Foraging and Optimal Body Size: An Overview, New Data and a Test of Alternative Models

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Studies of an optimal body size for individuals of different species based upon their foraging efficiency are reviewed and a detailed analysis of data specifically collected for this purpose is presented for *Microtus pennsylvanicus.* The natural selection of body sizes for some species is shown to be consistent with their foraging efficiency. However, a general model of optimal body size based on foraging efficiency (Reiss, 1986), unlike the species by species approach presented here, is shown to be incorrect.

Because energy transfers are ultimately limiting to all ecological systems (Odum, 1971), theories in foraging ecology have often been constructed with the assumption that feeding efficiency is subject to natural selection (Schoener, 1971; Pyke *et al.*, 1977; Krebs *et al.*, 1983; Stephens & Krebs, 1986). This includes the potential for the selection of body sizes during a species' life history based on foraging efficiency. Natural selection may not favor a body size that is most efficient for foraging, if predation, mate selection, microhabitat traits, etc., lead to stronger body size selection pressures. However, it is a possibility that ecologists must consider (Schoener, 1969*a,b*).

Because optimal foraging models (Schoener, 1969*b*; Pyke *et al.*, 1977; Krebs *et al.*, 1983; Pyke, 1984; Stephens & Krebs, 1986) are mathematically tractable, they can easily be adapted to look at the potential effect that foraging efficiency might have on the observed body sizes in a species' population. This is in contrast to another class of body size models that do not examine the mechanisms by which survival and reproduction vary with body size, and predict an optimal body size in terms of observed survival and reproductive parameters (Roff, 1981). In this paper, I wish to review briefly the existing data on this subject, present data on body size selection and foraging efficiency specifically collected to examine this question, and illustrate how a recently proposed model of optimal body size is incorrectly applied.

Previous Studies of Foraging Efficiency and Body Size Selection

Five empirical studies have tried to examine how foraging efficiency might act on body size selection (Belovsky, 1978, 1984*a*, 1987; Werner & Mittlebach, 1981; Reiss, 1986), after Schoener (1969*a,b*) initially raised this question. Werner & Mittlebach (1981) used bluegills (*Lepomis macrochirus*) to demonstrate that diet

and feeding patch choices by these fish were body size dependent. This should lead to selection for different body sizes in different habitats. However, it was found that predation pressure by bass (*Micropterus salmoides*) could largely override this body size selection in nature.

Using an optimal foraging model, Belovsky (1978, 1984a, 1987) has demonstrated for two herbivorous mammals (moose: *Alces alces*, and snowshoe hare: *Lepus americanus*) and the Kung! San human hunter-gatherers that an optimal diet choice model can be used to show that certain observed body sizes are consistent with the notion that selection for body size is dependent on foraging efficiency (size at weaning, maximum adult size and average adult size). Size at weaning and maximum adult size are set by the ability of individuals simply to satisfy their nutritional requirements, while average adult size is consistent with the size that provides the greatest nutritional intake above requirements (optimum body size). However, male moose were observed to exceed the optimum size presumably because foraging efficiency is of less importance than a male's need to be large for success in male–male competition for females.

Simple graphical presentations of these models appear in Fig. 1. The energy intake curves were computed using an optimal foraging model based on linear programming (Belovsky, 1978, 1984a, 1987), where the model was solved to predict maximum energy intake for individuals of different body sizes. The model is constructed incorporating digestive capacity, feeding times and nutritional limitations (constraints) that operate on the forager's diet choice. Each of the foraging model's constraints can be made functions of body size using regression analyses and the empirical data for each species or congeners. This leads to different predictions of maximum energy intake for different body-sized individuals. The minimum, maximum and optimal body sizes, as discussed above, are found by comparing the maximum energy intake and requirement levels for foragers of different body sizes.

Without any parameter value changes, Reiss (1982, 1986) applied my model for moose (Belovsky, 1978) directly to red deer (*Cervus elaphus*) to determine if an optimal body size existed for this species based on foraging. In this attempt, he was unable to find agreement between observed adult sizes and model predictions. Consequently, he found the moose model wanting. In response, he proposed a model for optimal body size based on foraging which he claimed to be more general since it incorporated commonly used interspecific allometric functions for digestive constraints to foraging.

