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Predicting Herbivore Feeding Times

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Abstract

An understanding of animal time budgets is crucial to behavioural biology. Although many studies have analysed time budgets of individual species, only a few have made interspecific comparisons. Here we take an interspecific look at one part of the time budget, feeding time. We hypothesize that feeding time can be predicted by the amount of time an animal needs to reach satiation. This time should be equal to the ratio of handling time to digestion time. For 19 herbivorous species from insects to mammals, we calculate this ratio and compare it to the observed feeding time. The mean difference between calculated and observed values is small (a half hour per 24 h-day), indicating that herbivore feeding times can often be approximated by the ratio of handling time to digestion time. We make three points concerning the time allocated to feeding in herbivores based on this interspecific comparison. First, our analysis suggests that herbivores often feed to satiation, which could mean that they are often released from time constraints. It is also possible, however, that while herbivores have enough time to reach satiation, they do not necessarily have sufficient time to choose the most desirable diet. Wilson's principle of stringency theoretically supports the former interpretation. It suggests that animals experience periods in their life in which they are time-constrained but that these periods are the exception rather than the rule. Most optimal foraging studies have assumed the opposite. The second point of this paper is therefore a recommendation: to consider the possibility that animals may often be released from time constraints. The third and final point is that feeding time is independent of body mass in our analysis. This is because handling time scales with body mass according to a parameter that is similar to the one for digestion time, and feeding time can be approximated by the ratio of handling time to digestion time.

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Introduction

Given that foraging time influences energy input and thus, indirectly, fitness (Schoener 1971; Stephens & Krebs 1986), why do, for example, mammals spend on average 61.5% of a 24 h-day or $14\frac{3}{4}$ h/d resting or sleeping (n = 222 species) and only 30.5% or 71/2 h/d foraging (n = 120) (Bunnell & Harestad 1990; see also Herbers 1981 and Owen-Smith 1988)? These and similar general questions on animal time budgets are crucial to behavioural biology. Although time budgets of individual species have attracted considerable attention, few studies have compared time budgets across species or have investigated general questions in this context (but see Herbers 1981, Owen-Smith 1988, or Bunnell & Harestad 1990). In this study, we take a general interspecific look at one part of the time budget, feeding time. We propose a null hypothesis for feeding time, namely that it should be equal to the time an animal needs to reach satiation.

Based on a review of empirical data, Jeschke et al. (2002) recently concluded that most animals need less time for handling a food item (i.e. capturing and eating it), than for digesting it (see also Karasov and McWilliams, in press). Because digestion is a passive process, it does not prevent animals from searching for food or handling it, nor from non-foraging activities such as avoiding predators or lying in the shade (Jeschke et al. 2002). Consequently, if food is sufficiently abundant to be found quickly, and if essential non-foraging activities do not take too much time, the foraging time of most species will be determined by their physiological needs (see also Herbers 1981). Foraging time is searching time plus feeding time. We here focus on the latter and hypothesize that feeding time can be predicted from the amount of time an animal needs to satisfy its physiological needs. We show that feeding time calculated in this way agrees well to observed feeding time and that, at least for the species analysed here, feeding time is independent of body mass.

The Model

Our model assumes that an animal's motivation to search for food or consume it is negatively correlated with the amount of food already present in its gut. This assumption is supported by work by McMahon & Rigler (1963), Holling (1966), and others. Our model also assumes that there exists a certain level of gut fullness beyond which the animal's motivation to search for food or consume it completely ceases, i.e. the animal is satiated. All animals that require less time for handling a food item than for digesting it, which appears to be true for most animals (Jeschke et al. 2002), can and do experience satiation under favourable environmental conditions (reviewed by Jeschke et al. 2002). Our model is not applicable to animals that cannot experience satiation. Note that the level of gut fullness that signals satiation is not a constant but can vary according to conditions. Mammals and birds, for example, need much more energy when faced with low temperature or during periods of production, e.g. lactation or migratory fattening (Weiner 1987; Diamond & Hammond 1992; Owen-Smith 1994; Winter

1998; Illius et al. 2002; Karasov and McWilliams, in press). Relative to baseline conditions, such hyperphagic animals need about twice as much energy to reach satiation (see Karasov and McWilliams in press for additional details). The level of gut fullness signalling satiation, therefore, is higher under hyperphagic than under baseline conditions.

We term the feeding time of an animal, as determined by its physiological needs, predicted feeding time $\hat{t}_{feed}$ (dimensionless), which is a fraction of time t. The predicted feeding time is the time an animal needs for handling one food item, b (time/food items), multiplied by the number of food items it needs to consume during t to reach satiation, y_s (food items/time):

$$\hat{t}_{feed} = b \cdot y_s. \tag{1}$$

Satiating food consumption rate y_s is the ratio of gut capacity g (food items), which is the number of food items that the gut of a satiated animal (i.e. one fed *ad libitum*) can hold, to the corresponding gut retention time t_g (time):

$$\hat{t}_{feed} = \frac{b \cdot g}{t_g} \tag{2}$$

Gut retention time is the average amount of time that a food item is retained in the gut of an individual. It is important to note, however, that t_g is a specific gut retention time: it relates to satiated individuals, i.e. it is the amount of time a food item is retained in the gut of a *satiated* individual. This specification is necessary because retention times are variable: they usually decrease with increasing gut fullness (Bernays & Simpson 1982; van Hoven & Boomker 1985). Equation (2) can be simplified by replacing the ratio of retention time to gut capacity, t_g/g, by digestion time c (time/food items), which, of course, also relates to satiated individuals:

$$\hat{t}_{feed} = \frac{b}{c} \tag{3}$$

This means that if an animal spends as much time feeding as it needs to reach satiation, its relative feeding time should equal the ratio of its handling time b to its digestion time c. Note that c is the reciprocal value of satiating food consumption rate y_s (compare eqn 3 with eqn 1), a theoretical result that is in accordance with Jeschke et al. (2002).

Data Considerations

Before comparing our model to empirical data, we describe the type of data needed for a reasonable comparison.

