

Optimal foraging and community structure: The allometry of herbivore food selection and competition

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Summary

I address the selection of plants with different characteristics by herbivores of different body sizes by incorporating allometric relationships for herbivore foraging into optimal foraging models developed for herbivores. Herbivores may use two criteria in maximizing their nutritional intake when confronted with a range of food resources: a minimum digestibility and a minimum cropping rate. Minimum digestibility should depend on plant chemical characteristics and minimum cropping rate should depend on the density of plant items and their size (mass). If herbivores do select for these plant characteristics, then herbivores of different body sizes should select different ranges of these characteristics due to allometric relationships in digestive physiology, cropping ability and nutritional demands. This selectivity follows a regular pattern such that a herbivore of each body size can exclusively utilize some plants, while it must share other plants with herbivores of other body sizes. I empirically test this hypothesis of herbivore diet selectivity and the pattern of resource use that it produces in the field and experimentally. The findings have important implications for competition among herbivores and their population and community ecology. Furthermore, the results may have general applicability to other types of foragers, with general implications for how biodiversity is influenced.

Keywords: allometry; competition; herbivory; optimal foraging

Introduction

Early formulations of optimal foraging theory (OFT) focused on foraging goals that natural selection might favour and how a forager would use its physiological and morphological abilities to attain these goals (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1969a,b, 1971). While early OFT models did not explicitly incorporate the physiological and morphological abilities of the forager, these abilities should influence each food's nutritional value and acquisition cost. The original OFT formulations sought to predict food resource selection by a forager, and thereby address how this affects the forager's population dynamics by defining the food availability in an environment for a forager. The hope was to create a foundation for population and community ecology issues that involve food-based carrying capacity, food-based competition, and predation. Even though the link between the behavioural ecology topic of OFT and population and community ecology was the initial motivating force, this linkage remains largely uninvestigated (Hughes, 1990).

A logical protocol for linking OFT with population and community ecology may be an allometric format, whereby OFT models explicitly include a forager's physiological and morphological abilities and these abilities are dependent on body mass. These models may provide insights into the abundance and distribution of species of different body sizes in various environments. The

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allometric link with OFT is not new (Schoener, 1969a,b; Belovsky, 1986a), nor are allometric applications to ecology (see Peters, 1983, 1991). These allometric approaches ‘build’ mechanistic population and community scenarios based on body size-dependent organismic characteristics (Schoener, 1986). This mechanistic approach differs from recent references to the importance of allometry in ecology where patterns in populations and communities are explained *post hoc* as being consistent with allometry (Brown, 1995).

As an example of this mechanistic approach, I will integrate allometry and OFT to examine the utilization of food resources by herbivores. An allometric model of diet selectivity by herbivores produces a unique pattern of plant utilization with body size that predicts that herbivores of each body size will have plant resources that only they can utilize, while still sharing most plant resources with herbivores of other sizes. The predicted pattern for food utilization has important implications for the diversity of herbivores and the potential for competition among them. Field observations on food selection by herbivores of different body sizes inhabiting a forest and a grassland support the theoretical predictions. Furthermore, experiments with common generalist herbivores, grasshoppers (Orthoptera, Acrididae), support the theoretical predictions – larger mammalian herbivores are not amenable to experimental examination.

A brief background on the allometry of herbivore feeding

The study of foraging by mammalian herbivores has a long-standing allometric tradition. First, speed of movement and mouth size, and their influence on cropping rates of plants, are dependent on body size (Spalinger and Hobbs, 1992; Gross *et al.*, 1993; Shipley *et al.*, 1994). Secondly, digestive efficiency and metabolic demands, and their influence on the necessary nutritional value (e.g. protein content, energy content, etc.) of plants selected as food and the amount that must be consumed, are also dependent on body size (Demment and Van Soest, 1985; Illius and Gordon, 1987, 1990, 1992). Both of the above aspects of herbivore foraging provide qualitative (Vesey-Fitzgerald, 1960; Gwynne and Bell, 1968; Bell, 1970, 1971; Geist, 1974; Jarman, 1974; Leuthold, 1977; Jarman and Sinclair, 1979) and quantitative (Demment and Van Soest, 1985; Illius and Gordon, 1987, 1990, 1992; Owen-Smith, 1988) predictions about which plants different mammalian herbivores should consume.

Regardless of whether a study makes qualitative or quantitative predictions, the general conclusions of these studies are:

1. Large-bodied mammalian herbivores, because of greater digestive efficiency and lower metabolic demands per unit body mass, can survive on foods of lower nutritional value than can small-bodied species.
2. Small-bodied mammalian herbivores, because of lower total metabolic demands, can survive in areas where food plants are in low abundance.

Observations on feeding by mammalian herbivores generally support the allometric predictions and the allometric predictions have been used to explain mammalian herbivore population and community ecology.

Allometric feeding relationships may produce ‘grazing successions’, whereby utilization of the plant community by a sequence of migrating mammalian herbivores, from larger to smaller, leads to facilitation of feeding by each successively smaller species (Vesey-Fitzgerald, 1960; Gwynne and Bell, 1968; Bell, 1970, 1971). This facilitation emerges when feeding by the larger herbivores on the larger plants of lower nutritional value exposes the smaller plants of higher nutritional value so that smaller herbivores can find and consume them more easily. Facilitation is enhanced further if consumption of larger plants of lower nutritional value increases the growth of smaller plants of

higher nutritional value by releasing them from competition. This is a mutualistic perspective, because the larger herbivores enhance the abundance of smaller herbivores, or may even create the necessary conditions for the smaller species' persistence. Under this scenario, large-bodied herbivores are 'keystone' species creating a more diverse herbivore community (Owen-Smith, 1988).

Employing the same allometric feeding perspective, other ecologists argue that a competitive scenario, not a mutualistic one, is operating (Jarman, 1974; Jarman and Sinclair, 1979). In this case, allometric feeding differences produce niche separations which permit competitive co-existence of different herbivores. Some ecologists argue that small herbivores competitively exclude the larger species after the larger species harvest the large plants of low nutritional value (Illius and Gordon, 1987, 1990, 1992).

The alternative explanations based on facilitation or competition raise critical issues:

1. Why should large-bodied species forego feeding on small plants of higher nutritional value, leaving them for small-bodied herbivores? Foragers should not ignore foods of high value just because a species can feed on foods of lower nutritional value (Schoener, 1974). Differential food selection by herbivores of different body sizes is the crux of either the facilitation or competition arguments.
2. Quantitatively, how does food utilization change with body mass? This question is key in determining how intense the competition or facilitation might be.
3. Quantitatively, how will the abundances of herbivores of different body masses be affected by the abundances of plants of different nutritional values? This question is critical for determining herbivore diversity in different environments, and should differ depending upon whether facilitation or competition is the dominant process.

I provide qualitative insights into these questions based on quantitative allometric studies. However, I demonstrate that the necessary precision required to test these ideas can only be attained with more explicit predictions of how herbivores select diets and OFT provides these insights. Finally, while the application of allometry to herbivore foraging has focused on mammals, there is no reason to restrict this approach to mammalian herbivores.

Herbivore OFT and allometry

I have developed an OFT model based on the same mechanisms invoked in the allometric analyses of mammalian herbivore foraging (digestive efficiency, metabolic demands and cropping rate) (Belovsky, 1978, 1984a,b,c, 1986a,b, 1987a,b,c, 1990a, 1991; Belovsky and Schmitz, 1991, 1994; Belovsky and Slade, 1987). The OFT model is based upon the mathematical optimization technique of linear programming (LP) and employs three constraints:

1. $T \geq \sum x_i/c_i$, where T is the herbivore's daily feeding time (time/day), c_i is the herbivore's cropping rate of food i (dry mass/time), and x_i is its intake of food i (dry mass/day).
2. $D \geq \sum b_i x_i/r_i$, where D is the herbivore's digestive organ capacity that limits food intake (rumen, crop, etc.: wet mass), b_i is the bulkiness of food i (wet mass/dry mass), and r_i is the mean retention time of food i in the digestive organ (r_i , in days);
3. $R \leq \sum d_i v_i x_i$, where R is the herbivore's daily nutritional requirement for some nutrient in short supply (e.g. energy, protein, etc./day), d_i is the herbivore's proportional digestion of food i , and v_i is the gross nutritional content of food i (protein, energy, etc./dry mass).

The LP model's feeding time constraint (1) assumes that different types of food plants are distributed in different patches in the environment, requiring the herbivore to search for and harvest each type independently (i.e. non-simultaneous search: Belovsky *et al.*, 1989). In contrast, classical

OFT models (Stephens and Krebs, 1986) do not employ a digestive constraint (2) and assume that the feeding time constraint is for foods that can be searched for and harvested simultaneously by the forager (i.e. foods are distributed either uniformly or randomly in the environment, and the functional form of the constraint would be different than (1): Belovsky *et al.*, 1989).

With the LP model, the food intake (x_i) which either maximizes the herbivore's nutritional intake (nutrient maximization) or minimizes the feeding time required to satisfy the herbivore's nutritional requirements (time minimization) is computed. A nutrient-maximizing goal assumes that the herbivore's fitness is maximized by having more nutrients for survival and reproduction, while a time-minimizing goal assumes that the herbivore's fitness is maximized by having more time for other activities such as mating, hiding from predators, care of young, and so on.

In earlier papers (Belovsky, 1986a; Belovsky and Slade, 1986), I framed the above constraint equations in terms of allometric relationships and biomasses of two plant types found in grasslands: grasses and forbs. I employed the allometric-plant biomass constraints (table 2 in Belovsky, 1986a) in the LP model to predict the diet composition selected by herbivores of different body masses in terms of grasses and forbs, where the biomasses of grasses and forbs and herbivore diets were reported in the literature. Comparing the LP predictions with observed herbivore diets from 46 grassland studies (27 species of mammalian, avian and insect herbivores, and body masses of 10^{-4} – 10^3 kg), I found that predicted diets, assuming a goal of nutrient (energy) maximization, explained 88% of the variance in observed diets (fig. 10 in Belovsky, 1986a: $r^2 = 0.88$, $N = 46$, $P < 0.0001$); the variance explained in different areas ranged from 69 to 95%. These allometric predictions explain an amount of the variance in diet selection comparable to that explained when observed constraint values for each species are employed ($r^2 = 0.87$, $N = 400$, $P < 0.001$; Belovsky, 1994). Therefore, the use of allometric constraints does not appear to markedly reduce precision.

Other diet selection models are not as predictive as the LP-OFT model. Classical OFT models produce diets that either contain only one food plant type or the food plant types selected by the forager are ingested in proportion to their relative abundances in the environment. Another class of models, not based on optimal choices, is referred to as 'satisficing' (Stephens and Krebs, 1986; Pierce and Ollason, 1987; Ward, 1992, 1993; Owen-Smith, 1993) and assumes that foragers simply select foods as they are encountered as long as they satisfy the forager's nutrient needs. 'Satisficing' has been criticized for being biologically unrealistic, unlikely to be a product of natural selection and scientifically untestable (Nonacs and Dill, 1993). Observed herbivore diets generally contain a mix of food types that are not in proportion to their relative abundance in the environment, which is counter to both the classical OFT model and 'satisficing' (Belovsky, 1986a, 1994). Furthermore, observed diets provide more energy or nutrients than the forager needs, which is counter to 'satisficing' (Belovsky, 1986a, 1994).