Reiss' (1982, 1986) conclusion that the moose model (Belovsky, 1978) is inappropriate may be misleading, because he made errors in applying the model to red deer. First, he decoupled the body size model from the optimal diet model which led him to misquote my equation [equation (15): Belovsky, 1978] as his equation (1). Because of this, Reiss' model is solely a function of digestive capacity, not a function of all three constraints: digestive capacity, feeding time and nutritional requirements, as were used for moose (Belovsky, 1978). Furthermore, his model does not allow differences in food choice for individuals of different sizes, i.e. only one diet is used, which is very different from my model in which diets are predicted to vary with body size.
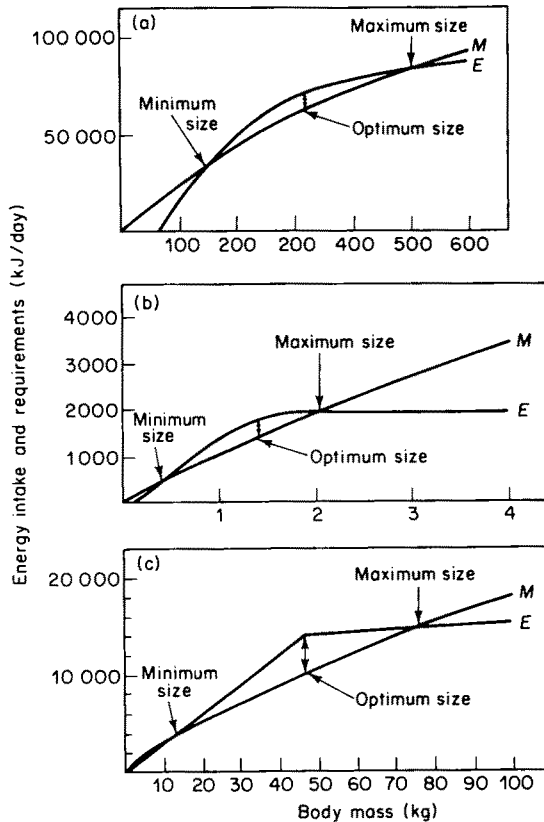
FIG. 1. The three figures simplify the body size models respectively presented in Belovsky (1978, 1984a, 1987) and do not present all the possibilities discussed in those papers. The energy intake function (E) is determined using an optimal foraging model employing the technique of linear programming with foraging constraints for digestive capacity, feeding time and other nutritional needs (e.g. sodium, protein, etc.) and solved to provide maximum energy intake. M is the maintenance metabolic requirement. For moose (a) and Kung! San (c), the minimum sizes correspond to the observed weaning sizes, while the minimum size for snowshoe hare (b) represents the size a juvenile must obtain to survive winter (another set of curves can be developed to predict weaning size). The predicted maximum size approaches the largest size observed for adult moose and Kung! San. The optimum sizes are near the observed sizes most adults asymptotically approach.

Second and most important, Reiss applied the empirical function that best fit the limited data on moose body mass vs. rumen capacity directly to red deer. A single allometric function for digestive capacity could not be applied in my prior studies, but Reiss attempted to do just this (see Belovsky, 1978, 1984a, 1987, below). Third, Reiss used a value of 3·42 times basal metabolic requirements for the red deer's maintenance metabolism, a value far exceeding that reported for most ruminants including red deer (av. value = 1·8–2·2: Moen, 1973; Parker & Robbins, 1983), except at peak lactation.

Because Reiss (1986) could not predict red deer sizes using my model for moose, he claimed that my empirical function for moose rumen capacity must be wrong.

This was his only choice since the digestive capacity was the only constraint in his model, unlike mine. Reiss criticized my function for this constraint on several grounds. First, Reiss (1986) argued that I used a constant digestive passage rate for moose of different sizes. It has not been demonstrated that there are large differences, if any, in passage rate with the growth of an individual ruminant.

Second, I measured stomach capacity, not rumen capacity; this was converted into rumen capacity using a proportion for rumen composition. This conversion was based on the ontogeny of white-tailed deer (*Odocoileus virginianus*) rumen proportions scaled by the relative body sizes of the two species. Reiss (1986) suggested that I should have used time rather than mass for scaling and data for dairy cattle rather than deer. However, mass is the most frequent scaling factor employed in these problems (Moen, 1973; Calder, 1984) especially since weight specific growth rates are slower for moose than deer (Moen, 1973). Also, data for scaling based on a wild congeneric species that is fed natural vegetation (deer) may be more appropriate than data from a domestic species from another genus that receives supplemental feed (cattle).