First, a species can only be used for our analysis if we have data on its feeding time, handling time, and digestion time. Alternatively, we need information to calculate these data.

Second, all data must be obtained under similar conditions. This is because for a given species, the values of the variables included in our model are condition-dependent. For example, hyperphagic animals need about twice as much energy to reach satiation as do animals living under baseline conditions. Hyperphagic animals consequently need more feeding time to reach satiation. Hence, when comparing our model to empirical data for a given species, it is necessary that all data have been obtained under similar conditions, e.g. that all data are either from hyperphagic individuals or from individuals living under baseline conditions. For animals with highly variable handling or digestion times that are dependent on their diet, e.g. for most mammalian herbivores (van Hoven & Boomker 1985; Appendix 1), the data must have been obtained for a roughly equal diet.

Third, we must be wary of tautology. For example, Owen-Smith & Novellie (1982) calculated the handling time of greater kudus (*Tragelaphus strepsiceros*) from the observed feeding time and an estimation of the consumption rate, which was, in turn, assumed to be satiating. In other words, the handling time of the kudus was calculated under the assumption that eqn (1) is valid, i.e. that our model is valid. It would be tautological to compare such data to our model.

Fourth, our model is not applicable to animals that cannot experience satiation. This is the case for a few species with special foraging characteristics: (1) The rare consumers that need as much or more time for handling their food than for digesting it ($b \geq c$), e.g. naticid gastropods of the species *Polinices duplicatus* that drill through the shells of *Mya arenaria* (Jeschke et al. 2002). (2) Predators such as pythons that are adapted to rare meals.

We searched the literature and found data from 19 species (one nectarivore and 18 herbivores) that meet these four requirements (Appendix 1). The body mass of these species ranges from 0.28 g (grasshoppers) to 636 kg [bison (*Bison bison*)], covering 7 orders of magnitude. One of these species is the yellow-bellied marmot (*Marmota flaviventris*), which we use as an example to briefly show how we assessed eqn (3) using empirical data: an average marmot observed by Belovsky (1986) at the National Bison Range, Montana, needed 0.425 min for handling 1 g-dry mass of its diet (i.e. for biting, chewing, and swallowing its food), and needed 3.40 min for digesting this amount of food under *ad libitum* conditions (Appendix 1). Hence, the predicted feeding time $\hat{t}_{\mathrm{feed}} = (0.425\ \mathrm{min/g\text{-}dry\ mass})/(3.40\ \mathrm{min/g\text{-}dry\ mass}) = 0.125 = 12.5\%$ of a 24 h-day or 3 h/d. The observed feeding time was 13.6% or $3\frac{1}{4}$ h/d. See Appendix 1 for a detailed outline of all data used in the analysis and of the computations made.

Results and Discussion

Predicted and Observed Feeding Times

The observed feeding times agree well with our predicted values (Fig. 1). For all species, the mean difference between $\hat{t}_{\mathrm{feed}}$ and t_{feed} is only 1.9 percentage points or 27 min/d (100% would equal 24 h/d), and the median difference, which is not

