67} + 5.02 \times 10^{-4}P_g^{.25}W^{.76}) \\ \text{if: } 3.25P_g^{-.25}W^{-.67} < 1 \end{array} \right\} \times g \\ \\ + \\ \\ 1/5.78P_f^{-.25}W \left\{ \begin{array}{l} \times 1, \\ \text{if: } 3.91P_f^{-.25}W^{-.67} \geq 1 \\ \times (3.91P_f^{-.25}W^{-.67}) \\ \text{if: } 3.91P_f^{-.25}W^{-.67} < 1 \end{array} \right\} \times f \end{array} \right.$$

Processing constraint:

For homeotherms:

$$\left\{ \frac{24 \text{ for homeotherms or 6 for poikilotherms}}{\left[.87W^{.67} + 11.84P_t^{-.44} + \frac{((23.67P_t^{-.44})^2 + 7.76W^{.67})^{.5}}{2} \right]} \right\}$$

$$+ \left\{ \begin{array}{l} 0 \text{ for homeotherms} \\ 1 \text{ for poikilotherms} \end{array} \right\} \times \left\{ \begin{array}{l} 95.7W^{.96} \text{ for homeotherms} \\ 8.4W^{.75} \text{ for poikilotherms} \end{array} \right\} \frac{\text{g-wet}}{\text{day}} \geq 1.64g + 2.67f$$

Energy constraint:

$$\left\{ \begin{array}{l} 140W^{.75} \text{ for homeotherms} \\ 59W^{.75} \text{ for poikilotherms} \end{array} \right\} \frac{\text{kcal}}{\text{day}} \leq 3.25e^{-.26W^{-.14}}g + 3.52e^{-.26W^{.14}}f$$

CONCLUSION

Implications for generalist-herbivore evolution and guild assembly

We know from the studies of generalist herbivores reported here:

1) all the generalist herbivores appear to be energy/nutrient maximizers,

2) all the generalist herbivores appear to select food plants based upon minimum quality and item size characteristics which provide the herbivore with its energy/nutrient requirements within its digestive capacity and feeding time constraints, and

3) differences in species-specific minimum food quality and item size may explain food allocation between herbivores that are limited by food and are potentially competing.

Even with this consistency of the observations, the generality of these findings is limited by the small number of species and systems studied. Therefore, an assessment of whether generalist herbivore populations are generally food limited and compete must await an expansion of the data base.

To expand the number of cases studied would require considerable work, given that the results summarized here represent 11 years of effort. Therefore, an expedient for generalizing from these findings must be found.

A logical general concept that might account for differences in species' foraging parameters, resulting in different diets and resource partitioning, is body size. Body size is a logical choice for two reasons. First, the foraging constraints (digestive capacity, cropping rate, energy requirements and nutrient requirements) are probably physiological/anatomical functions of body size. Second, a number of investigators have documented that foraging behavior, diet and resource partitioning for generalist
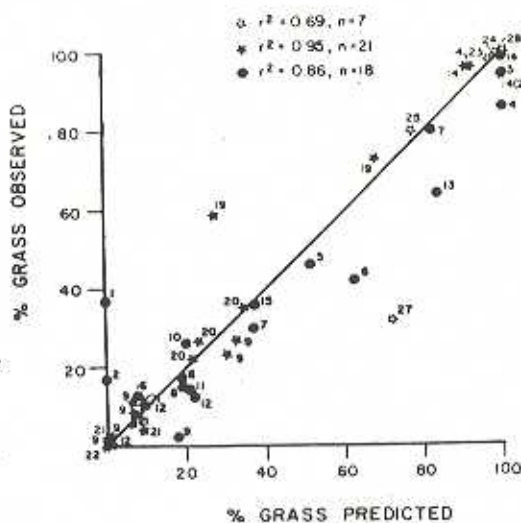
FIG. 10. Observed diet proportions of grass *versus* the proportions predicted using the equations in Table 2 and parameter values from the literature in an energy-maximizing diet model. Bison Range data are represented by ●s, other North American grassland herbivores by ★s and East African grassland herbivores by ☆s. Each number represents a different species: 1) grasshopper, *M. femur-rubrum*; 2) grasshopper, *M. sanguinipes*; 3) grasshopper, *Circotettix undulatus*; 4) grasshopper, *Dissosteira carolina*; 5) meadow vole, *Microtus pennsylvanicus*; 6) Columbian ground squirrel, *Spermophilus columbianus*; 7) cottontail, *Sylvilagus nuttalli*; 8) yellow-bellied marmot, *Marmota flaviventris*; 9) pronghorn antelope, *Antilocapra americana*; 10) white-tailed deer, *Odocoileus virginiana*; 11) bighorn sheep, *Ovis canadensis*; 12) mule deer, *Odocoileus hemionus*; 13) elk, *Cervus elaphus*; 14) buffalo, *Bison bison*; 15) spruce grouse, *Canachites canadensis*; 16) porcupine, *Erithizon dorsatum*; 19) blacktailed jackrabbit, *Lepus californicus*; 20) hoary marmot, *Marmota caligata*; 21) California ground squirrel, *Spermophilus beecheryi*; 22) walkingstick, *Diapheromera velii*; 23) wildebeest, *Connochaetes taurinus*; 24) Bubal hartebeest, *Alcelaphus buselaphus*; 25) Thomson's gazelle, *Gazella thomsoni*; 26) impala, *Aepyceros melampus*; 27) Grant's gazelle, *Gazella granti*; 28) blesbok, *Damaliscus dorcas*. (References: Severson and May, 1967; Sparks, 1968; Du Plessis, 1972; Ueckert and Hansen, 1972; Peden *et al.*, 1974; Hansen, 1975; Schwartz and Nagy, 1976; Schwartz *et al.*, 1977; Schitoskey and Woodmansee, 1978; Tieszen *et al.*, 1979; Spalinger, 1980; Belovsky, 1984a, manuscript.)

herbivores may be related to body size (Vesey-Fitzgerald, 1960; Gwynne and Bell, 1968; Bell, 1970, 1971; Geist, 1974; Jarman, 1974; Schwartz and Nagy, 1976; Leuthold, 1977).

Detailed development of the relation-

ship between body size and foraging goals for generalist herbivores is not possible here. However, as a cursory review of the idea's potential, the linear program foraging model's constraint values can be constructed as functions of body weight and plant abundance. A preliminary assessment was accomplished using non-linear regression analysis (Marquardt, 1963) and data from 14 species of generalist herbivores studied at the Bison Range (Belovsky, 1985). Each constraint parameter is a physiological/anatomical function which scales to body size (Calder, 1983; Peters, 1983); detailed description of these functions will be presented elsewhere (Belovsky, manuscript). The regression functions are for grassland herbivores because they were constructed with data for herbivores from this habitat, and are in some instances rather complex due to the combination of several body size relationships (Table 2).

There are some studies of generalist herbivore diets from grasslands that also present the biomass of grasses and forbs in the environment. Using the body size functions for the linear program constraints with the food biomass values and the herbivores' adult body masses from the study, if reported, or from a field guide (*e.g.*, Burt and Grossenheider, 1964), diets were predicted for comparison with observed diets (Fig. 10). A remarkably good fit was found ($r^2 = 0.88$, n = 46, $P \leq 0.001$) for generalist herbivores ranging in mass from 2.5×10^{-4} kg to >1,000 kg, which suggests that body size may provide a general concept to address differences in herbivore diets and resource partitioning. Therefore, with a body size approach, the ecologist may be able to employ available information to test the foraging strategies presented here and the potential for competition to shape generalist herbivore guilds.

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