Third, the function I used for body mass vs. rumen capacity was a log–linear function, whereas Reiss (1986) argued that it should have been a power function with the exponent equal to $1 \cdot 0$ based upon interspecific allometry. Given the 21 observations available for moose stomach capacity, a log–linear regression provides a better fit on total stomach or computed rumen capacity (Pearson Correlation Coefficient $= 0 \cdot 92$ and $0 \cdot 96$), than Reiss' suggested power function (exponent $= 0 \cdot 93$: Pearson Correlation Coefficient $= 0 \cdot 80$ and $0 \cdot 87$, respectively). I originally chose to use the log–linear function on the basis of its better statistical fit.

If Reiss' criticisms of the moose model for body size are correct, then all my published analyses for other species (Fig. 1) should be incorrect. To examine the idea that body size may be selected on the basis of foraging efficiency and to address Reiss' (1982, 1986) criticisms directly, a data set collected specifically for this purpose is needed. Such data have been collected for *Microtus pennsylvanicus*. After this analysis is completed, an alternative model (Reiss, 1986) based on interspecific allometry will be examined.

Data for Optimal Body Size Analysis from *Microtus pennsylvanicus*

In the three studies of optimal body size that I have conducted (Belovsky, 1978, 1984*a*, 1987), the modeling of body size was not the primary goal. Rather these studies were directed toward examining optimal diet choices by the forager. To test my optimal body size model explicitly, a species is required that provides the opportunity to study a large number of individuals of different body sizes. *Microtus pennsylvanicus* satisfies these criteria.

The data collection for *M. pennsylvanicus* was conducted at the National Bison Range, Montana, and was described elsewhere (Belovsky, 1984*c*, 1986*a*; Belovsky & Slade, 1986). Rather than using average adult values as in Belovsky (1984*c*, 1986*a*), similar data were collected from 1981 to 1984, on *Microtus*, except observations were divided into body size categories (>10 g, $10 < 20$ g, $20 < 30$ g, $30 < 40$ g, $40 <$

50 g, and 50 + g) and analyzed for body mass relationships. The necessary parameters for the optimal diet model are presented in Table 1, as well as the allometric functions.

The foraging model employs the optimization technique of linear programming and has been described in detail in a number of papers (Belovsky, 1978, 1984a-c, 1986a,b, 1987). The linear programming model for *Microtus* employs three foraging constraints: daily digestive capacity, daily feeding time, and daily maintenance metabolic requirements (Belovsky, 1984c, 1986b). These constraint equations are

TABLE 1

The foraging model parameters used to model the diets of Microtus pennsylvanicus *of different sizes. The best fit function for the foraging parameter with body mass are presented, along with the predicted allometric function for comparison with Reiss' proposed values. Comparison with standard errors and sample sizes are also presented*

		Allometric function		
	Best fit	Best fit	Reiss' proposed	Sig. diff.
Digestive constraint:				
Capacity (g wet wt)	$-6.39 + 7.56 \log M$ $r = 0.85, N = 91$ $P < 0.001$	$0.29 M^{0.80 \pm 0.05}$ $r = 0.84, N = 91$ $P < 0.001$	$\propto M^{1.0}$	Yes
Turnover (times/day)	Constant $= 6.8$ ± 0.56 $N = 5$	$9.32 M^{-0.09 \pm 0.18}$ $r = 0.28, N = 5$ N.S.	$\propto M^{-0.33}$	No
Food bulk (wet wt/dry wt):				
Monocot[a]	1.64	—	—	—
Dicot[a]	2.67	—	—	—
Time constraint:				
Feeding time	265; $M \le 30$ g— 48 hr total observations			
(min/day)	231; $M > 30$ g— 48 hr total observations			
Cropping rate (min/g dry wt):				
Monocot	$1142.15 M^{-1.12 \pm 0.18}$ $r = 0.98, N = 30$ $P < 0.001$ Constant for $M \ge 40$ g	—	—	—
Dicot[b]	$591.31 M^{-1.12}$ Constant for $M \ge 40$ g	—	—	—
Energy requirements:				
Metabolism (kJ/day)[c]	$4.11 M^{0.80}$	—	$\propto M^{0.75}$	No
Digestible energy value (kJ/g dry wt):				
Monocot	$8.84 \pm 0.21, N = 6$	—	—	—
Dicot	$9.63 \pm 0.32, N = 7$	—	—	—

[a] Belovsky (1986b).
[b] Based on function for monocot since only 40 g individuals were studied feeding on dicots.
[c] Packard (1968), Wiegert (1961).

written in the form:

$C \geq aM + bD$ (e.g. digestive and feeding time constraints)

$C \leq aM + bD$ (e.g. metabolic requirements)

(1)

where C is the constraint value, M is the dry mass intake of monocots, D is the dry mass intake of dicots, and a and b convert this ingestion into the constraint units.