Therefore, LP models for herbivore diet selection appear to be very predictive. This does not mean that LP models have not been criticized as being too simplistic, logically circular or mechanistically in error (Hobbs, 1990; Owen-Smith, 1993, 1996; Huggard, 1994; but see Belovsky, 1990b, 1994; Belovsky and Schmitz, 1993, 1994). Rosenzweig (1995) argues that OFT has generally been attacked for the same reasons, but it has withstood these assaults because it remains the single most predictive body of theory in ecology. Likewise, the OFT model based on LP for herbivores continues to exhibit remarkable predictive power for a wide range of organisms and environments (e.g. marine snails, Grantham *et al.*, 1995; desert tortoises, C.R. Tracy, personal communication).

What the herbivore 'looks for' in a plant

The LP-OFT model can predict plant characteristics that a herbivore seeks in a given environment if it forages optimally (i.e. maximizes its nutritional intake or minimizes its feeding time). To do

this, the three LP foraging constraints (feeding time, digestive capacity and nutritional requirements) are rewritten in terms of plant characteristics as they affect the herbivore's ability to harvest and process plants. The rewritten constraints produce two minimum values sought by the herbivore that depend in part upon plant characteristics for a given plant type (e.g. grasses, forbs, shrubs) (Belovsky, 1981a, 1986a):

1. *Minimum digestibility* ($d_{m,i}$: proportion of plant matter digested) is defined by combining the Digestion (2) and Nutrient (3) Constraints:

$$d_{m,i} = (Rb_i r_i) / (Dv_i) \quad (1)$$

Minimum digestibility is how digestible an item must be if the herbivore can satisfy its nutritional needs when it fills its entire digestive capacity with this plant type.

2. *Minimum cropping rate* ($c_{m,i}$: g dry/min) is defined by combining the Time (1) and Nutrient (3) Constraints, and the solution for $d_{m,i}$ (Equation 1):

$$c_{m,i} = R / (v_i d_{m,i} T) \quad (2a)$$

Minimum cropping rate is how quickly an item must be harvested if the herbivore can satisfy its nutritional needs when it fills its digestive tract. Digestive tract fill enters the solution for minimum cropping rate because minimum digestibility ($d_{m,i}$) is included in Equation (2a).

Each plant type defines its own minimum values because each differs in characteristics from other plant types. For an item of a food type to be consumed, the item must have characteristics that produce digestibility and cropping rate values greater than the minimum values for both. These minimum values are defined when the herbivore must trade-off consumption of plant types that are limited by cropping rate with plant types that are limited by digestion rate. This trade-off occurs when plants are abundant enough that the herbivore is constrained by digestive capacity as well as feeding time; that is, the herbivore can ingest more of some foods in a time period than can be processed by the digestive tract (Belovsky, 1986b).

On the other hand, if the herbivore cannot ingest more food than can be digestively processed, the herbivore is strictly time-limited and digestion is set by the rate at which food can be ingested. In this situation, the minimum digestibility, ($d_{m,i}$), is no longer a selection criterion and cannot influence the minimum cropping rate, so that minimum cropping rate becomes:

$$c_{m,i} = R / (v_i d_i T) \quad (2b)$$

In this case, only the nutritional benefit relative to cropping rate is considered, the classic approach to OFT (Stephens and Krebs, 1986). I have argued that this case for herbivores should only occur at times and in environments where food is at a very low abundance (Belovsky, 1984b). Others have placed a greater emphasis on it, considering it more common in time and space (Spalinger and Hobbs, 1992; Gross *et al.*, 1993; Shipley *et al.*, 1994). With proper measures, this issue can be resolved and will be addressed in my allometric analysis.

Minimum digestibility and cropping rate values are also predicted by the 'satisficing' approach, but the OFT definitions are different (Schmitz and Ritchie, 1991). For example, one 'satisficing' allometric approach (Hobbs and Swift, 1985) argues that herbivores select the range of foods that provides an average nutritional benefit equal to requirements. This means that the poorest foods consumed are set by the nutritional content and relative abundance of better foods in the environment, so that the weighted mean of nutritional value and relative abundance just satisfies the herbivore's nutritional requirements. This is in contrast to the OFT perspective, where the herbivore selects foods to maximize its fitness by maximizing its nutritional intake or minimizing its time spent feeding while still satisfying nutritional needs (Maynard Smith, 1978).

What an allometric herbivore ‘looks for’ in a plant

An OFT perspective

Assuming that all herbivores are identical in geometry and simply increase in body mass (Fig. 1), three basic relationships emerge (Peters, 1983; Calder, 1984):

1. Body masses (M) or capacities of body structures (e.g. stomach, mouth, etc.) are proportional to body volume ($M \propto V$).
2. Therefore, body or body structure lengths (L) are proportional to body mass raised to the 1/3 power ($L \propto M^{1/3}$).
3. Therefore, body or body structure surface areas (S) are proportional to body mass raised to the 2/3 power ($S \propto M^{2/3}$).

This is an overly simplistic perspective because taxon-specific differences are ignored (e.g. ruminants vs caecal-digestors: Janis, 1976; Owen-Smith, 1988), but it provides a starting point.

With the above relationships, the parameters in Equations (1), (2) and (3) can be allometrically defined (summarized in Fig. 1):

1. *Metabolic requirements* (R) are proportional to $V^{2/3}$ or $M^{2/3}$, because the animal’s loss of energy or nutrients should be related to surface area (Kleiber, 1961). Others (Hemmingsen, 1960; McMahon, 1973; Peters, 1983; Calder, 1984) have claimed that the power should approach 3/4 due to other scaling considerations.

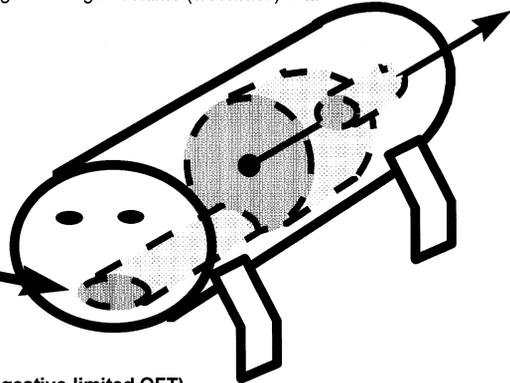
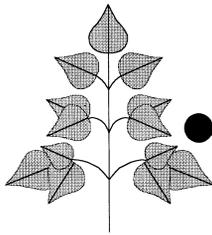
CONSTANTS-- $\alpha, \beta, \gamma, \varepsilon, \theta, \zeta, \kappa$.

PLANT TRAITS --

- v: nutritional value of plant (mass/mass)
- A: density of plant items in environment (items/area)
- I: mass of a plant item in environment (dry mass/item)
- b: plant fill of gut (bulk) (dry mass/mass)

HERBIVORE TRAITS --

- M: herbivore size (wet mass)
- R: herbivore nutritional requirements (dry mass/time) $\propto M^{2/3}$
- T_T : herbivore’s activity time (time) $\propto k_2 + k_3 M^{2/3} + k_4 M$
- D: digestive organ volume (wet mass) $\propto M$



HERBIVORE RESPONSE --

(scenario: S = “satisficing”, T = time-limited OFT, TD = time- & digestive-limited OFT)

- c: herbivore cropping rate (mass/time): $c \propto (IA)^{\gamma} M^{2/3}$
- r: retention time in gut (time/mass)
 - S: $\propto M^{1/4}$ or $1/3$
 - T: $\propto M^{1/3}$
 - TD: $\propto k_8 + k_7 M^{1/3} / v_i^2 + (k_8^2 + k_9 M^{1/3} / v_i^2)^{1/2}$

- E: total herbivore food intake (mass/time)
 - S: $\propto M^{2/3}$ or $3/4$
 - T: $c(T_T - T_S) \propto \zeta(IA)^{\gamma} T_T M^{2/3} / \{1 + \beta(IA)^{\theta - 1} / \alpha\}$
 - TD: $= D/r \propto k_{16} M + k_{16} M^{2/3}$
- T_S : herbivore’s time searching for food (time) $\propto E / \alpha IAM^{2/3}$
 - S: $\propto M^{1/12}$
 - T: $= k_{11} / \alpha IA$
 - TD: $\propto k_{10} M^{1/3} / \alpha IA$

Figure 1. A summary of parameters and foraging goals used to address plant selection by hypothetical herbivores that have a regular geometric body plan.

2. *Digestive capacity* (D : wet mass) should be proportional to M (Schmidt-Nielsen, 1975). This relationship has been reported for closely related species (e.g. ungulates: Demment and Van Soest, 1985; Illius and Gordon, 1987, 1990, 1992), but also holds for a greater diversity of herbivores (insects to mammals, 10^{-4} – 10^3 kg; Fig. 2a).

3. *Cropping rate* (c : dry mass/time) is a function of plant item size (I : dry mass/item), number of items ingested per bite (C : items/bite) and number of bites per time (B : bites/time):

$$c = ICB$$

Items harvested per bite (C) depends on the density of items in the environment (A : items/area) and the area of the herbivore's open mouth ($\propto M^{2/3}$: area/bite):

$$C \propto AM^{2/3}$$

This formulation of items harvested per bite (C) assumes that the mass of plants per area (IA) is not greater than the mass that the herbivore can hold in its mouth (Spalinger and Hobbs, 1992).

Bite rate (B) depends on number of bites needed to deplete the items in a patch (A/C) and time spent moving between patches, which is a product of the herbivore's travel speed ($\propto M^{1/3}$: distance/time) and its reach as it feeds ($\propto M^{1/3}$: distance):

$$B \propto AM^{2/3}/C = k_1$$

where k_1 is a constant when C is substituted. The formulation of bite rate (B) assumes that time spent biting and chewing is minimal or is done while moving (Spalinger and Hobbs, 1992). Shipley *et al.* (1994) found bite rate (B) to be a constant regardless of herbivore body mass.

Using the functions for C and B , c increases linearly with plant biomass per area (IA), a Type I functional response:

$$c \propto IAM^{2/3}$$

If the mass of plants per area is greater than mouth size and/or time spent biting and chewing are not minimal, then c increases to an asymptote as plant biomass per area (IA) increases (Type II functional response: see Spalinger and Hobbs, 1992). Assuming that plant biomass per area (IA) never becomes so large that cropping rate (c) asymptotes, c can be written as:

$$c \propto (IA)^\gamma M^{2/3} \quad (3)$$

where γ is less than 1. Using cropping rate data for a range of herbivore species in different seasons (i.e. different IA in g dry/m²) at the National Bison Range (Belovsky, 1986b; Belovsky and Schmitz, 1994), a non-linear regression (Wilkinson *et al.*, 1992) indicates that c is proportional to $M^{2/3}$ and γ is less than 1 (Fig. 2b)

4. *Feeding time* (T) depends on the maximum amount of time that a herbivore can be active in a day (T_T) less time spent searching for food (T_S).