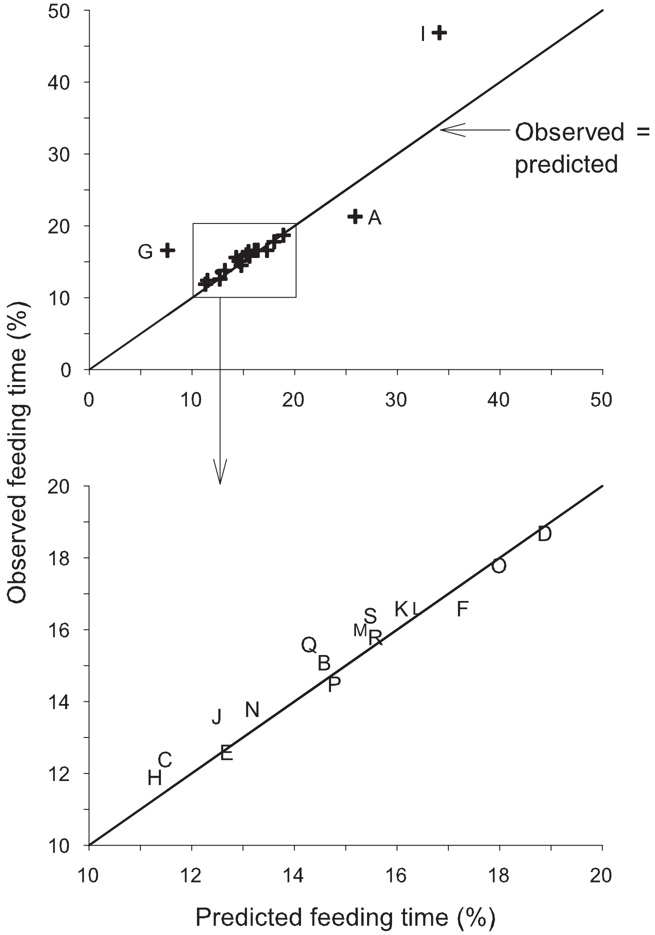

Fig. 1: Scatter plots of observed feeding times t_{feed} vs. predicted values $\hat{t}_{\mathrm{feed}}$. The latter were calculated with eqn (3); see Appendix 1 for details and references. Both t_{feed} and $\hat{t}_{\mathrm{feed}}$ are given as fractions of 24 h-days. Letters indicate species: (A) moose (*Alces alces*)$^{\mathrm{T}}$, (B) pronghorn antelope (*Antilocapra americana*)$^{\mathrm{T}}$, (C) bison (*Bison bison*)$^{\mathrm{T}}$, (D) beaver (*Castor canadensis*)$^{\mathrm{T}}$, (E) elk (*Cervus elaphus*)$^{\mathrm{T}}$, (F) undulant-winged grasshopper (*Circotettix undulatus*)$^{\mathrm{T}}$, (G) Carolina grasshopper (*Dissosteira carolina*)$^{\mathrm{T}}$, (H) snowshoe hare (*Lepus americanus*)$^{\mathrm{M}}$, (I) giant rams-horn snail (*Marisa cornuarietis*)$^{\mathrm{C,M}}$, (J) yellow-bellied marmot (*Marmota flaviventris*), (K) red-legged locust (*Melanoplus femur-rubrum*)$^{\mathrm{T}}$, (L) migratory grasshopper (*Melanoplus sanguinipes*)$^{\mathrm{T}}$, (M) meadow vole (*Microtus pennsylvanicus*)$^{\mathrm{C}}$, (N) mule deer (*Odocoileus hemionus*)$^{\mathrm{T}}$, (O) white-tailed deer (*Odocoileus virginianus*)$^{\mathrm{M}}$, (P) bighorn sheep (*Ovis canadensis*)$^{\mathrm{T}}$, (Q) rufous hummingbird (*Selasphorus rufus*), (R) Columbian ground squirrel (*Spermophilus columbianus*), (S) Rocky Mountain cottontail (*Sylvilagus nuttali*)

$^{\mathrm{C}}$Captive animals.

$^{\mathrm{M}}$Mean $|\hat{t}_{\mathrm{feed}} - t_{\mathrm{feed}}|$, calculated from the values reported in Appendix 1.

$^{\mathrm{T}}$Negative correlation between daily activity time and temperature.

so sensitive to outliers, is only 0.6% or 9 min/d. To account for phylogenetic dependence within the data, we calculated standardized independent contrasts of $\hat{t}_{\mathrm{feed}}$ and t_{feed} (see Appendix 2 for details). The correlation coefficient r between these contrasts is 0.821 (ANOVA: $F_{1,17} = 35.2$, $p < 0.001$; SPSS 11.5.0, SPSS Inc. 2002). Captive animals have little reason to look out for predators and do not spend much time searching for food. It is therefore not surprising that captive animals were able to spend as much time feeding as they needed to reach satiation. However, all analysed feeding times were observed in the field except for the giant rams-horn snails (*Marisa cornuarietis*) and meadow voles (*Microtus pennsylvanicus*). Excluding these two species from the analysis does not significantly change the result (mean $|\hat{t}_{\mathrm{feed}} - t_{\mathrm{feed}}| = 1.3\%$ or 19 min/d, median $|\hat{t}_{\mathrm{feed}} - t_{\mathrm{feed}}| = 0.6\%$ or 9 min/d, $r = 0.827$, $F_{1,15} = 32.6$, $p < 0.001$).

Thus, many herbivores seem to feed naturally to satiation, with their feeding time dependent on handling and digestion time. To our knowledge, only Diamond et al. (1986), whose data on rufous hummingbirds are included in our study, have explicitly shown this for any species before. Our analysis extends their finding to herbivores and thereby questions the general validity of classical optimal foraging models in which consumers cannot become satiated (MacArthur & Pianka 1966; Schoener 1971; Charnov 1976a,b; Parker & Stuart 1976; Stephens & Krebs 1986). We next consider the possibility that feeding time is constrained by environmental temperature because such a feeding time constraint underlies other, more recent optimal foraging models that account for consumer satiation.

Feeding Time and Temperature

The observed feeding times given in Fig. 1 are mean values averaged over several days varying in temperature. In some of the studies analysed here, animal activity time at single days was plotted against environmental temperature, giving further insights: eleven species became less active with increasing temperature (see caption below Fig. 1) and three species were most active at intermediate temperatures [yellow-bellied marmots (*Marmota flaviventris*), white-tailed deer (*Odocoileus virginianus*), and Columbian ground squirrels (*Spermophilus columbianus*)]. The remaining five species were not analysed (Belovsky & Jordan 1978; Belovsky 1984a, 1986; Belovsky & Slade 1986; Schmitz 1991).

Given that feeding time is correlated with activity time, these observations suggest that daily feeding time depends on temperature and may thus be limited by temperature. This interpretation is corroborated by Belovsky's (1984b) study on snowshoe hares (*Lepus americanus*) in which he showed that hourly and daily activity time in summer can be adequately predicted by a thermal balance model not accounting for digestion time.

It is unclear, however, whether this result for snowshoe hares can be generalized, especially because many arctic species have severe problems with overheating in summer (reviewed by Begon et al. 1996). Furthermore, using a correlation between daily activity time and environmental temperature as an indication of time constraints has several weaknesses. First, these correlations do not necessarily imply correlations between feeding time and temperature because the animals may have merely avoided unnecessary activities on unsuitably warm days. Second, a decreased daily feeding time would not necessarily imply a decreased daily food consumption because herbivores are able to compensate for restricted food access by increasing their foraging effort (Smith 1961; Bunnell & Harestad 1990; Romney et al. 1996; Emmans & Kyriazakis 2001). This may also be true for the animals analysed here. According to Fig. 1, these species actually fed to satiation. Finally, if animals were pressed for time on hot days, this would not necessarily be the case on other days (Owen-Smith 1998). In conclusion, feeding time is often influenced by environmental temperature, but it is doubtful whether it is often *constrained* by temperature (see also Kenagy et al. 2002).