The linear programming model's constraint for feeding time reflects the *Microtus'* maximum available daily feeding time as limited by the thermal environment and *Microtus* physiology (Belovsky, 1986b; Belovsky & Slade, 1986), and how this time can be used in cropping foods whose acquisition require different amounts of time (cropping rate). The model's digestive capacity constraint represents the *Microtus'* stomach and caecal capacity multiplied by the daily passage rate of digesta through these organs and how this capacity can be filled by foods with different bulkiness (wet wt/dry wt). The metabolic requirement represents the *Microtus'* energy needs for survival and its satisfaction by the energy content of different foods.

From previous studies of *Microtus* foraging using this model (Belovsky, 1984c, 1986b), adults were shown to select a diet which maximizes daily energy intake, rather than minimizing their daily feeding time. Energy maximization is the expected goal if energy intake limits survival and reproduction, while time minimization is the goal if time spent in other activities (hiding from predators, mating, etc.) determines survival and reproduction, after minimal nutritional needs are satisfied (Belovsky, 1984c, 1986a).

Diet composition was predicted by the model in terms of the ingestion of monocots and dicots. These two food types differ nutritionally and in their feeding constraint parameters (a and b, above), while the plant species composing each category are similar in these traits. Most important, the two food categories are distributed in different patches in the environment requiring the forager to search for each separately (Belovsky, 1984c, 1986a,b).

Making the model's constraint parameters functions of body size (Table 1), the energy-maximizing and time-minimizing diets for individuals of different body sizes can be predicted. The model's predicted energy-maximized diets for *Microtus* of different body sizes appear in Fig. 2(a) and are compared with the observed diets. The observed diets were measured using microhistological examination of stomach contents (Belovsky, 1984c, 1986b) from snap-trapped individuals of different body masses. The model predicts changes in diet composition very similar to those observed for individuals of different body size categories (predicted diet vs. observed: Pearson Correlation Coefficient $= 0.87$, $N = 6$ body size categories, $P < 0.05$). If these microtines were time minimizers, the diet would contain no monocots for any body size category, and if they chose foods in proportion to their encounters with them in the environment, the diet would be 70% monocots. Therefore, *Microtus* of all body sizes appear to be energy maximizers.

The observed *Microtus* diets are significantly different for *Microtus* of different body sizes (ANOVA: $F_{5,9} = 3.77$, $P < 0.04$). These results indicate that the model presents real diet choice differences for individuals of different body sizes. The
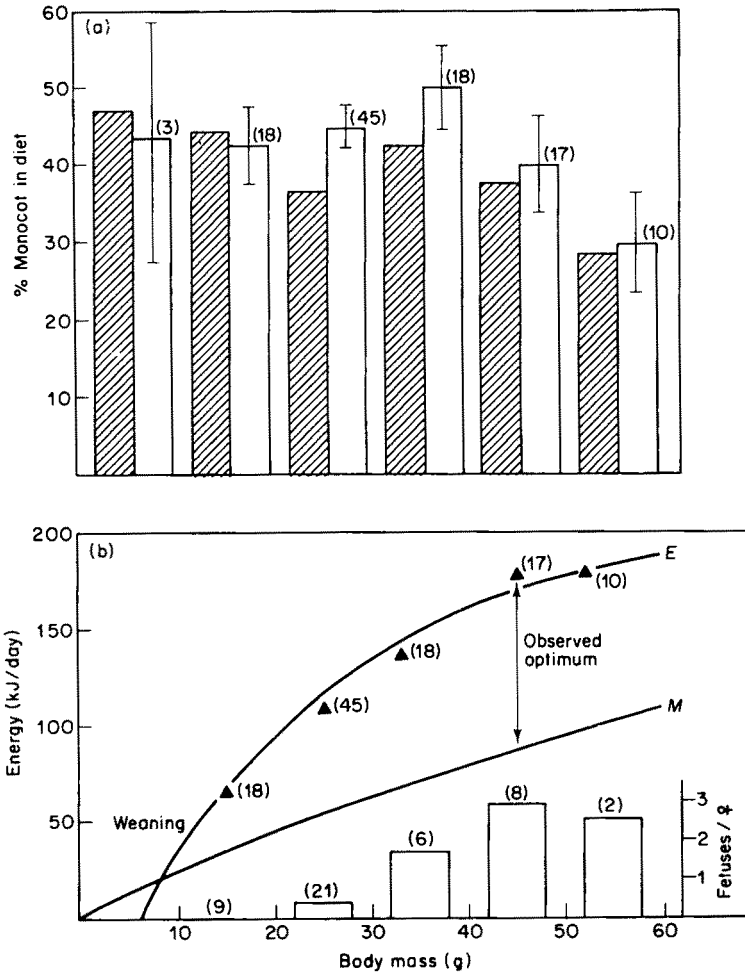
FIG. 2. (a) The observed diets for *Microtus pennsylvanicus* of different sizes (non-cross-hatched area ±S.E. and sample size in brackets) are compared with the optimal foraging model's predictions for a diet which maximizes energy intake. (b) The maximum energy intake predicted (triangles) by the foraging model and the best fit regression using a log-linear function (E) are presented for *Microtus pennsylvanicus* of different body sizes. M is their maintenance requirement. A minimum size corresponding to weaning and an optimum size corresponding to the body size with peak reproductive output are shown. Reproductive output is measured as average number of fetuses/♀ (sample sizes in parentheses and are too small to demonstrate significant differences for the body size categories, 30–60 g).