Active time (T_T) may be set by abiotic conditions and herbivore physiology (e.g. thermal and water balance: Belovsky, 1981b, 1984c, 1986a,b; Schmitz, 1991). Based upon models of thermal physiology, two allometric relationships are important (Monteith, 1973; Bakken and Gates, 1975; Gates, 1980). First, animal surface area ($M^{2/3}$) affects the amount of environmental heat absorbed, the amount of heat radiated, the amount of heat lost to convection, and the amount of heat metabolically produced by an animal. Secondly, animal thermal inertia (ability to store heat) depends on body mass (M). Belovsky and Slade (1986) found T_T to be a function of these relationships:

$$T_T = k_2 + k_3 M^{2/3} - k_4 M \quad (4)$$

where the k values are constants.

Time spent searching for food (T_S) depends upon the amount of food consumed by the herbivore (E), food biomass per area as it affects harvesting by the herbivore (see Cropping rate: IA), and the speed at which the herbivore can cover an area while searching for food (see Cropping rate: $\propto M^{2/3}$):

$$T_S \propto E/[\alpha(IA)M^{2/3}] \quad (5)$$

where α is a constant.

The amount of food consumed (E) depends on whether the herbivore seeks to maximize its nutritional intake or to minimize its feeding time. Because herbivores generally appear to maximize their nutritional intake (see Herbivore OFT and allometry), I restrict further analysis to this foraging goal. In addition, the amount of food consumed by a nutrition-maximizing herbivore and the food's mean retention time in the digestive tract will depend on whether the herbivore's consumption is solely limited by feeding time or by feeding time and digestive capacity.

5. *Amount of food consumed and its mean retention time in the digestive tract when consumption is solely time-limited.* In this case, the amount of food consumed determines mean retention time of food in the digestive tract, because digestive capacity is greater than food consumption.

Amount of food consumed (E) depends on conversion of feeding time ($T_T - T_S$) into intake by the cropping rate (c):

$$E = c(T_T - T_S) \propto k_{24}M^{2/3} + k_{25}M^{4/3} - k_{26}M^{5/3}$$

or, if ($T_T - T_S$) is constant as empirically observed (Belovsky and Slade, 1986), then:

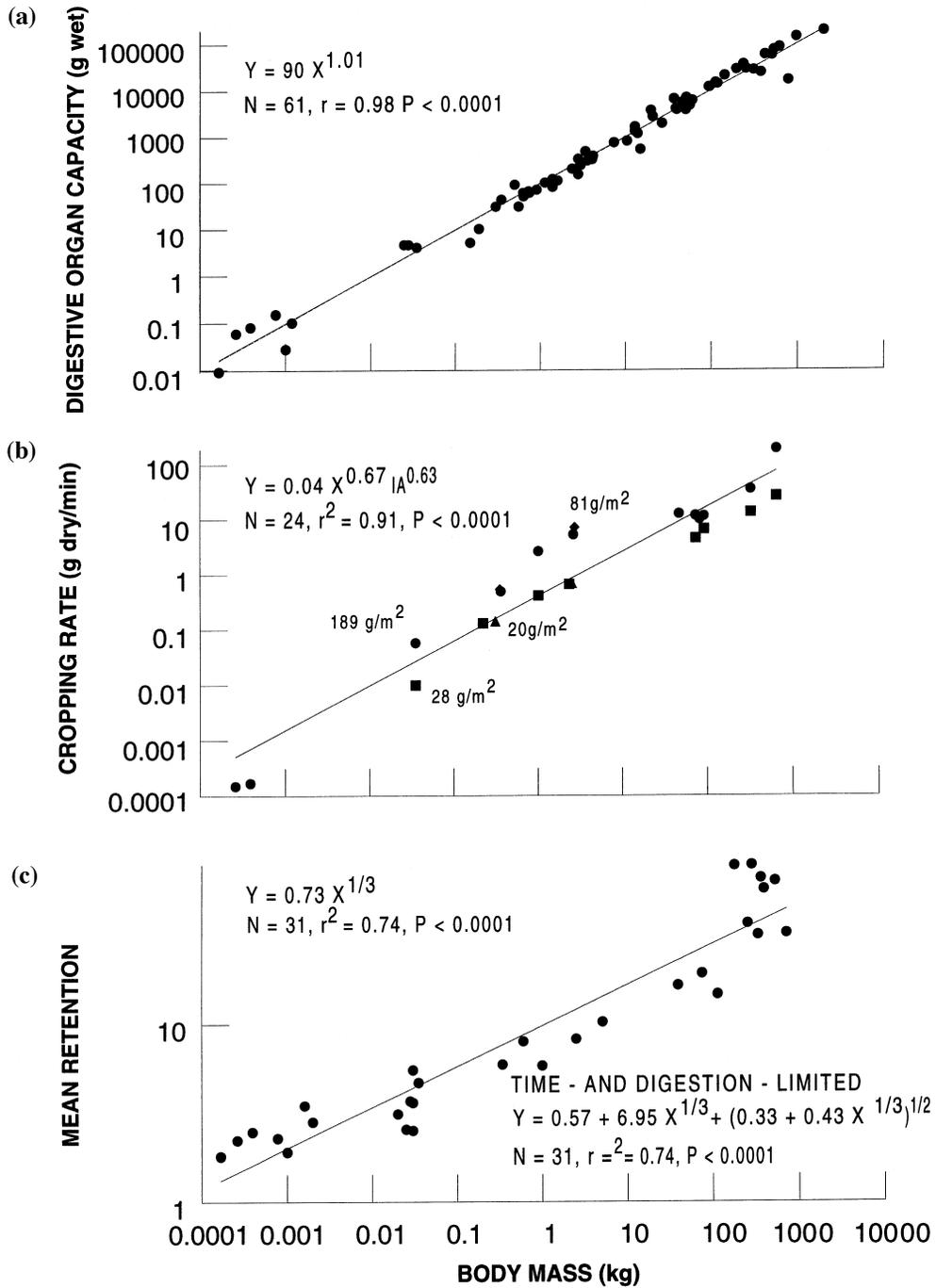
$$E \propto \zeta(IA)^{\gamma}M^{2/3}/[1 + \beta(IA)^{\gamma-1}/\alpha] \quad (6)$$

where β and ζ are constants. With this amount of food consumed, time spent searching for it (T_S ; Equation 5) is independent of body mass.

Mean retention time of food in the digestive tract (r) is set by the herbivore's digestive capacity ($D \propto M$: mass) divided by the quantity of food that is harvested ($E \propto M^{2/3}$: mass/time, Equation 6) (Belovsky, 1984b), which makes r proportional to $M^{1/3}$.

6. *Amount of food consumed and its mean retention time in the digestive tract when consumption is both time- and digestion-limited.* In this case, the amount of food consumed and its mean retention

Figure 2. Herbivore allometric relationships described in the text are presented: (a) digestive organ capacity (Hamilton, 1934, 1955; Gelting, 1937; Grinnel *et al.*, 1937; Swenk and Silko, 1938; Longhurst, 1944; Fitch, 1948; Peters, 1958; Bookhout, 1959; Dexter, 1959; Hungate *et al.*, 1959; Golley, 1960; Buss, 1961; Eddy, 1961; Hewson, 1962; Jonkel and Greer, 1963; Short, 1963, 1964; Storr, 1963, 1964; Ledger and Smith, 1964; Watson, 1964; Short *et al.*, 1965, 1966, 1969; Johnson and Maxwell, 1966; Tileston and Lechleitner, 1966; Egorov, 1967; Johnson and McBee, 1967; Berwick, 1968; Laws and Parker, 1968; Walker and Farley, 1968; Clough and Hassom, 1970; Eley, 1970; O'Gara, 1970; Pendergast and Boag, 1970; Flux, 1971; McBee, 1971; Prins and Geelen, 1971; Bernays and Chapman, 1972; Allo *et al.*, 1973; Arman and Field, 1973; Meagher, 1973; Nagy, 1973; Fitzgerald and Lechleitner, 1974; Schoonveld *et al.*, 1974; Dean *et al.*, 1975; Nagy and Regelin, 1975; Hoppe, 1977; Parker, 1977; Belovsky, 1978, 1984b,c, 1986b, unpublished results; Van Hoven *et al.*, 1981; Demment, 1982); (b) cropping rate where the plant biomasses for the four symbols are presented (Belovsky, 1986b, unpublished results; Belovsky and Schmitz, 1994); (c) mean retention time of food in the digestive tract (Ritzman and Benedict, 1938; Alexander, 1952, 1963; Chapman, 1957; Gill and Bieguszewski, 1960; Campling *et al.*, 1961; Bergerud and Russell, 1964; Kostelecka-Myrcha and Myrcha, 1964; Balch and Campling, 1965; Hainlein *et al.*, 1966; Hintz and Loy, 1966; Stewart, 1967; Vander Noot *et al.*, 1967; Lee and Horvath, 1969; Bernays and Chapman, 1970a,b, 1973; Maloiy and Kay, 1971; Mautz and Petrides, 1971; Milne *et al.*, 1976; Staines, 1976; Schaeffer *et al.*, 1978; Karasov and Diamond, 1985; Belovsky, 1986b, unpublished results).



time in the digestive tract are functions of each other, because there is now an optimal trade-off between the two constraints.

Mean retention time for food i (r_i) is not fixed, but under the animal's control so that the rate at which nutrients are obtained is maximized (Yang and Joern, 1994). The rate that nutrients are released from an item of food i (N_i/t : nutrients/time) depends on the Digestive Constraint (2) and values from the Nutrient Constraint (3):

$$N_i/t = (Dv_i d_i)/(b_i r_i) \quad (7)$$

The optimal mean retention time of food i ($r_{opt.i}$) is the value for r_i that maximizes N_i/t , an approach that is identical to chemical reactor models of digestion (Cork, 1994).

Let us assume, for ease of attaining an analytical solution, that very simple digestive kinetics are operating, which makes incorporation of the optimal mean retention time ($r_{opt.i}$) in further calculations easier. This assumption is not made in most chemical reactor studies of digestion (e.g. Cork, 1994). Consider the digestive organ (D) to be a container in which a meal (set of food items) is broken down (digested) and then emptied through a pipe, where the released nutrients are absorbed (Fig. 1). Nutrients are absorbed more rapidly in the pipe when the food has a greater nutrient concentration, and this leads to more rapid movement of food through the pipe. This formulation is similar to digestive kinetics based upon chemical reactors, especially 'batch reactors' and 'constant stirred tank reactors' for the digestive organ and a 'plug flow reactor' for the pipe (Penry and Jumars, 1986, 1987; Dade *et al.*, 1990; Martinez del Rio *et al.*, 1994).

r_i is then composed of two components:

$$r_i = s_i + p_i \quad (8)$$

where s_i is time that a meal of food i is held in the digestive organ, and p_i is mean time required for an item of food i in a meal to traverse the pipe. The time required to empty the digestive organ depends on its capacity ($D \propto M$), the pipe's cross-sectional area ($P \propto M^{2/3}$) and the velocity of contents passing through the pipe (v) so that:

$$p_i = D/2Pv = M^{1/3}/2v \quad (9)$$

Velocity (v) depends on the rate that nutrients are absorbed in the pipe (i.e. nutrient concentration: $d_i v_i$), so that:

$$p_i \propto M^{1/3}/d_i v_i \quad (10)$$

The proportion of a food item that is digested (d_i) increases at a decreasing rate with time spent in the digestive organ:

$$d_i = \varepsilon - \theta/s_i \quad (11)$$

where ε and θ are constants defining plant resistance to digestion (e.g. fibre). If θ is greater than or equal to ε , then there is a minimum time that food must reside in the digestive tract before any nutrients are released.