Optimal Foraging Models with Satiation

The results presented above not only suggest that many herbivores naturally feed to satiation, but that they are often also released from time constraints, because such constraints would likely lead to trade-offs in time allocation and thus to a non-satiating food consumption. However, it is also possible that food abundance and the time available to forage allowed the species analysed here to feed to satiation but not to choose the absolutely most desirable diet. Such a situation can occur when abundant or easily handled food is only slowly digestible while quickly digestible food is rare or difficult to handle. Hence, if an animal feeds to satiation, it might or might not be time-constrained. It seems likely that some animals are, while others are not. We do not argue that all animals are permanently released from time constraints, but rather, that many animals are occasionally or often released from them. The problem we see with published optimal foraging studies is that the vast majority of them, including those that consider satiation effects (Belovsky 1978; Owen-Smith & Novellie 1982; Verlinden & Wiley 1989; Fryxell 1991), have only been conducted under the assumption that consumers are time-constrained (but see also Newman et al. 1995 and Fortin et al. 2002). We join others by pointing out that this crucial assumption has not been verified (Owen-Smith 1994; Illius et al. 2002; Kenagy et al. 2002). We do not even know whether foraging time is limited by sleeping time, because the determinants of sleeping time as well as the function of sleep have remained elusive (Rechtschaffen 1998). Some readers might object that pressure of time is a reasonable *a priori* assumption because 'lazy' animals are unlikely to be naturally selected. However, this objection is challenged by Wilson's Principle of Stringency and by the observation that herbivores, as well as carnivores, are able to compensate for restricted food access, decreased food abundance, or increased food requirements by increasing their foraging time or effort (Smith 1961; Chacon & Stobbs 1976; Masman et al. 1989; Swennen et al. 1989; Bayer 1990; Bunnell & Harestad 1990; Romney et al. 1996; Emmans & Kyriazakis 2001; Jeschke et al. 2002).

Wilson's Principle of Stringency

An evolutionary explanation for 'lazy' animals has been offered by Wilson (1975) with his principle of stringency (Fig. 2): 'time-energy budgets evolve so as

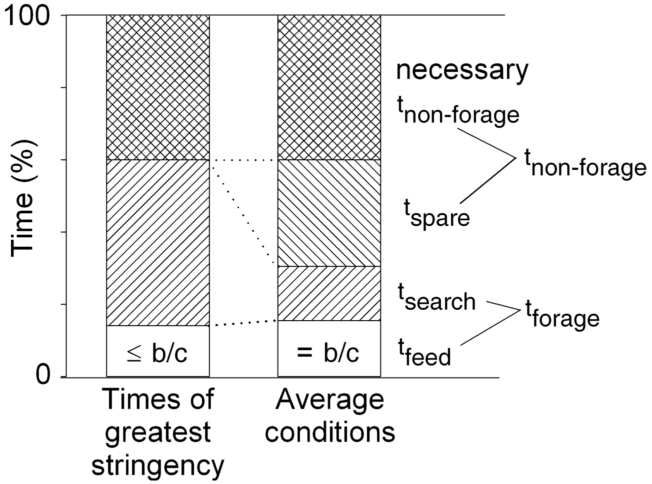

Fig. 2: An illustration of Wilson's (1975) principle of stringency. An animal's total 24 h per day can be divided into foraging time t_{forage} (consisting of searching time t_{search} and feeding time t_{feed}) and non-foraging time $t_{\text{non-forage}}$ (consisting of necessary non-foraging time, e.g. predator avoidance or prevention of overheating, and non-necessary non-foraging time, i.e. spare time t_{spare}). At the times of greatest stringency, an animal has no spare time. Under average conditions, however, it needs less time searching for food and thus has spare time. See main body text for more details on this. The values shown for t_{search} and t_{feed} are realistic for mammals under average conditions (Bunnell & Harestad 1990); other time allocations shown are arbitrary. With respect to birds, Ettinger & King (1980) suggested that the most stringent period for the female willow flycatchers (*Empidonax traillii*) they investigated was the incubation phase. They estimated the spare time of these birds as 52.6% or $12\frac{1}{2}$ h/d during the pre-nesting phase, 20.3% or 5 h/d during the nest-construction phase, and 25% or 6 h/d during the nestling phase

to fit to the times of greatest stringency', such as periods of low food abundance (e.g. severe winters), large food requirements (e.g. rearing of offspring), or greatest alternative demands (e.g. reproductive activities). For simplicity, energy-conserving mechanisms such as fat reserves are not considered. According to the principle of stringency, animals are time-constrained on an evolutionary time scale but, as a result of limited phenotypic plasticity, they are not time-constrained on most days of their life. That is, although they spend all the time foraging needed to fill their gut with the absolutely most desirable diet, and spend the additional time needed to fulfil non-foraging needs (e.g. to watch out for predators or prevent overheating), they still have some spare time left (Fig. 2). The principle of stringency relies on the assumption that the fittest animals are those whose traits fit to the times of greatest stringency, especially those traits that determine their time budgets. As long as these traits cannot be adjusted to the environmental conditions as greatly and as rapidly as these conditions vary, animals are pressed for time during, but not outside the times of greatest stringency. Because these periods are rare, animals are seldom pressed for time. Indeed, the traits that determine one part of the time budget, feeding time t_{feed}, are probably not sufficiently plastic. According to our study, these traits are handling time b and digestion time c, which is in turn determined by gut capacity g and retention time t_g (eqns 2 and 3). An animal usually has a relatively constant handling time for a given type of food. Furthermore, an animal is obviously unable to either increase its gut capacity or decrease its retention time beyond a certain limit (Karasov and McWilliams, in press). Under given environmental conditions and according to eqn (3), therefore, there is a certain portion of its time an individual needs to spend feeding to reach satiation ($\hat{t}_{feed}$ in eqn 3 and Fig. 2).

Feeding Time and Body Mass

According to Fig. 3, all species except rams-horn snails spent similar portions of the day feeding [phylogenetically weighted mean excluding snails, beavers (*Castor canadensis*), and rufous hummingbirds (*Selasphorus rufus*) = 15.5% or $3\frac{3}{4}$ h/d, range = 11.9–21.3% or $2\frac{3}{4}$–$5\frac{1}{4}$ h/d]. Beavers and hummingbirds were excluded from Fig. 3 because of incomparable data: the values given for these species for ‘observed feeding time’ in Fig. 1 actually are observed foraging times (see also Appendix 1; the ‘predicted feeding times’ given in Fig. 1 for these species consequently are predicted foraging times). Why the rams-horn snails showed exceptionally high feeding times is currently unclear and should be examined in future studies.