ANOVA was conducted using a single average diet value for each body size category/year, providing up to three values for each body size category, one for each year that diets were studied. This was necessary since stomach contents reflect a single meal, not an individual's average diet.

Curves which represent the linear programming model's predictions of maximum energy intake for *Microtus* of different body sizes and their maintenance energy requirements are presented in Fig. 2(b). The intersections of these two curves predict

the energetic limits to body size: weaning (lower intersection) and maximum body size (upper limit is not shown). The size at which the distance is greatest between the two curves is the optimal adult body size. This approach is the body size model I have used for moose, snowshoe hare and Kung! San (Belovsky, 1978, 1984a, 1987), not Reiss' (1986) model that he attributed to me.

The minimum size predicted for weaning, 8 g, corresponds very well with the observed weaning sizes, 7–9 g, determined by rearing a litter of five young at the study site. The maximum size predicted, 156 g, is much larger than that observed, 60 g; the same degree of discrepancy was reported for snowshoe hare (Belovsky, 1984a). Perhaps the selection pressure to have a body size near optimum is severe, or other selection pressures against a very large body size prevent the observation of individuals near this maximum, as was observed for larger species (e.g. moose and humans: Belovsky, 1978, 1987).

Finally, and most importantly, an optimum body size of 40–50 g is predicted. The observed average body size in the field for a reproductive female was found to be $44 \cdot 2 \pm 10 \cdot 7$ g ($N = 17$) and for males, $42 \cdot 2 \pm 9 \cdot 9$ g ($N = 19$); these weights were used to define adult body sizes. Reproductive females were defined as those pregnant or lactating, while reproductive males were those with distended testes. Many individuals of the same size as reproductive individuals were not reproductive; using all individuals larger than the smallest observed reproductive individual (female = 29 g; male = 27 g) gives mean adult sizes of $41 \cdot 6 \pm 9 \cdot 9$ g ($N = 21$) for females and $38 \cdot 5 \pm 9 \cdot 8$ g ($N = 38$) for males. Using either measure, the average adult size is not different from the predicted optimal size range.

Another way of examining the optimal body size is to compare the number of fetuses per female (reproductive potential) with her predicted energy intake based on foraging efficiency. Reproductive potential is highly correlated with energy intake less maintenance metabolism [Fig. 2(b): Pearson Correlation Coefficient = 0·91, $N = 5$, $P < 0 \cdot 05$]. The largest observed number of fetuses per female occurs in the optimum body size range; this value is not significantly different from the size class values on either side of it (ANOVA, $P < 0 \cdot 05$). A larger sample size is needed.

The results for *Microtus* are consistent with the body size findings for other species (Belovsky, 1978, 1984a, 1987), but the data for *Microtus* are more complete and can be used to address Reiss' (1982, 1986) criticisms of my approach. Reiss (1986) suggests that digestive passage rate and capacity should be power functions of body size with specific exponents. The observed digestive passage rate and body mass data, when fit to a power function, are not significant (Table 1), contrary to Reiss. Therefore, a constant value was used in the model. The observed digestive capacity data are highly correlated with body mass, but the exponent in the power function is significantly different from Reiss' (1986) suggested interspecific value of 1·0 (Table 1). This last difference is very important since it negates Reiss' main criticism of my earlier moose model. In particular, the "best fit" function for *Microtus* is the same function I used for moose, a log–linear function.