Substituting Equations (8), (10) and (11) into Equation (7), we obtain:

$$N_i/t \propto [v_i M(\varepsilon - \theta/s_i)]/[b_i(s_i + M^{1/3}/v_i(\varepsilon - \theta/s_i))]$$

The optimal mean retention time ($r_{opt.i}$) occurs when $\partial N/t/\partial s_i = 0$:

$$s_i = k_8 + \sqrt{(k_8^2 + k_9 M^{1/3}/v_i^2)}$$

and

$$r_{opt.i} = k_8 + k_7 M^{1/3}/v_i^2 + \sqrt{(k_8^2 + k_9 M^{1/3}/v_i^2)} \quad (12)$$

The function for the optimal mean retention time is consistent with many observations on digestive physiology and makes a distinction commonly overlooked. First, as plant resistance to digestion increases (ϵ small and θ large), mean retention time increases. Secondly, as nutrient content of the plants (v_i) increases, mean retention time decreases. Therefore, two plant characteristics (resistance to digestibility and nutrient content) operate in opposite ways to influence retention time; this solves the apparent anomaly in chemical reactor models of digestion reported by Martinez del Rio *et al.* (1994), when they considered the two characteristics as synonymous. Finally, the mean retention time model considers both digestion and absorption as rate-limiting processes.

Amount of food consumed (E) is the digestive organ's capacity divided by mean retention time (D/r). Given the relationships for D and r , E can be written as:

$$E \propto M/[k_8 + k_7M^{1/3} + \sqrt{(k_8^2 + k_9M^{1/3}/v_i)}]$$

or

$$E \approx k_{15}M + k_{16}M^{2/3} \quad (13)$$

With this amount of food consumed, time spent searching for it (T_S) is:

$$T_S \approx k_{10}M^{1/3}/\alpha IA \quad (14)$$

The traditional perspective

The traditional allometric studies of herbivore foraging reviewed above deal with the same traits for herbivores of different body sizes that were addressed with OFT. The traditional projections, although usually not identified as such, represent a 'satisficing' perspective, because the herbivore only seeks to consume a food based on whether the food can *just satisfy* its nutritional needs. This approach produces the following allometric relationships:

1. *Mean retention time* (r) is predicted to be $\propto M^{1/4}$ or $\propto M^{1/3}$ based upon the food's rate of movement along a linear dimension (Demment and Van Soest, 1985; Illius and Gordon, 1987, 1990, 1992).

2. *Amount of food consumed* (E) is predicted to be $\propto M^{2/3}$ or $\propto M^{3/4}$ based upon digestive capacity ($\propto M$) divided by the mean retention time ($\propto M^{1/3}$ or $\propto M^{1/4}$) (Demment and Van Soest, 1985; Illius and Gordon, 1987, 1990, 1992).

3. *Search time* (T_S) is predicted to be a constant or $\propto M^{1/12}$ based upon the amount of food consumed (E) divided by biomass of plants per area (IA) divided by the speed of searching an area ($\propto M^{2/3}$: see above).

Evidence supporting one of the allometric formulations

The allometric relationships developed for the two OFT scenarios and the traditional perspective can be compared with observations for herbivores. The observations are for herbivores spanning eight orders of magnitude in body mass (1×10^{-4} – 2×10^3 kg), which should be sufficient because Cork (1994) argues that more than three orders of magnitude are necessary to make these comparisons.

1. *Mean retention times* (r) for herbivores of different body masses that consumed the same type of plants (fresh green) were fit to a simple allometric relationship and the more complex Equation (12). Both approaches did very well (Fig. 2c: $r^2 = 0.74$, $P < 0.0001$, $N = 31$). However, the simple allometric relationship ($M^{1/3}$) provided significant residuals ($r = 0.6$, $P < 0.001$) that underestimated r at both small and large body masses; that is, it was unable to account for the decreasing slope as herbivore body size declines (Fig. 2c). The more complex Equation (11) did not

produce significant residuals. Therefore, the OFT scenario of both time and digestive capacity being limiting is supported.

2. *Amount of food consumed (E)* increases faster with body mass than predicted by ‘satisficing’ ($\propto M^{2/3}$ or $\propto M^{3/4}$) and the OFT scenario where time is only limiting ($\propto M^{2/3}$) (Belovsky, 1986b, 1987b). This supports the OFT scenario where time and digestive capacity are limiting.

There is debate over whether herbivore food consumption is solely time-limited (Equation 6) or limited by both time and digestive capacity (Equation 13 = D/br). Food consumption (E) under each of these scenarios can be compared to ascertain at what food abundance (IA) each scenario is limiting. The condition for time and digestive capacity being limiting is:

$$\beta(IA)^\gamma T_T M^{2/3} / [1 + \beta(IA)^{\gamma-1} / \alpha] \geq D/br \quad (15)$$

Using empirical values from Table 1, the value of IA at which both time and digestive capacity are limiting can be computed for herbivores of different body masses (Fig. 3a). As I have suggested previously (Belovsky, 1984b), IA must be very small for time to be solely limiting (for a 1×10^{-4} kg herbivore: $IA < 1-5$ g dry/m²; for a 1×10^3 kg herbivore: $IA < 7-40$ g dry/m²). Comparing predicted IA values in seasons with the lowest plant abundances for four environments (grassland, boreal forest, tundra and desert shrubland), time is never solely limiting (Fig. 3b).

Table 1. The parameters (defined in Fig. 1 and text) used to compute $I_m A_m$

T_T	Prairie (Bison Range)		
	summer	250 min/day	Belovsky and Slade (1986)
	winter	400 min/day	Belovsky and Slade (1986, unpublished results)
	Boreal forest (Isle Royale)		
	summer	200 min/day	Belovsky (1978, 1981a, 1984b)
	winter	400 min/day	Belovsky (1978, 1981a, 1984b)
	Australian desert shrubland	450 min/day	Belovsky (unpublished results)
	Arctic tundra	350 min/day	White and Trudell (1980a,b)
α		0.04 g dry/min	This study (Fig. 2b)
γ		0.63	This study (Fig. 2b)
β		3.38 m ² /min	Peters (1983), McMahon and Bonner (1983)
k_1		50–90 g wet/kg (mean = 70)	Demment (1982), Demment and Van Soest (1985), Illius and Gordon (1992), Owen-Smith (1988)
k_7^a		6.93 h/kg ^{1/3}	This study (Fig. 2c)
k_8^a		0.58 h	This study (Fig. 2c)
k_9^a		0.43 h ² /kg ^{1/3}	This study (Fig. 2c)
b	(approx. mean value of all plants consumed)		
	Prairie (Bison Range)		
	summer	2 g wet/g dry	Belovsky (1986b)
	winter	2 g wet/g dry	Belovsky (1986b)
	Boreal forest (Isle Royale)		
	summer	4 g wet/g dry	Belovsky (1978)
	winter	2.5 g wet/g dry	Belovsky (1981a)
	Australian desert shrubland	2 g wet/g dry	Belovsky <i>et al.</i> (1991)
	Arctic tundra	2.5 g wet/g dry	Belovsky (1991)

^a The computed mean retention time (r) must be divided into 24 h/day to obtain the correct units.

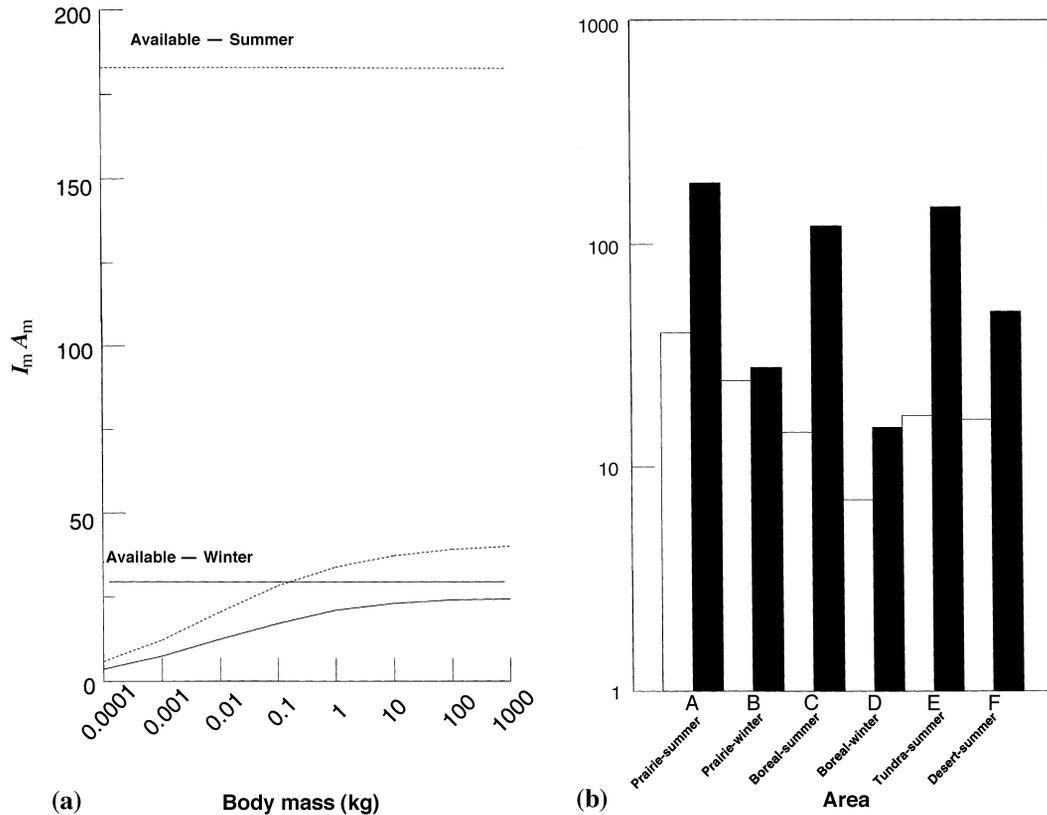


Figure 3. Predictions of the relationship between minimum plant biomass required in the environment and observed mean biomasses are presented. Parameters used in the calculations are presented in Table 1. (a) The relationship calculated for the National Bison Range (Belovsky, 1986b; Belovsky and Schmitz, 1994, unpublished results) for peak summer (early July) and minimum winter (early April) plant biomasses are presented as a function of herbivore body mass. (b) Because large herbivores require greater plant biomasses than small herbivores, calculations for the minimum required value for a 1000 kg herbivore (open bars) are compared with mean plant biomasses (filled bars) in different environments and seasons (Belovsky and Jordan, 1978; White and Trudell, 1980a; Belovsky 1984b, 1986b; Belovsky *et al.*, 1991, unpublished results). A, Prairie-summer; B, prairie-winter; C, boreal-summer; D, boreal-winter; E, tundra-summer; F, tundra-winter.