An extension of eqn (3) using allometric functions suggests constancy in feeding time: A huge number of animal traits scale allometrically to body mass, including the two parameters in eqn (3), handling time b and digestion time c

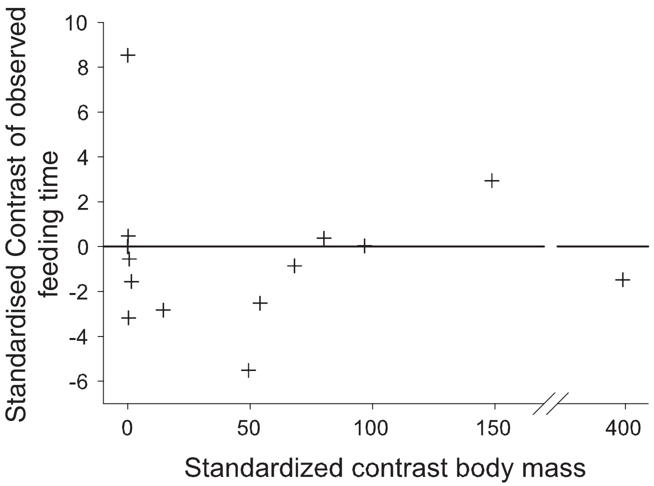

Fig. 3: For the species analysed here, feeding time is independent of body mass. Species included are as in Fig. 1, but beavers and rufous hummingbirds were excluded because of incomparable data (see main body text). Top, raw data as given in Appendix 1; the letters are as in Fig. 1 and the solid line is the phylogenetically weighted mean feeding time excluding giant rams-horn snails (15.5% or 33/4 h/d). Bottom, independent contrasts (for their calculation, see Appendix 2)

(Calder 1984; Belovsky 1997). That is, each of these parameters can be expressed as an allometric function of body mass:

$$b(m) = \alpha_b m^{\beta_b}, \tag{4}$$

$$c(m) = \alpha_c m^{\beta_c}, \tag{5}$$

where m is the coefficient of body mass (dimensionless), e.g. in case of a body mass of 8 kg, m is 8 (cf. Brown et al. 1996); α_b (time/food items), α_c (time/food items), β_b (dimensionless), and β_c (dimensionless) are allometric parameters. Inserting eqns (4 and 5) in eqn (3) yields:

$$\hat{t}_{feed}(m) = \frac{b(m)}{c(m)} = \frac{\alpha_b m^{\beta_b}}{\alpha_c m^{\beta_c}} = \frac{\alpha_b}{\alpha_c} m^{\beta_b - \beta_c}. \tag{6}$$

According to Fig. 4, β_b is similar to β_c: the slopes of the two lines are similar. Biologically speaking, both handling time b and digestion time c decrease with increasing body mass in a similar way: a doubling in mass leads roughly to a 40%

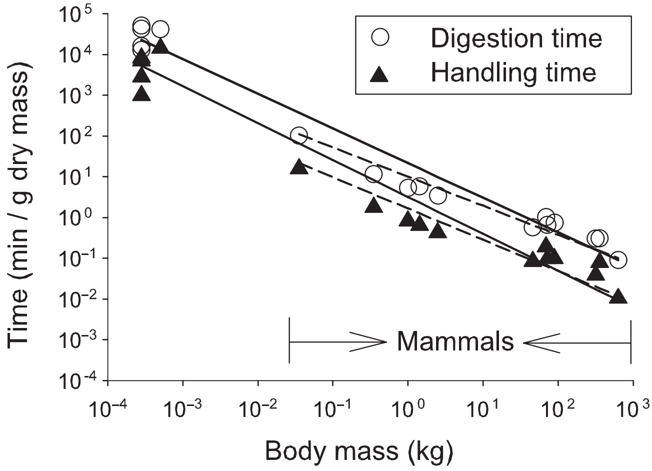

Fig. 4: Allometric relationships in herbivores between either handling time $\hat{b}$ (closed triangles) or digestion time $\hat{c}$ (open circles) and body mass. Each symbol represents one species. Species included are as in Fig. 1, but beavers and rufous hummingbirds were excluded because of incomparable data (see Appendix 1). Solid lines are OLSBISIC regressions (*o*rdinary *l*east *s*quares-*bis*ector *i*ndependent *c*ontrasts regressions) for all species: $\tilde{b} = 3.19\ m^{-0.904}$, $r^2 = 0.880$ [OLSIC regression (*o*rdinary *l*east *s*quares *i*ndependent *c*ontrasts regression): $\tilde{b} = 3.62\ m^{-0.848}$, r^2 identical], $\tilde{c} = 21.49\ m^{-0.849}$, $r^2 = 0.926$ (OLSIC regression: $\tilde{c} = 23.13\ m^{-0.817}$); dashed lines are OLSBISIC regressions for mammals only: $\tilde{b} = 1.65\ m^{-0.766}$, $r^2 = 0.855$ (OLSIC regression: $\tilde{b} = 1.49\ m^{-0.727}$), $\tilde{c} = 10.02\ ^{-0.714}$, $r^2 = 0.943$ (OLSIC regression: $\tilde{c} = 9.51\ ^{-0.693}$). For data or information on independent contrasts regressions, see Appendix 1 or 2, respectively. For information on least squares-bisector regressions, see Babu & Feigelson (1992)

reduction in handling and digestion time. As the difference between β_b and β_c is roughly 0, eqn (6) can be simplified to $\hat{t}_{feed} = \alpha_b/\alpha_c$, i.e. feeding time is constant and thus independent of body mass. Although Fig. 3 seems to support these considerations and feeding time is not significantly correlated with body mass in the species analysed here, the low power of these significance tests – either with and without rams-horn snails – calls for further data (including snails: independent contrasts $r = 0.116$; ANOVA: $F_{1,15} = 0.205$, $p = 0.657$, observed power$_{\alpha=0.05} = 0.071$; excluding rams-horn snails: $r = 0.134$; ANOVA: $F_{1,14} = 0.255$, $p = 0.621$, observed power $= 0.076$).

A broader comparative analysis by Belovsky (1997) indicates that β_b is generally similar to β_c in herbivores: using ordinary least squares regression analysis, he found β_b to be −0.67. Furthermore, gut capacity g scaled as $m^{1.0}$ and retention time t_g as $m^{0.33}$, thus – given that $c = t_g/g$ (see above) – $c \propto m^{0.33}/m^{1.0}$, i.e. $\beta_c = -0.67$. Hence, β_b is equal to β_c, suggesting that feeding time is independent of body mass for herbivores in general. However, future studies are clearly needed to test the validity of this suggestion as well.