Even more important, Reiss (1986) argues that the energy intake function should be proportional to body mass raised to the 0·67 power; however, the empirical function for *Microtus* has an exponent of $0 \cdot 93 \pm 0 \cdot 15$ (95% confidence interval),

which does not encompass his suggested value ($P < 0.05$, significant difference). Furthermore, this is not the "best fit" function, since a log-linear function explains more variance, 99% vs. 94%. Finally, even the "best fit" regression for *Microtus* net energy intake based on observed values is not adequate to develop a simple model of body size since the changes in diet choice with body size cannot be expressed by a simple regression. Therefore, Reiss' (1986) allometric arguments are not only inappropriate for modeling body size selection based on foraging efficiency, but his suggested functions do not apply.

An Alternative Model

In lieu of collecting the necessary empirical data to test the above model for optimal body size using red deer, Reiss (1986) offers an alternative model based on allometry. Reiss (1982, 1986) attempts to find the body size that has the highest energy intake above maintenance energy requirements, as I do. So what is the difference between our approaches?

I use an optimal foraging model to determine energy intake for individuals of different body sizes (Belovsky, 1978, 1984a, 1987) which employs the optimization technique of linear programming with constraint equations for digestive capacity, feeding time and other nutritional requirements. Reiss (1986) does not use an optimal diet model but sets energy intake equal to only one of my proposed feeding constraints, digestive capacity. Reiss' model is written as:

$$E = R(KD - S)/B, \qquad (2)$$

where E is energy intake, R is digestive capacity, K is the gross energy content of ingested food, D is the percent digestibility, S is the energetic cost of moving to collect a unit mass of food and B is the food bulkiness (wet wt/dry wt). This is the equation Reiss incorrectly calls my model (Belovsky, 1978).

Reiss (1986) assumes that the digestible energy content (KD) of foods is constant for animals of different body sizes if they eat the same food types (e.g. plants). However, KD changes for each foraging species due to differences in the food parts and species it selects and its digestive capabilities. Therefore, the model proposed by Reiss (1986) is not as appropriate as it first appeared.

Next, Reiss (1986) uses standard interspecific allometric functions for digestive organ capacity and passage rates in his model. Table 2 presents the allometric

TABLE 2

Comparison of Reiss' (1986) suggested allometric functions for his model of body size and empirical values from my studies, using data in Table 3

	Reiss (1986)	Belovsky (1986b)	Significant difference
Function:			
Digestive capacity	$\propto M^{1.0}$	$\propto M^{0.96}$	N.S.
Digestive turnover	$\propto M^{-0.33}$	$\propto M^{-0.35}$	N.S.
Energy intake	$\propto M^{0.67}$	$\propto M^{0.63}$	N.S.
Metabolism	$\propto M^{0.75}$	—	—

functions Reiss used for each model parameter. Table 3 presents field data used and generated from my studies of the optimal foraging of 15 species of herbivores at one study site (Belovsky, 1986*b*), including the *Microtus* data used above. In no case do my data lead to interspecific allometric functions different from those proposed by Reiss (see comparison in Table 2). I have used these allometric functions to develop a general optimal foraging model for herbivores of different body sizes (Belovsky, 1986*a*).

However, the most important difference in our approaches is that Reiss (1982, 1986) uses the standard interspecific allometric functions, rather than unspecified functions which are determined for each species, as I do. Interspecific allometric functions represent average values for different species. Calder (1984), in his review of ecological applications of allometry, bluntly states that interspecific allometric functions *do not* necessarily apply to intraspecific ontogenetic relationships (pp. 5, 358–365; also see Harvey, 1982).

Allometric power functions are written as αM^{β}, where α and β are constants and M is body mass. If Reiss' model parameters for individuals of different body sizes within a species scale allometrically, then for his model to predict each species' optimal body size, the α values must be species specific. Furthermore, the α values for different species must also be mass dependent, if the model predicts a smaller optimum size for small species than for large species (see Calder, 1984; pp. 358–365). Therefore, it is virtually impossible for species specific allometric functions and the interspecific allometric functions to have the same exponent (β) of body mass, since α must also be an allometric function.