3. Search time (T_S) increases with $M^{1/3}$ (Belovsky and Slade, 1986), which is consistent with the OFT scenario where both time and digestive capacity are limiting.

Therefore, herbivores allometrically forage as predicted by OFT, not 'satisficing'. The OFT scenario supported occurs when time and digestive constraints are both operating, unless food abundance (IA) is severely restricted. Further analyses are restricted to this scenario.

Plant characteristics sought by the optimal-foraging allometric herbivore

Minimum foraging values sought

Given the allometric relationships when time and digestive capacity are limiting, the minimum digestibility ($d_{m,i}$: Equation 1) can be written as:

$$d_{m:i} \approx k_{17}/v_i^3 + k_{18}M^{-1/6}/v_i^3 + k_{19}M^{-1/3}/v_i \quad (16)$$

and the minimum cropping rate ($c_{m:i}$: Equation 2a) can be written as:

$$c_{m:i} \approx IAM^{2/3}/[(k_{17}/v_i^3 + k_{18}M^{-1/6}/v_i^3 + k_{19}M^{-1/3}/v_i)(k_{20}IA - k_{21}M^{-1/3})] \quad (17)$$

The minimum digestibility ($d_{m:i}$) decreases for larger herbivores and the minimum cropping rate ($c_{m:i}$) increases for larger herbivores, the same qualitative pattern that is obtained for 'satisficing' and time-only limited results. Neither $d_{m:i}$ nor $c_{m:i}$ are plant characteristics that the herbivore can seek in food selection, but they are outcomes sought by the herbivore. Therefore, $d_{m:i}$ and $c_{m:i}$ need to be redefined in terms of the plant characteristics that produce them.

Digestibility of plants (d_i) with similar resistance to digestion (i.e. lignin, cellulose, hemicellulose) is often proportional to plant chemical content (e.g. protein, minerals, etc.: Belovsky, 1981b, 1986a,b; Larter, 1992; Belovsky and Slade, 1995). In this case, minimum digestibility ($d_{m:i}$) can be rewritten as a function of minimum plant chemical quality (Q_m) and retention time in the digestive organ (s_i : see Appendix):

$$d_{m:i} = Q_m(\varepsilon' - \theta'/s_i) \quad (18)$$

where ε' and θ' are new constants that depend on the plant's resistance to digestion. Plant chemical quality (Q_m), retention time in the digestive organ (s_i) and ε' increase minimum digestibility, whereas θ' decreases minimum digestibility.

Likewise, the minimum cropping rate ($c_{m:i}$) can be defined (Equation 3) in terms of a minimum density of plant items (A_m) and a minimum plant item size (I_m) selected by the herbivore:

$$c_{m:i} \propto I_m A_m M^{2/3} \quad (19)$$

Minimum plant item size (I_m) and minimum item density (A_m) are not independent of each other, because the herbivore will trade-off these two values; that is, the herbivore can select a smaller item size if items are at high density, or can select a lower density of items if items are large.

Minimum plant characteristics sought by different herbivore body masses

Minimum chemical quality (Q_m), minimum item size (I_m) and minimum item density (A_m) are plant characteristics that the herbivore can ascertain using chemo-, tactile- and visual-sensory abilities prior to stopping in an area or feeding on a plant.

Because the minimum cropping rate ($c_{m:i}$: Equation 2a) is a function of minimum digestibility ($d_{m:i}$: Equation 2), then the product of minimum item size and minimum item density ($I_m A_m$) becomes a function of minimum plant quality (Q_m). Combining Equations (16) and (18) and substituting the result into Equation (17), the function relating I_m and A_m with Q_m can be found:

$$I_m A_m \approx 1/(\lambda Q_m^\omega - \phi) \quad (20)$$

where λ , ϕ and ω are constants. The intriguing aspect of the function relating $I_m A_m$ to Q_m is that any combination of these minimum plant characteristics that satisfy the function is unique to a herbivore of a given body mass.

If gross nutritional value (v_i) is not correlated with chemical quality defining digestibility (Q_i), then ω equals 1. If a perfect positive correlation is found, then ω equals 2. If a negative perfect correlation is found, then ω equals 0. This defines the limits for ω , because Q_i and v_i can be positively or negatively correlated to varying degrees. Q_i and v_i might be expected to be positively correlated because plants high in nutritional content will not be resistant to digestion; however, digestion-inhibiting plant secondary compounds (Belovsky and Schmitz, 1991, 1994) could pro-

duce a negative correlation, because plants might not evolve defences if they are already unattractive to herbivores.

ϕ is proportional to the ratio of plant bulk (b_i) to mean plant biomass in the environment (IA), and this produces some interesting results. Holding λ and minimum plant quality (Q_m) constant, as b_i decreases or IA increases, the product of the minimum plant item size and item density ($I_m A_m$) selected by the herbivore decreases. This means that herbivores are becoming less selective in their feeding as plant abundance increases or plant bulk decreases.

There is no analogous relationship between Q_m and $I_m A_m$ with the 'satisficing' perspective or the OFT scenario, when time only is limiting. This occurs because there is no trade-off between $d_{m;i}$ and $c_{m;i}$, so that for a given IA in the environment, Q_m only varies for herbivores of different body sizes. The relationship relating Q_m with IA contains a value equivalent to ω (Equation 20) which can only be positive (0 to 1), and as IA increases (i.e. cropping rates approach the asymptote of the Type II functional response), ω approaches 0. Furthermore, the parameters equivalent to λ and ϕ are not constants, but proportional to $M^{-1/3}$. Therefore, in this case, the relationship relating Q_m with IA will not resemble the simple function (Equation 20) that emerges with the OFT perspective, when time and digestive capacity are limiting.

Empirical evidence for a relationship between $I_m A_m$ and Q_m

Two datasets are available to examine whether the selection of plants by herbivores of different body masses conforms to the relationship between $I_m A_m$ and Q_m . The first dataset comes from field observations at Isle Royale National Park, Michigan, on two mammalian herbivores (Belovsky, 1981a, 1984b), and at the National Bison Range, Montana, on ten mammalian and two insect herbivores (Belovsky, 1986b). The second dataset is from a laboratory experiment designed to examine the relationship with five grasshopper species at different developmental stages: *Age-neotettix deorum*, *Melanoplus sanguinipes*, *M. femurrubrum*, *Arphia pseudonietana* and *Dissosteira carolina*.

Field observations

I measured in the field the minimum plant item sizes and densities selected by a herbivore of a given body mass ($I_m A_m$) by averaging the smallest 10% of the plant biomass per area values (IA) observed to be utilized by each species. Knowing the distribution of Q values for each common plant species in the environment and assuming that individuals of each herbivore species consumed items with Q values greater than or equal to Q_m , Q_m can be estimated as the smallest value such that the observed proportional use of each plant species by each herbivore species would be obtained if all plants with higher Q values were consumed (Fig. 4). Each herbivore species' Q_m was computed separately for different plant categories (e.g. grasses, forbs, twigs, deciduous leaves) by averaging the Q_m value estimated for each plant species comprising the category. Q_m at Isle Royale was measured as plant mineral plus protein content (% /g dry), and at the National Bison Range as plant solubility in HCl and pepsin (% soluble/g dry); both measures have been shown to be related to the herbivores' dry matter digestibility of plants (Belovsky, 1981a, 1984a, 1986a; Larter, 1992; Belovsky and Slade, 1995). At Isle Royale, $I_m A_m$ and Q_m values for each herbivore species were based upon an inventory of plants fed upon over a season without observing which herbivore had fed on each plant. This was possible because each herbivore species had a unique manner of cutting an item; for example, hare leave a diagonal cut when they bite and moose leave a jagged edge from tearing the item. However, at the Bison Range, $I_m A_m$ and Q_m had to be computed by measuring each herbivore's proportional use of plants in a feeding bout that was directly observed, because the remnants of consumed plant items provided no clues that could be used to identify the par-

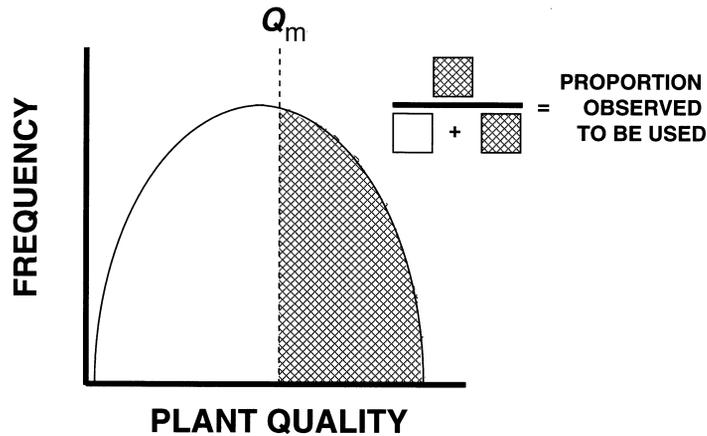


Figure 4. The method for computing Q_m is presented, where the herbivore consumes all plants encountered that are greater than this value (cross-hatched area). Therefore, knowing the distribution of plant quality (Q) values and the proportion of encountered plants that the herbivore consumed, Q_m can be computed.

ticular herbivore species that had fed upon the item. These methods are described in detail elsewhere (Belovsky, 1981a, 1984b) and data collection is reported in Belovsky (1981a, 1984b, 1986a).

$I_m A_m$ and Q_m (Fig. 5a, b) were fit to the proposed relationship (Equation 20) employing non-linear regression methods (Wilkinson *et al.*, 1992); even with limited data, interesting patterns emerge. The power of $Q_m(\omega$: Equation 20) was never significantly different from 1 (Table 2), but there was a tendency for woody plants at Isle Royale to provide a power less than 1. This might be expected given the number of structural compounds (e.g. lignin, cellulose, etc.) and secondary compounds (e.g. tannins) in woody plants that serve as defences by reducing digestibility; that is, v_i and Q may be negatively correlated. Finally, in no case were residuals significantly correlated with body mass as expected if 'satisficing' or OFT when time is only limiting occurred.