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Appendix 1: Calculation of predicted feeding times

Species (references)	Duration of observation (animal 24 h-days)	Body mass (kg)	Plant class i	$Bulk_i$ (g-wet mass/g-dry mass)	$Diet_i$	b_i (min/g-dry mass)	$\hat{b}$ (min/g-dry mass)	dig. cap. (g-wet mass/min)	$\hat{c}$ (min/g-dry mass)	$\hat{t}_{feed}$ (%)	t_{feed} (%)	$\lvert\hat{t}_{feed} - t_{feed}\rvert$ (%)
(A) Moose (1–3) (*Alces alces*)	15.0 (summer)	358	Terrestrial	4.04	0.75	0.09	0.07902	22.85	0.306	25.9	21.3	4.6
			Herbs	4.4	0.08	0.054						
			Aquatics	20	0.18	0.04						
(B) Pronghorn antelope (4) (*Antilocapra americana*)	42.9 (summer)	46	Monocots	1.64	0.02	0.207	0.08254	4.7	0.564	14.6	15.1	0.5
			Dicots	2.67	0.98	0.08						
(C) Bison (4) (*Bison bison*)	137.1 (summer)	636	Monocots	1.64	0.99	0.01	0.01035	18.27	0.0903	11.5	12.4	0.9
			Dicots	2.67	0.01	0.045						
(D) Beaver (5) (*Castor canadensis*)	5.0 (summer)	15	Leaves	4.04	0.89	0.49	0.457	2.4	2.415	18.9	18.7	0.2
			Aquatics	20	0.11	0.19						
(E) Elk (4) (*Cervus elaphus*)	51.3 (summer)	318	Monocots	1.64	0.64	0.029	0.03872	6.61	0.304	12.7	12.6	0.1
			Dicots	2.67	0.36	0.056						
(F) Undulant-winged grasshopper (4) (*Circotettix undulatus*)	7.5 (summer)	0.00028	Monocots	1.64	0.96	2860	2768.8	0.000105	16011	17.3	16.6	0.7
			Dicots	2.67	0.04	580						
(G) Carolina grasshopper (4) (*Dissosteira carolina*)	7.5 (summer)	0.00028	Monocots	1.64	0.85	1100	977	0.00014	12818	7.6	16.6	9.0
			Dicots	2.67	0.15	280						

Appendix 1: Continued

Species (references)	Duration of observation (animal 24 h-days)	Body mass (kg)	Plant class i	Bulk_i (g-wet mass/g-dry mass)	Diet_i	b_i (min/ g-dry mass)	$\hat{b}$ (min/ g-dry mass)	dig. cap. (g-wet mass/min)	$\hat{c}$ (min/ g-dry mass)	$\hat{t}_{feed}$ (%)	t_{feed} (%)	$\lvert\hat{t}_{feed} - t_{feed}\rvert$ (%)
(H) Snowshoe hare (6) (*Lepus americanus*)	? (summer)	1.35	Leaves	4.04	0.11	0.26	0.4798	0.766	5.766	8.3	9.1	0.8
			Herbs	4.4	0.88	0.49						
			Fungus	10	0.01	2						
snowshoe hare	? (winter)	1.5	Deciduous	2	0.79	0.8	0.8	0.374	5.628	14.2	14.6	0.4
			Coniferous	2.5	0.21	0.8						
(I) Giant rams-horn snail; snail 4 (7) (*Marisa cornuarietis*)	1.0 (captive animals)	0.000501	*Ludwigia*	13430	0.94	15780	16087	0.324	42093	38.2	45.8	7.6
			Vallisneria	16900	0.06	20890						
Giant rams-horn snail; snail 8	1.0 (captive animals)	0.000614	*Ludwigia*	13430	0.87	10100	9854.3	0.329	42192	23.4	45.8	22.4
			Vallisneria	16900	0.13	8210						
Giant rams-horn snail; snail 14	1.0 (captive animals)	0.000655	*Ludwigia*	13430	0.98	14430	14371	0.329	41032	35.0	52.8	17.8
			Vallisneria	16900	0.02	11490						
Giant rams-horn snail; snail 16	1.0 (captive animals)	0.000655	*Ludwigia*	13430	0.92	16630	16085.2	0.342	40081	40.1	43.1	3.0
			Vallisneria	16900	0.08	9820						
(J) Yellow-bellied marmot (4) (*Marmota flaviventris*)	10.7 (summer)	2.5	Monocots	1.64	0.11	1.52	0.4253	0.751	3.404	12.5	13.6	1.1
			Dicots	2.67	0.89	0.29						
(K) Red-legged locust (4) (*Melanoplus femur-rubrum*)	7.5 (summer)	0.00028	Monocots	1.64	0.22	10000	8198.2	0.000048	50904	16.1	16.6	0.5
			Dicots	2.67	0.78	7690						