Given the above problem in using interspecific allometric functions, Reiss' model will not predict the optimal body size for a species. Rather, the model predicts the optimal body size for a species in an ecological guild, i.e. the species which feeds on a type of food (e.g. herbivore) that has the greatest absolute energy intake above its needs. For herbivores, Case (1979) has theoretically argued and I have empirically

TABLE 3

Data used to compute allometric functions for a set of herbivores in the same environment (Belovsky, 1986b)

	Mass (kg)	Digestive capacity (g wet wt)	Digestive turnover (times/day)	Energy intake (kJ/day)
Microtus pennsylvanicus	0·035	4·0	7·8	133
Spermophilus columbianus	0·35	43·0	7·3	1282
Sylvilagus nutalli	1·0	92·0	6·9	3017
Marmota flaviventris	2·5	230·0	4·7	5046
Antilocapra americana	46·0	5942·0	1·14	25 725
Ovis canadensis	72·0	4653·0	1·14	27 063
Odocoileus virginianus	80·0	4200·0	1·14	18 713
Odocoileus hemionus	90·0	4386·0	1·14	19 664
Cervus elaphus	318·0	21 159·0	0·45	59 379
Bison bison	636·0	87 700·0	0·30	198 929

demonstrated that there may exist an optimal body size within a guild for a given environment. This body size identifies the most abundant and productive species' populations. Also, this body size should be represented by the largest number of species. Rather than using the absolute energy intake above needs as Reiss (1986) does, these studies use energy intake divided by needs which is more appropriate to make interspecific comparisons over a wide range of body sizes (Schoener, 1969a, 1971).

The optimum body size for a guild in a given environment will not competitively exclude other species with different body sizes. I have argued elsewhere (1986b) that herbivore species of different body sizes will persist together in an environment because they partially use different food plant resources due to their different foraging constraints that are body size dependent. This assumes that the different food plant resources that each body size uses are sufficiently abundant in the environment.

An example of this community ecology approach, which is similar to Reiss' model, is presented in Fig. 3 using the data in Table 3. The intersections of the energy requirement and intake lines reflect the smallest and largest species body sizes expected in the guild. The size at which the two lines are farthest apart (greatest ratio of intake to needs because the logarithms of the data are plotted) reflects the
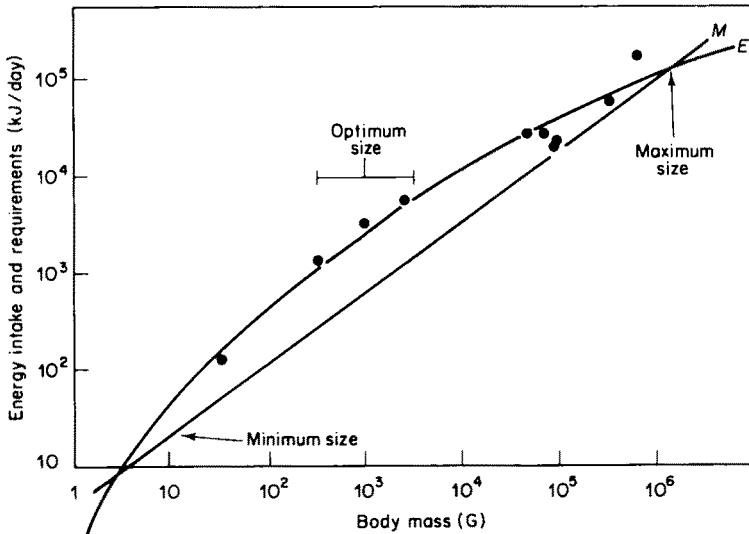

FIG. 3. The relationship for the observed energy intake (E) and maintenance metabolic (M) needs for different mammalian herbivores in the same environment, the National Bison Range, Montana (Belovsky, 1986b), are presented. Because the arithmetic and log-log data are non-linear, a best-fit function was sought for the different observed energy intake values (E line) and was not intended to have any particular biological interpretation. A polynomial regression [$3\cdot32 + 2\cdot06(\log(x^{0\cdot33})) - 0\cdot29(\log(x^{0\cdot33}))^2$] provides the best fit (Pearson Correlation Coefficient = $0\cdot99$). This and a number of other curvilinear regressions (log-linear, power, etc.) using the log-log data provide a minimum size between 10^{-3} and 10^{-2} kg which corresponds to an 8×10^{-3} kg newly weaned microtine, and a maximum size slightly larger than 10^3 kg which corresponds to the largest mammalian herbivore, a $1\cdot2 \times 10^3$ kg bull bison; the optimum size range corresponds to a species size range that is represented by the greatest number of herbivore species (Belovsky, 1986b).

species body sizes in a guild that are most efficient for that environment and are presented by the greatest number of species. All predicted sizes are consistent with the observed body sizes (Belovsky, 1986b). Although the model is similar to my optimal body size model for each species, it is not the same.