As expected, observed changes in the ratios of plant bulk (b) to mean plant biomass (IA) in different environments are proportional to the regression estimates of ϕ (Table 2). At the Bison Range, ϕ increases from summer grasses to winter grasses to summer forbs. Summer grasses at the Bison Range had the greatest biomass (132 g/m²); however, with comparable biomasses of winter grasses (28 g/m²) and summer forbs (37 g/m²), ϕ was greater for summer forbs, because they had a greater bulk (b : 2.67 vs 1.67). At Isle Royale, ϕ increases from winter to summer. Even though

Figure 5. The empirical Q_m and $I_m A_m$ for different herbivores in different environments are presented; regression analyses of these data are presented in Tables 2 and 3. (a) Moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) at Isle Royale National Park consuming leaves in summer (circles) and twigs in winter (squares). (b) Bison (*Bison bison*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), yellow-bellied marmot (*Marmota flaviventris*), mountain cottontail (*Sylvilagus nuttali*), Columbian ground squirrel (*Spermophilus columbianus*), meadow vole (*Microtus pennsylvanicus*), migratory grasshopper (*Melanoplus sanguinipes*) and red-legged grasshopper (*M. femurrubrum*) at the National Bison Range consuming summer grasses (circles), summer forbs (squares) and winter grasses (triangles). (c) Experimental studies with mixed-feeding grasshoppers (filled symbols: *M. sanguinipes* and *M. femurrubrum*) and grass-feeding grasshoppers (open symbols: *Ageneottettix deorum*, *Arphia pseudonietana* and *Dissosteira carolina*) at different developmental stages eating grasses (circles) and forbs (squares).

summer leaves have a greater plant biomass (27 g/m^2) than winter twigs (14 g/m^2) at Isle Royale, the twigs are less bulky ($b: 2 \text{ vs } 4$).

Little can be determined about the third constant, λ , in Equation 20 from the field data alone, so that discussion of this regression parameter will be deferred until the experimental results can be combined with the field results.

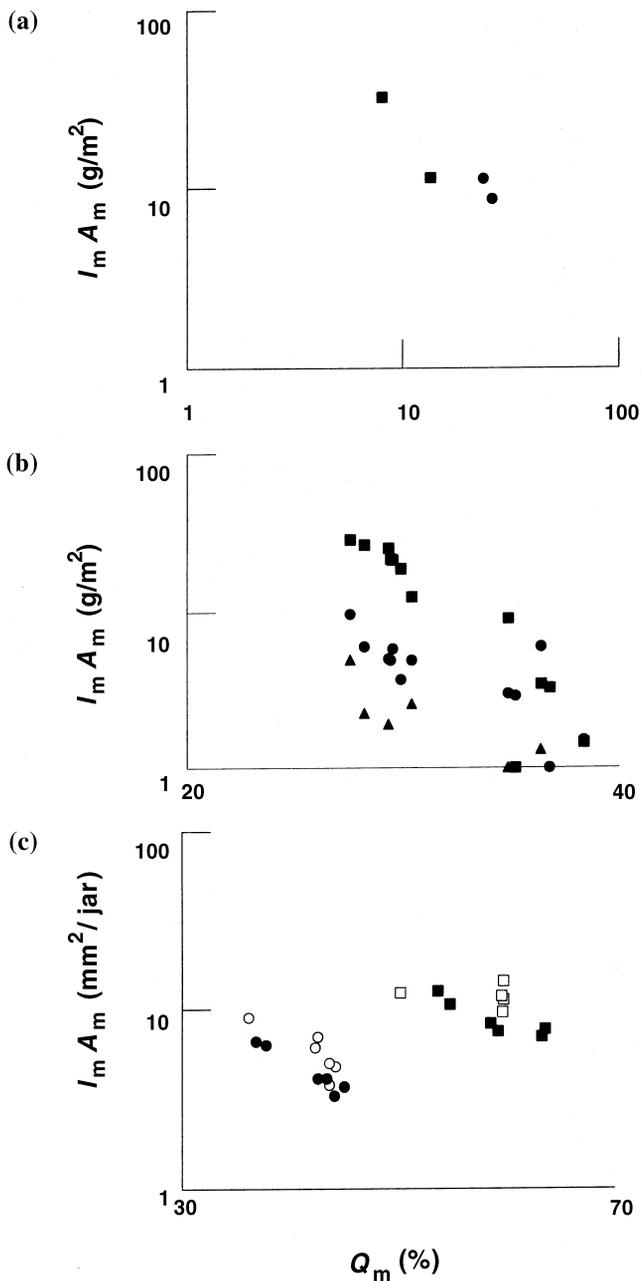


Table 2. The non-linear regression results, including regression statistics (r^2 ; sample size, N ; and significance, P) when Equation 17 (γ, ϕ, ω) is fit to the field observations of Q_m and $I_m A_m$ (Fig. 5a,b). The standard error for ω is provided in parentheses

	γ	ϕ	ω	r^2	N	P
Isle Royale						
Summer	0.06	0.51	0.63	0.64*	4*	0.13*
Winter	0.14	0.31	0.35			
Bison Range						
Summer grass	0.054	0.76	0.86 (0.06)	0.46	11	0.01
Summer forb	0.025	1.16	1.18 (0.05)	0.51	11	0.005
Winter grass	0.021	0.93	1.26 (0.06)	0.74	6	0.05

* All data were entered into a single regression, because two values (species) within each season do not permit the calculation of statistics.

Laboratory experiment

I reared field-caught hatchlings of each grasshopper species' developmental stages in the laboratory on *ad libitum* food. I used individuals in feeding trials in which they were presented with a food item that varied in size (IA) and quality (Q). By cutting different-sized rectangles from leaves of different individual plants and plant species, I varied IA and Q . Before a feeding trial, I starved individuals of each grasshopper species' developmental stage for 3 h, and I placed each individual in a 1 litre jar with a plant item (rectangle) suspended on a pin for 20 min. I recorded whether the grasshopper consumed the item.

I varied IA by starting with an item size that an individual of the grasshopper species' developmental stage could not completely consume in 20 min, and in each subsequent trial I reduced item size by 20%. This reduction in size continued until I found the size at which no consumption occurred in a minimum of five trials with different individuals. $I_m A_m$ for a developmental stage of a species was the smallest item size for which I observed consumption in at least one trial of at least five trials with different individuals. The trials used a grass (*Dactylis glomerata*) or a forb (*Taraxacum officinale*) that had very high Q values and all developmental stages of the grasshoppers readily consumed these plants.

I varied Q by cutting rectangles from leaves of different individual plants (> 20) and plant species (2–3 grass species and 2–3 forb species). The plant rectangle's size was large enough so that individuals of a grasshopper species' developmental stage could not completely consume it in 20 min. I conducted a minimum of 80–120 feeding trials for each developmental stage of a grasshopper species. Knowing the distribution of Q values (solubility in HCl and pepsin) for each plant species used in the trials and assuming that individual grasshoppers only consumed items with Q values greater than or equal to Q_m , I estimated Q_m as the smallest value such that the observed proportional use of each plant species by each developmental stage of a grasshopper species would be obtained if all plants with higher Q values were consumed (Fig. 4). For each developmental stage of a grasshopper species, I computed Q_m separately for grasses and forbs by averaging the Q_m value estimated for each plant species in the category.

I employed non-linear regression (Wilkinson *et al.*, 1992) with the experimental results to estimate the parameters relating minimum plant quality (Q_m) with minimum plant abundance ($I_m A_m$) (Equation 20, Fig. 5c). The power of Q_m (ω) for grasses was not different from 1, whether all species' developmental stages were pooled or analysed separately by feeding type (Table 3); this indicates that all grasshoppers responded similarly to grasses. This is surprising, because specialists are expected to be more efficient at feeding on the foods for which they have specialized. The power of Q_m (ω) computed for forbs was less than 1, when the grasshopper species were categorized as being grass-specialists or mixed-feeders, but not different from 1 when feeding types were pooled. This indicated that the two feeding types did not respond similarly to forbs. Forbs are expected to produce a power of Q_m that is less than 1, because the forb species used (*Taraxacum officinale*, *Heterotheca villosa*, *Achillea millefolium*, *Erodium cicutarium*) contain secondary compounds which reduce digestion. Grass-specialists had a power of Q_m that approached 0 for forbs (Table 3), which is expected if these herbivores were unable to cope with the secondary compounds.

Interpreting the ϕ value (Equation 20), which should be proportional to the ratio of plant bulk (b) to plant abundance (IA), was less straightforward than for the field data. In the field, at an instant in time, food depletion is probably not important (i.e. IA is constant); however, in the laboratory experiment, food depletion occurs (i.e. IA declines) because the rectangles of food are small. Therefore, in the experiment, the average IA experienced by a grasshopper is a value between the initial IA used in the trial (largest plant rectangle used) and $I_m A_m$ (the smallest plant rectangle consumed). Because the largest rectangle used in all trials was the same and the $I_m A_m$ for forbs is larger than for grasses, the individuals should perceive the average IA to be greater for forbs than grasses. Consequently, with the same plant bulk values as the field for grasses and forbs, ϕ should be larger for grasses than forbs, which is observed.

The relationships between $I_m A_m$ and Q_m (Equation 20) from the field and experimental studies appear to shift away from the origin (Fig. 5a,b,c) as the food's average quality increases (summer vegetation > winter vegetation; forbs > grasses). This indicates that the constants λ and ω are more

Table 3. The non-linear regression results, including regression statistics (r^2 ; sample size, N ; and significance, P) when Equation 17 (γ , ϕ , ω) is fit to the field observations of Q_m and $I_m A_m$ (Fig. 5c). The standard error for ω is provided in parentheses

	γ	ϕ	ω	r^2	N	P
All species-stages						
Grass	0.02	0.51	0.99 (0.08)	0.58	12	0.004
Forb	0.07	0.31	0.94 (0.13)	0.36	11	0.05
Mixed-feeders						
Grass	0.01	0.49	1.14 (0.11)	0.92	6	0.002
Forb	0.02	0.26	0.68 (0.15)	0.83	6	0.01
Grass-feeders						
Grass	0.02	0.50	0.99 (0.11)	0.58	6	0.06
Forb	0.11	0.11	0.14 (0.35)	0.03	5	n.s.

important than the constant ϕ , because ω depends on the correlation between plant quality (Q) and v_i , and λ depends on plant resistance to digestion (ε and θ : Equation 11) and plant nutritional value (v_i), which are related to plant quality. ϕ depends on plant bulk (b) and the average food abundance (IA), neither of which is related to plant quality.

Relationship between $I_m A_m$ and Q_m and herbivore community ecology

Competition between herbivores of different body masses

The function relating $I_m A_m$ with Q_m has important implications for niche separation based on food utilization if food is limiting to herbivore populations (Fig. 6). (1) A minimum plant quality Q_m is associated with a single herbivore body mass, where Q_m decreases with increasing body mass. (2) A plant item of quality (Q) greater than Q_m *might* be utilized by a herbivore with the body mass associated with Q_m . (3) For a plant item with quality (Q) greater than Q_m *to be utilized*, the item must also be found at a location where the product of item density (items/area) and item size (mass) are greater than $I_m A_m$ for the herbivore body mass associated with Q_m . Therefore, a Q_m value and its associated $I_m A_m$ define a rectangular region of plant characteristics that can be utilized by a herbivore of a particular body mass (Fig. 6a–c). If the power of Q_m in the relationship (ω : Equation 20) is greater than 0, then the largest herbivore in an environment can utilize all of the food quality values (Q) that smaller herbivores can use as well as lower values. However, the smallest herbivore can utilize all of the $I_m A_m$ values that the largest herbivore can use as well as lower values (Fig. 6b,c). This means that herbivores of each body size will utilize plants with a set of plant characteristics (Q and IA) that herbivores of other body sizes can use, but will also be able to use plants with a set of characteristics unique for its body size (Fig. 6b,c).