Appendix 1: Continued

Species (references)	Duration of observation (animal 24 h-days)	Body mass (kg)	Plant class i	Bulk_i (g-wet mass/g-dry mass)	Diet_i	b_i (min/g-dry mass)	$\hat{b}$ (min/g-dry mass)	dig. cap. (g-wet mass/min)	$\hat{c}$ (min/g-dry mass)	$\hat{t}_{feed}$ (%)	t_{feed} (%)	$\lvert\hat{t}_{feed} - t_{feed}\rvert$ (%)
(L) Migratory grasshopper (4) (*Melanoplus sanguinipes*)	7.5 (summer)	0.00028	Monocots Dicots	1.64 2.67	0.29 0.71	6250 7140	6881.9	0.0000564	42044	16.4	16.6	0.2
(M) Meadow vole (4) (*Microtus pennsylvanicus*)	2.0 (captive animals)	0.035	Monocots Dicots	1.64 2.67	0.45 0.55	21.17 10.97	15.56	0.0217	101.68	15.3	16.0	0.7
(N) Mule deer (4) (*Odocoileus hemionus*)	28.1 (summer)	90	Monocots Dicots	1.64 2.67	0.09 0.91	0.18 0.09	0.0981	3.47	0.743	13.2	13.8	0.6
(O) White-tailed deer; Montana (4) (*Odocoileus virginianus*)	23.4 (summer)	80	Monocots Dicots	1.64 2.67	0.14 0.86	0.18 0.1	0.1112	3.33	0.758	14.7	14.1	0.6
White-tailed deer; Ontario (8, 9)	2.1 (early winter)	59	Deciduous Coniferous	1.85 2.25	0.94 0.06	0.28 0.14	0.2716	1.52	1.233	22.0	22.0	0.0
White-tailed deer; Ontario	2.1 (mid winter)	59	Deciduous Coniferous	1.85 2.25	0.68 0.32	0.35 0.16	0.2892	1.52	1.301	22.2	22.0	0.2
White-tailed deer; Ontario	2.1 (late winter)	59	Deciduous Coniferous	1.85 2.25	0.48 0.52	0.42 0.12	0.264	1.52	1.354	19.5	20.7	1.2
(P) Bighorn sheep (4) (*Ovis canadensis*)	37.8 (summer)	72	Monocots Dicots	1.64 2.67	0.26 0.74	0.128 0.086	0.09692	3.68	0.653	14.8	14.5	0.3
(Q) Rufous hummingbird (*Selasphorus rufus*) (10, 11)	0.6 (summer)	≈0.004	–	–	–	–	0.588	–	4.1	14.3	15.6	1.3

Appendix 1: Continued

Species (references)	Duration of observation (animal 24 h-days)	Body mass (kg)	Plant class i	$Bulk_i$ (g-wet mass/g-dry mass)	$Diet_i$	b_i (min/ g-dry mass)	$\hat{b}$ (min/ g-dry mass)	dig. cap. (g-wet mass/min)	$\hat{c}$ (min/ g-dry mass)	$\hat{t}_{feed}$ (%)	t_{feed} (%)	$\lvert\hat{t}_{feed} - t_{feed}\rvert$ (%)
(R) Columbian ground squirrel (4) (*Spermophilus columbianus*)	4.8 (summer)	0.35	Monocots Dicots	1.64 2.67	0.19 0.81	3.49 1.37	1.7728	0.218	11.350	15.6	15.8	0.2
(S) Rocky Mountain cottontail (4) (*Sylvilagus nuttali*)	4.6 (summer)	1	Monocots Dicots	1.64 2.67	0.35 0.65	1.61 0.38	0.8105	0.441	5.237	15.5	16.4	0.9

References

(1) Belovsky (1978); (2) Belovsky & Jordan (1978); (3) Belovsky (1984c); (4) Belovsky (1986); (5) Belovsky (1984a); (6) Belovsky (1984b); (7) Grantham et al. (1995); (8) Schmitz (1990); (9) Schmitz (1991); (10) Hixon et al. (1983); (11) Diamond et al. (1986).

Notes

Estimated handling time $\hat{b} = \sum b_i \cdot \mathrm{diet}_i$, where b_i is the handling time for plant class i and diet_i is the relative frequency of plant class i in the species' diet (with respect to dry mass). Estimated digestion time $\hat{c} = (\sum \mathrm{bulk}_i \cdot \mathrm{diet}_i)/\mathrm{dig.cap.}$, where bulk_i is the ratio of wet mass to dry mass in plant class i and dig. cap. is the species digestive capacity. Predicted feeding time $\hat{t}_{\mathrm{feed}} = \hat{b}/\hat{c}$ (eqn 3). Beaver: the given value for t_{feed} is actually t_{forage}, but $\hat{b}$ is corrected for this. Giant rams-horn snail: g-wet mass has to be replaced by mm^3. Rufous hummingbird: g-dry mass has to be replaced by foraging bout; t_{feed} and $\hat{t}_{\mathrm{feed}}$ are related to daylight hours (6 AM–8 PM ⇒ 14 h); the given value for t_{feed} is actually t_{forage} at a high flower density (Fig. 3 in Hixon et al. 1983), but $\hat{b}$ is corrected for this.