Finally, Reiss discounts his own model and any model of optimal intraspecific body size, claiming that these models are too sensitive to parameter changes. This makes the models' predictions too volatile with slight errors in parameter estimates. Given that Reiss' model does not depict an optimal intraspecific body size and is different from my models presented above, his sensitivity analyses are not applicable. My models of intraspecific optimal body size are not nearly as sensitive as Reiss' model, since my energy intake functions are not as "flat" as Reiss'. The "flatness" of the energy intake functions is defined by the exponent of the allometric power function defining intake; the nearer the exponent is to zero, the "flatter" the curve. The empirical exponents measured in my analyses are much larger than Reiss claims.

Conclusion

Modeling and the investigation of body size selection on the basis of foraging efficiency alone may not always be completely appropriate (Werner & Mittlebach, 1981), but the successes reported here and elsewhere (Belovsky, 1978, 1984a, 1987) indicate the need for further investigation. The handful of successes, however, do not constitute a general model, nor can a simple general model based on allometric functions with known interspecific constants be expected, contrary to Reiss' (1986) claims. Rather a species by species approach is required.

REFERENCES

BELOVSKY, G. E. (1978). Theor. Pop. Biol. 14, 105.
BELOVSKY, G. E. (1984a). Theor. Pop. Biol. 25, 235.
BELOVSKY, G. E. (1984b). Am. Midl. Nat. 111, 209.
BELOVSKY, G. E. (1984c). Am. Nat. 124, 97.
BELOVSKY, G. E. (1986a). Am. Zool. 26, 51.
BELOVSKY, G. E. (1986b). Oecologia, Berl. 70, 35.
BELOVSKY, G. E. (1987). J. Anthrop. Arch. 6, 29.
BELOVSKY, G. E. & SLADE, J. B. (1986). Oecologia, Berl. 70, 53.
CALDER, W. A. III. (1984). Size, Function, and Life History. Cambridge, Massachusetts: Harvard University Press.
CASE, T. J. (1979). Acta Biotheor. 28, 54.
HARVEY, P. H. (1982). J. theor. Biol. 95, 37.
KREBS, J. R., STEPHENS, D. W. & SUTHERLAND, W. J. (1983). In: Perspectives in Ornithology: Essays Presented for the Centennial of the American Ornithologists' Union. (Brush, A. H. & Clark, G. A. Jr, eds). Cambridge: Cambridge University Press.
MOEN, A. (1973). Wildlife Ecology: An Analytical Approach. San Francisco: W. H. Freeman.
ODUM, E. P. (1971). Fundamentals of Ecology. Philadelphia: W. B. Saunders.

PACKARD, G. C. (1968). *J. Mamm.* **49,** 215.

PARKER, K. L. & ROBBINS, C. T. (1983). *Can. J. Zool.* **62,** 1409.

PYKE, G. H. (1984). *Ann. Rev. Ecol. Syst.* **15,** 523.

PYKE, G. H., PULLIAM, H. R. & CHARNOV, E. L. (1977). *Quart. Rev. Biol.* **55,** 137.

REISS, M. J. (1982). *New Sci.* **96,** 226.

REISS, M. J. (1986). *J. theor. Biol.* **122,** 237.

ROFF, D. (1981). *Am. Nat.* **118,** 405.

SCHOENER, T. W. (1969*a*). *Am. Nat.* **103,** 277.

SCHOENER, T. W. (1969*b*). *Brookhaven Symp. Biol.* **22,** 103.

SCHOENER, T. W. (1971). *Ann. Rev. Ecol. Syst.* **2,** 369.

STEPHENS, D. W. & KREBS, J. R. (1986). *Foraging Theory.* Monographs in Behavior and Ecology. Princeton, New Jersey: Princeton University Press.

WERNER, E. E. & MITTLEBACH, G. G. (1981). *Am. Zool.* **21,** 813.

WIEGERT, R. G. (1961). *Ecology* **42,** 245.