The presence of exclusive resources in Fig. 6b and Fig. 6c ensures competitive co-existence among herbivores, if plants with the characteristics defining the exclusive resource are abundant enough in the environment to permit a population of herbivores of the associated body mass to persist. Food competition and the mechanism of competitive co-existence described above has been verified empirically in experimental field studies of competition using moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) at Isle Royale (Belovsky, 1984b, 1986b), and grasshoppers at the National Bison Range (Belovsky, 1986b; Chase and Belovsky, 1994; Chase, 1996a,b). I summarize these findings in Fig. 7.

The relationship between Q_m and $I_m A_m$ (Equation 20 with $\omega > 0$) leads to predictions about how similar in body mass herbivores can be and still competitively co-exist:

1. I assume that the ability of each herbivore body mass to competitively co-exist depends upon the amount of exclusive food resources available to it. The availability of shared food resources is not considered in determining competitive co-existence, because these resources, as demonstrated above, will be utilized among many competitors. In my assessment of competitive co-existence, two necessary levels of exclusive resources are examined: a constant amount (biomass) or an increasing amount (biomass) as herbivore body mass increases to account for allometric minimum viable population projections ($\propto M^{1/3}$: Belovsky, 1987a).

2. I assume that plants of all Q and IA characteristics are equally abundant by biomass in the environment. This means that plants with high IA values constitute fewer patches in the environment than plants with low IA values.

3. With the above assumptions and the Q_m and $I_m A_m$ relationship (Equation 20), the different herbivore body sizes that can co-exist in the environment can be determined. The smallest body size, H1, is arbitrarily set. Given the maximum plant quality (Q_{\max}) and abundance ($I_{\max} A_{\max}$) values observed in the environment, H1's total resource availability can be defined

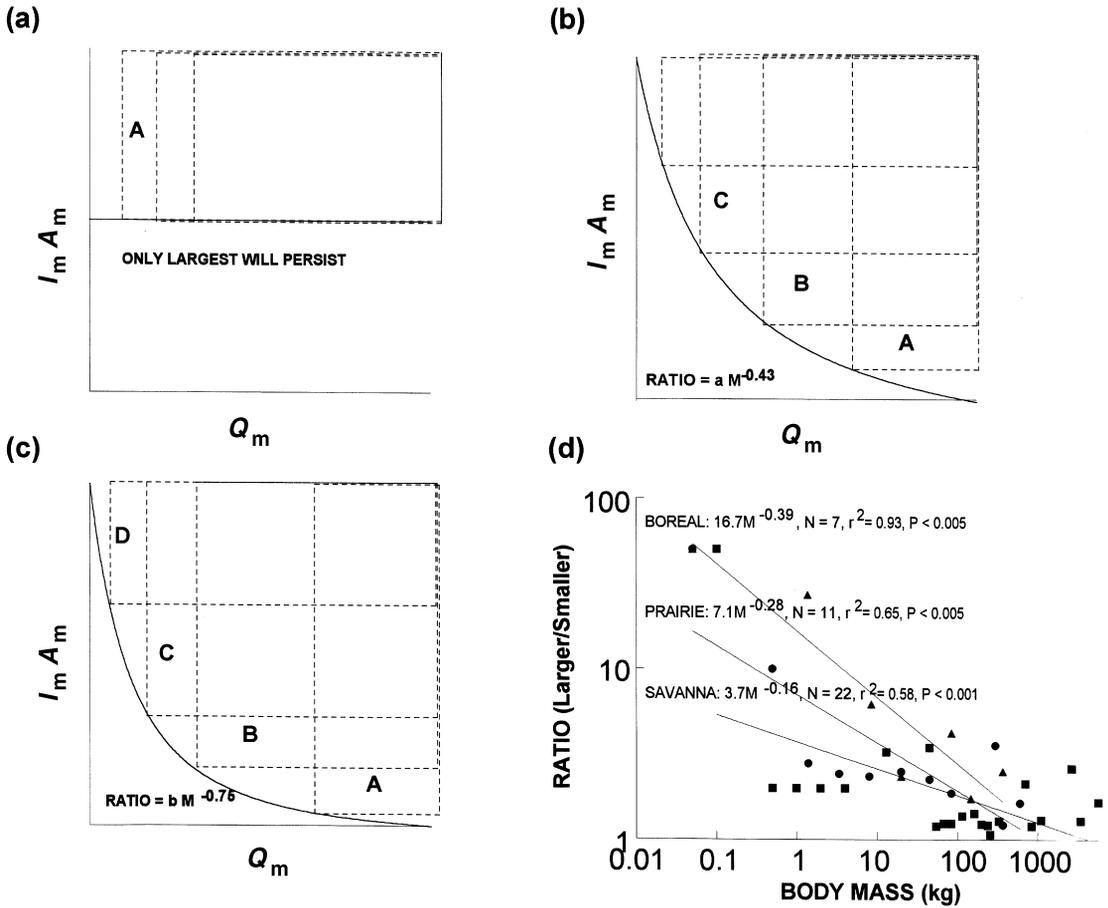


Figure 6. The relationship between Q_m and $I_m A_m$ is presented for $\gamma = 0$ (a), $\gamma = 1$ (b) and $\gamma = 2$ (c). Assuming that plants are uniformly distributed by Q and IA , (a), (b) and (c) portray the amount (rectangle area) of exclusive food resource available to the herbivore of the body size defined by the Q_m and $I_m A_m$ at the lower left-hand corner of the rectangle (see text). If the rectangle areas are set equal, more herbivore body sizes can competitively co-exist in an environment as γ increases from 0 to 2: $\gamma = 0$ (1 size in a), $\gamma = 1$ (3 sizes in b) and $\gamma = 2$ (4 sizes in c). If herbivores are ranked by size from smallest to largest, the limiting similarity ratio of the larger to smaller body sizes for two consecutively ranked herbivores (RATIO) will decrease as the size of the larger of the pair increases; this indicates that large sizes can be more similar than small sizes and still co-exist. This pattern is addressed by comparing co-existing herbivore species (RATIO) from the North American boreal forest and prairie (Shelford, 1963, where mammalian body masses are from Burt and Grossenheider, 1964) and an East African savanna (Lamprey, 1963, where mammalian body masses are from Dorst and Dandelot, 1969) in (d). Similarity is predicted to increase (RATIO decreases) as γ increases from (a) to (c).

(area = $[Q_{\max} - Q_{m:H1}][I_{\max}A_{\max} - I_{m:H1}A_{m:H1}]$). Only a portion of the total resource will be used exclusively by H1, depending upon the next larger herbivore's (H2) Q_m and $I_m A_m$. H2's body size is defined as the body size with a $Q_{m:H2}$ that leaves H1 with the amount of exclusive resource assumed above (2). This computation is then repeated for body size H2 and the next larger size, H3; then H3 and the next larger body size, H4, etc., until a larger body size cannot be added because it cannot

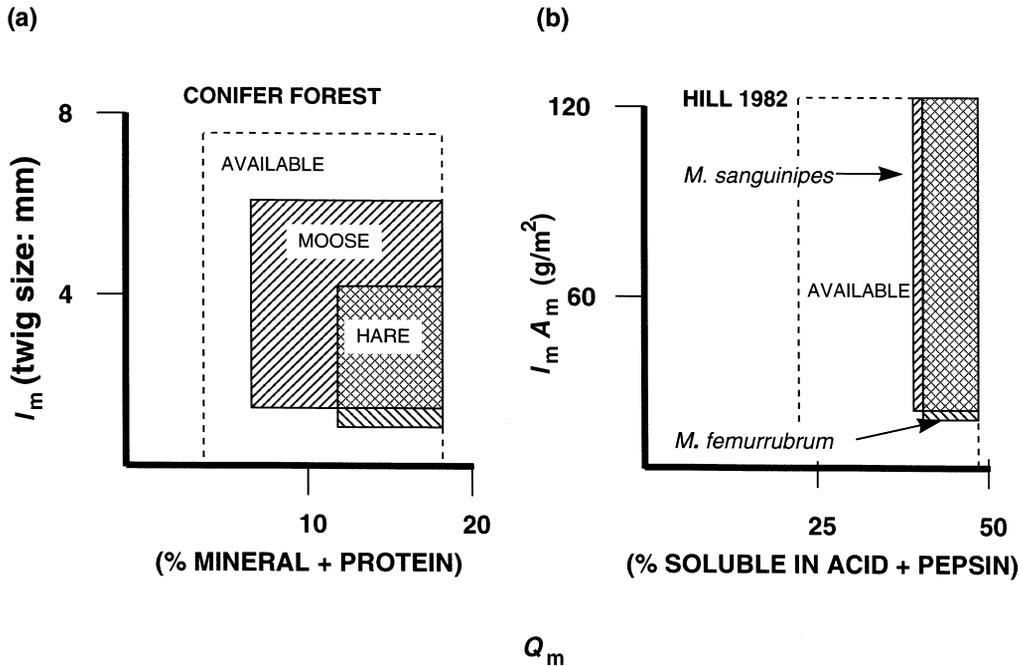


Figure 7. The measured Q_m and $I_m A_m$ values are used to define the exclusive and shared resources for competing species of herbivores: (a) moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) at Isle Royale, and (b) grasshoppers, *Melanoplus sanguinipes* and *M. femurrubrum* at the National Bison Range. The areas with hatching going in a single direction represent exclusive resources for one species and cross-hatched areas represent shared resources. The area defined by the dashed lines represents the available plant characteristics in the environment (modified from Belovsky, 1986a).

attain sufficient exclusive resources. These computations are straightforward because each body mass possesses unique Q_m and $I_m A_m$ values.

4. As in traditional analyses of limiting similarity (Hutchinson, 1959), herbivores (H1, H2...) were ranked by body mass from smallest to largest. For pairs of consecutively ranked herbivores, the ratio of the larger body mass to the smaller was computed and these ratios were plotted against the body mass of the larger herbivore.

Four main patterns emerge from the Q_m and $I_m A_m$ relationship, regardless of which assumption about the amount of exclusive resources is employed (2) (Fig. 6b,c). First, as herbivores increase in body mass, larger herbivores can be more similar in size; that is, the limiting similarity ratio becomes smaller. Secondly, as herbivore body mass increases, the limiting similarity ratio approaches an asymptote. A survey of the distributions of herbivore body sizes in different environments supports the first two predictions (Fig. 6d). Thirdly, as plant biomass increases, the asymptote of the limiting similarity ratio is predicted and observed to be approached at smaller body sizes (African savanna > prairie > boreal forest: Fig. 6d). Fourthly, as the value of ω (the power of Q in Equation 20) increases from 0 to 2, more species are able to co-exist and body sizes are more similar (Fig. 6a–c). At the extreme when $\omega = 0$ (Fig. 6a), only the largest herbivore will be present, because it will be able to utilize all of the food resources that smaller herbivores use, as well as plants of lower Q values. At this extreme, if competition for food is regulating herbivore abundance, then the largest herbivore will eliminate all smaller herbivores.