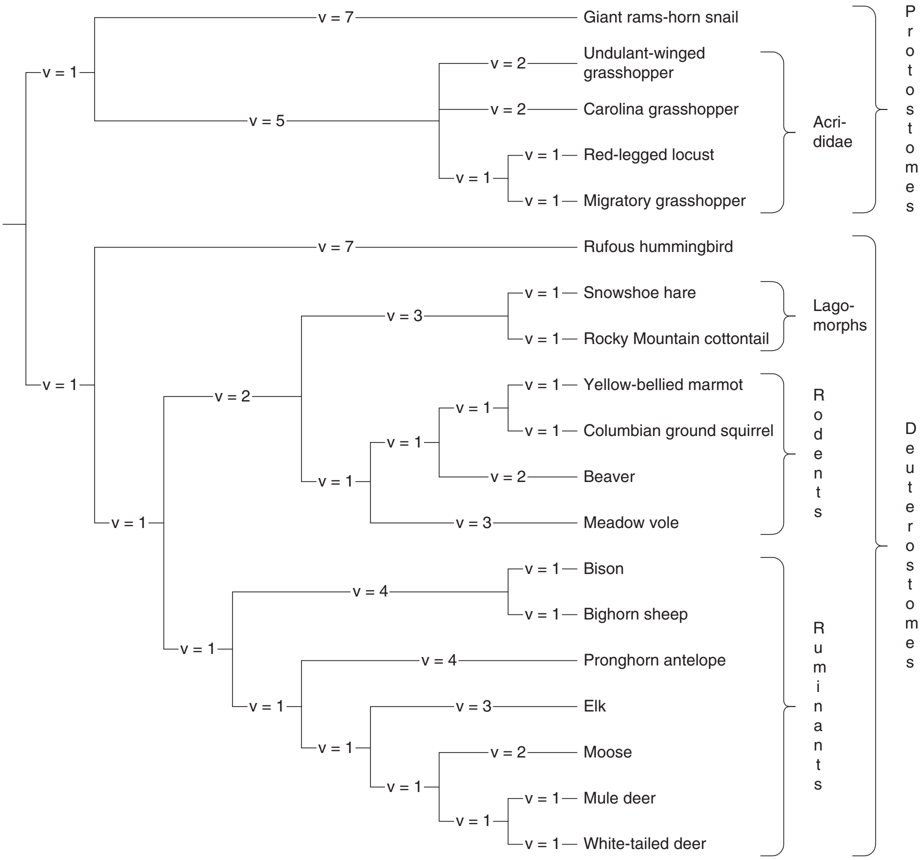
To make it easier for readers to critically inspect the table, we explain in detail for a sample species, the yellow-bellied marmot (J), how the quantities given here have been derived from the raw data reported in the cited study, in this case Belovsky (1986). Regarding the first column, duration of observation, Belovsky & Slade (1986), their Table 1) reported that the marmots were scanned for 257 h, i.e. for 10.7 d. Belovsky (1986) (his Table 3), in a companion paper, measured an average marmot body mass of 2.5 kg, a monocot bulk ($\mathrm{bulk}_{\mathrm{monocots}}$) of 1.64 g-wet mass/g-dry mass, and a dicot bulk ($\mathrm{bulk}_{\mathrm{dicots}}$) of 2.67 wet mass/g-dry mass. According to his Fig. 3, the marmots' diets included 11% monocots and 89% dicots ($\mathrm{diet}_{\mathrm{monocots}} = 0.11$, $\mathrm{diet}_{\mathrm{dicots}} = 0.89$). Furthermore, these animals needed 1.52 min for handling 1 g-dry mass of monocots (b_{monocots}) and 0.29 min for dicots (b_{dicots}) ('cropping rate' in his Table 3). We can now calculate the average marmot handling time $\hat{b}$ as $\sum b_i \cdot \mathrm{diet}_i$ (see above) $= b_{\mathrm{monocots}} \cdot \mathrm{diet}_{\mathrm{monocots}} + b_{\mathrm{dicots}} \cdot \mathrm{diet}_{\mathrm{dicots}} = 1.52$ min/g-dry mass $\cdot\ 0.11 + 0.29$ min/g-dry mass $\cdot\ 0.89 = 0.4253$ min/g-dry mass. The next column includes digestive capacity (in g-wet mass/min) which is Belovsky's (his Table 3) 'digestion organ volume' (230 g-wet mass for yellow-bellied marmots) multiplied by his 'digestive turnover' (4.7 times per day) and a correction factor for transferring days to minutes (1 day = 1440 min):

$$\text{dig. cap.} = \frac{230\,\mathrm{g} - \text{wet mass} \cdot 4.7/\mathrm{d}}{1440\,\mathrm{min/d}} = 0.751\,\text{g-wet mass/min.}$$

This digestive capacity relates to satiated marmots because Belovsky obtained the 'digestion organ volume' as well as the 'digestive turnover' under *ad libitum* conditions. Digestive capacity is given in g-wet mass/min so its reciprocal value is the digestion time of a satiated marmot in min/g-wet mass. To compare digestion time to handling time, we transform the dimension of digestion time to that of handling time which is min/g-dry mass. For this transformation, we need to know the portion of the gut occupied by monocots (= $\text{diet}_{\text{monocots}} = 0.11$), the portion occupied by dicots ($\text{diet}_{\text{dicots}} = 0.89$), the bulk of monocots ($\text{bulk}_{\text{monocots}} = 1.64$ g-wet mass/g-dry mass), and the bulk of dicots ($\text{bulk}_{\text{dicots}} = 2.67$ g-wet mass/g-dry mass): digestion time $\hat{c}$ in min/g-dry mass is, according to the equation given above, equal to $(\sum \text{bulk}_i \cdot \text{diet}_i)/\text{dig.cap.} = (\text{bulk}_{\text{monocots}} \cdot \text{diet}_{\text{monocots}} + \text{bulk}_{\text{dicots}} \cdot \text{diet}_{\text{dicots}})/\text{dig. cap.} = (1.64$ g-wet mass/g-dry mass $\cdot\ 0.11 + 2.67$ g-wet mass/g-dry mass $\cdot\ 0.89)/0.751$ g-wet mass/min $= 3.404$ min/g-dry mass. We are now able to compute the predicted feeding time $\hat{t}_{\text{feed}}$ as $\hat{b}/\hat{c}$ (eqn 3) $= (0.4253$ min/g-dry mass$)/(3.404$ min/g-dry mass$) = 0.125 = 12.5\%$. Finally, the observed marmot feeding time t_{feed} is 196 min/d $= 196/1440 = 13.6\%$ (Belovsky's Table 3), so the difference between predicted and observed feeding time, $|\hat{t}_{\text{feed}} - t_{\text{feed}}|$, is $|12.5\text{–}13.6\%| = 1.1\%$.

Most of the data given here come from Belovsky and his colleagues, and the validity of these data has been questioned: first, because they fit the values predicted by Belovsky and colleagues better than what is statistically likely (Hobbs 1990; Huggard 1994). This 'too good fit' is in our eyes not the result of erroneous empirical data but of the circularity involved in the application of the linear programming model (Owen-Smith 1993, 1994, 1996). The second criticism of the data of Belovsky et al. has been the use of inaccurate methods to estimate retention times and gut capacities (Hobbs 1990). Belovsky (1990) has already responded to these criticisms.

Appendix 2: Information on Independent Contrasts Analyses



This is the phylogenetic tree that underlies our analyses (Pérez-Barbería & Gordon 1999; Maddison 2004), v are arbitrary branch lengths. We calculated the independent contrasts and the regressions with PDTREE 5.0 (Garland et al. 2001 based on Garland et al. 1993, 1999 and Garland & Ives 2000). In case of regressions, we log-transformed the data.