Therefore, the relationship between Q_m and $I_m A_m$ (Equation 20) provides insights into herbivore community structure, if competition for food were the mechanism structuring them. The community predictions appear to be consistent with empirical patterns. A critical assumption in this analysis, which needs future investigation, is what happens if the assumption that plants of all Q and IA characteristics are equally abundant is relaxed?

Competition between different body sizes versus different species

In the analyses conducted above, I refer to herbivore body sizes, not species, because several species of very similar sizes often co-exist in an environment in different habitats. This accounts for much of the observed deviation in body size ratios in different environments from the predictions of the Q_m and $I_m A_m$ relationship (Equation 20; see Fig. 6d). The richness of species with similar body masses in the same environment may be related to the foraging efficiencies (optimal nutrient intake/requirements) of different body sizes, so that more efficient body sizes can be represented by more species. If a body size provides optimal efficiency, there must be a solution to the following expression:

$$\partial(Edv - R)/\partial M = 0 \quad (21)$$

where E is food consumption (mass/time), d is proportion digestible, v is the nutrient content of the food (nutrient mass/mass ingested) and R is nutrient requirement (nutrient mass/time).

In the 'satisficing' approach, there is no body mass that leads to an optimal foraging efficiency, because food intake and requirements are proportional to $M^{2/3}$ and digestibility is a constant (see above). In the OFT scenario where time is only limiting, the largest herbivore that can live in an environment has the greatest foraging efficiency, because food intake is proportional to $M^{2/3}$ less a constant and requirements are proportional to $M^{2/3}$ (see above). However, in the OFT scenario when time and digestive capacity are limiting, the most efficient body sizes are intermediate. This occurs because the amount eaten (E : Equation 13), digestibility (d : Equation 12) and nutritional requirements ($R: \propto M^{2/3}$) do not create a function that is proportional to a single power of M :

$$E = D/r = k_1 M / \{k_8 + k_7 M^{1/3} + (k_8 + k_9 M^{1/3})^{1/2}\}$$

$$d = \varepsilon - \theta / \{k_8 + (k_8 + k_9 M^{1/3})^{1/2}\}$$

$$Ed \cong k_{22} M^\varphi + k_{23}$$

where $0.67 < \varphi < 1.0$. Because φ is different from the power of mass (0.67) defining nutrient requirements (R), there now is a solution to Equation (21) for the body mass that has optimal efficiency of resource use and this occurs at an intermediate herbivore body size.

Even though there is an optimal body size, this does not imply that a herbivore with that body size will out-compete all herbivores of other body sizes, because herbivores of other sizes have different exclusive resources. However, herbivores of this size will be able to survive and reproduce better on their exclusive and shared resources, than will herbivores of other sizes on their exclusive and shared resources. Furthermore, as herbivore body sizes increase or decrease from the optimum size, foraging efficiency declines. This general pattern of foraging efficiency with herbivore body size was supported by studies at the National Bison Range, and it was observed that sizes of greater efficiency were represented by more species (Belovsky, 1986a, 1987b) (Fig. 8). A similar phenomenological pattern was reported for energetic efficiency and species diversity in general (Holling, 1992; Brown, 1995).

Therefore, two levels of competitive interactions operate to affect herbivore diversity: between species in different body size categories and between species of a common body size. The level of competitive interactions between body sizes requires a perspective on competition that includes exclusive and shared resources (Schoener, 1974) and this perspective has been applied to herbivores

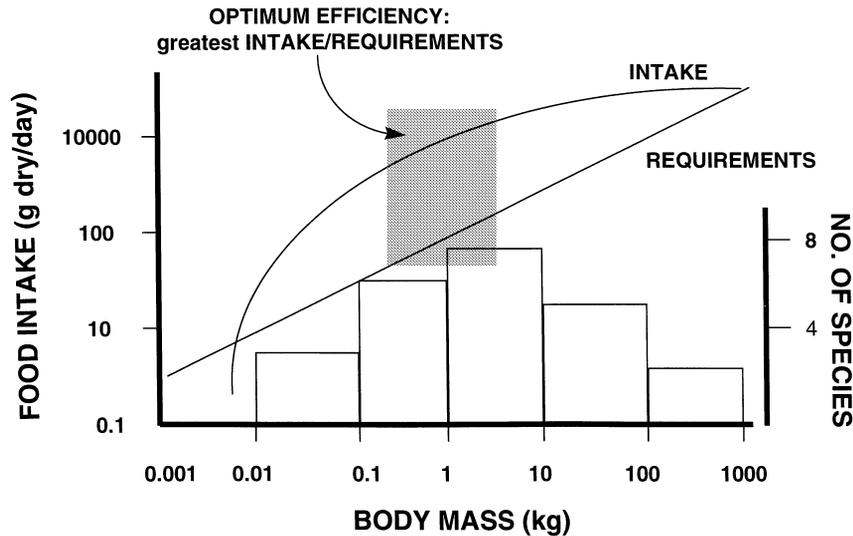


Figure 8. The observed energy intake is compared to energy requirements for herbivores of different body sizes at the National Bison Range. The difference between these two values defines foraging efficiency because of the log-log plot (greater difference, greater efficiency: shaded area) and body sizes with greater efficiency are represented by more species (modified from Belovsky, 1986b).

(Belovsky, 1984b, 1986b; Chase and Belovsky, 1994). The level of competition between species of similar size has not been addressed for herbivores, but I suspect that a perspective similar to Rosenzweig's (1981) model for segregation of species in different habitat patches may be fruitful. In fact, Schoener (1975) found that abundances of anole lizard species of different sizes on islands were consistent with competition when exclusive and shared resources were available, but the abundances of species of similar size were consistent with competition for different habitat patches. This perspective of competition at two levels is not commonly employed by ecologists, but may be very important for understanding biodiversity.

Facilitation between herbivores of different body masses

Facilitation cannot be examined in as straightforward a manner as competition, although the relationship between Q_m and $I_m A_m$ (Equation 20) clarifies the likelihood of observing facilitation. Facilitation by definition occurs when one herbivore body size enhances the abundance of plants with characteristics that are exclusively used by herbivores of another body size. For example, this would occur if large herbivores enhance the abundance of plants that provide low IA and high Q values, the characteristics sought by small-bodied herbivores, or enhance the ability of the small-bodied herbivores to find these plants. Because large herbivores will not feed in patches of plants with low IA , they cannot affect existing low- IA patches, but by feeding in patches of high- IA , they can convert them to low- IA .

How this enhancement might occur is not apparent. First, in the case of the large herbivore increasing the abundance of low- IA patches, although these patches can be used by small-bodied herbivores, they provide a lower nutritional benefit in a given time than high- IA patches for the small-bodied herbivores. This is unlikely to facilitate the small-bodied herbivores. Secondly, in the case of the large-bodied herbivores enhancing the ability of the small-bodied herbivores to find

foods, it is questionable how this would occur, because the small-bodied herbivores require plants of high- Q , but these are also preferred by the large-bodied herbivores. This means that even if the large-bodied herbivores 'opened' the vegetation so that small-bodied herbivores could find their foods more easily, it is likely that many of the foods required by the small-bodied species would have been eaten by the large-bodied species. Similar arguments can be made for the actions of small-bodied herbivores on large-bodied herbivores.

Therefore, facilitation does not naturally emerge from the analysis of herbivore foraging behaviour and its allometry, as do competitive predictions. In fact, the allometric analysis of foraging behaviour indicates that as the power of Q (ω) decreases in the relationship between Q_m and $I_m A_m$ (Equation 20), the likelihood of observing competition instead of facilitation increases. It is not surprising that the majority of claims for facilitation come from the East African savanna, the community with the largest value for ω (see above). However, there is also strong evidence from these communities that competition, rather than facilitation, occurs (see above).

Conclusions

I have applied several hypotheses about herbivore foraging ('satisficing', an OFT scenario when time is only limiting, and an OFT scenario when time and digestive capacity are limiting) in an allometric context to predict the minimum plant characteristics (chemical content or quality, and abundance or biomass per area) sought by herbivores of different body sizes. Considerable empirical evidence indicates that herbivores of different body sizes seek the plant characteristics predicted by the OFT scenario when time and digestive capacity are limiting.

I employ these results for the minimum plant characteristics sought by herbivores of different body sizes to demonstrate how the availability of plants with these different characteristics in the environment might influence herbivore community structure through competition or facilitation. Observations on herbivore body size distributions in different communities indicate that this OFT scenario is consistent with these distributions if herbivores compete for food.

The complex equations with numerous parameters needed to define the allometric perspective of the OFT scenario when time and digestive capacity are limiting become quite simple for defining the minimum plant quality and minimum plant abundance sought by a herbivore of a given body size. A remarkable result is that each herbivore body size possesses a unique minimum plant quality and minimum plant abundance in an environment. In this relationship, the minimum plant quality increases and minimum plant abundance decreases as herbivore body size declines. The form of competition depends on the ability of herbivores of each body size to utilize a range of plant characteristics that no other body size can use (exclusive resource), and a much larger range of plant characteristics that many other body sizes can use (shared resource).

The results indicate the utility of combining the long-standing allometric approach in ecology with OFT to examine differences in food selection between herbivores of different body sizes. But even more enticing, this allows us to realize at least in part the long sought linkage between behavioural/physiological ecology with population ecology, and population ecology with community ecology (Schoener, 1986; Hughes, 1990). This approach may help to unravel important issues related to the maintenance of biodiversity.

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Appendix

For the situation where feeding time and digestive capacity are both limiting feeding behaviour, the following relationship is obtained starting with Equations (2a) and (3):

$$\alpha(I_m A_m)^2 M^{2/3} = R/d_m v(T_T - T_S)$$

Because $T_S \propto D/(\alpha rIAM^{2/3})$ and $d_m \propto M^{2/3}br/vD$ (from Equation 1), T_S can be rewritten as:

$$T_S = k_{24}b/vLAd$$

Because $R \propto M^{2/3}$, we now have:

$$(I_m A_m)^\gamma = k_{25}/(dvT_T - k_{24}b/LA)$$

Because $d_m = Q_m (\varepsilon' - \theta'/s)$ (Equation 17), we have:

$$(I_m A_m)^\gamma = k_{24}/[vT_T Q_m (\varepsilon' - \theta'/s) - k_{24}b/LA]$$

θ'/s is expected to be relatively invariant, given the relationship for s (Equation 11) and the empirical values for s (Fig. 3c). This permits us to rewrite the function as:

$$(I_m A_m)^\gamma \approx 1/[\lambda Q_m - \phi]$$

Finally, because $\gamma \rightarrow 1$, we have:

$$I_m A_m \approx 1/[\lambda Q_m - \phi] \tag{1A}$$