

A unifying approach to allometric scaling of resource ingestion rates under limiting conditions

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Abstract. Individual resource ingestion rates depend on both individual body size and resource supply. A component of the latter, namely resource availability, is also body-size dependent. This raises the question of the adequacy of simple scaling laws to describe the body-size dependency of resource ingestion. Here we propose a model which integrates resource ingestion drivers by merging a scaling law for feeding metabolism and Holling's functional responses into a single mathematical framework. At any fixed level of resource supply, the model predicts a log-log concave-down relationship between resource ingestion rates and body size, rather than a simple scaling law. Deviations from the latter are accounted for by the body size dependency of resource limitations. Experimental and literature data describing patterns of perceived resource availability and individual intake rates under limiting conditions with increasing individual body size are used to validate the model's assumptions and predictions. The model incorporates and extends well-established theoretical approaches and is intended as a step towards the integration of metabolic theory with behavioral ecology and population dynamics.

Key words: body size; Holling's functional response; individual-based resource perception; Kleiber's law; metabolic theory; resource availability.

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INTRODUCTION

The rate at which individuals ingest resources depends on both their body size and the overall supply of those resources in their fundamental niche. Ecological energetics and metabolic theory have addressed the relationship between resource ingestion rates and individual body mass (Peters 1983, Brown et al. 2004), while behavioral ecology has quantitatively addressed the relationship between resource ingestion rates and resource supply. Holling's functional responses (Holling 1959*a, b*) represent a simple and widely used quantitative description of the relationship

between individual resource ingestion rates and resource supply. The relevance of consumer-resource functional responses has recently been emphasized for regional population dynamics (Englund and Leonardsson 2008), species interaction dynamics and community structure (Holland and De Angelis 2009, Petchey et al. 2008).

The influences of body size and resource supply on individual resource ingestion rates have often been studied separately. This may lead to contrasting predictions regarding the scaling of resource intake. Only recently has interest grown in their combined effect (Woodward et al. 2005, Brose et al. 2006, Weitz and

Levin 2006, Basset and DeAngelis 2007, Petchey et al. 2008, Berlow et al. 2009, Beckerman et al. 2010, Brose 2010, Vucic-Pestic et al. 2010). Much attention has also been paid to the allometric scaling of attack rates, the instantaneous search coefficient, and handling time, which determine the coefficients of Holling's functions (see Beckerman et al. 2010, Brose 2010 for short reviews on this topic). Fractal geometry arguments have been used to highlight an allometric scaling component of resource supply, showing that body size affects home-range size (Haskell et al. 2002) and determines patch selection (Belovsky 1997, Ritchie 1998). Evidence that large individuals give up the patch earlier and at higher densities of remaining resources than small individuals (Brown et al. 1994, Wilson et al. 1999, Basset and DeAngelis 2007) suggests that individual perception of available resources has a body-size dependent component. We define here the perceived resource availability as the absolute amount of resources available to a single individual normalized for the individual's metabolic requirement; therefore, if individuals of different body size experience the same absolute resource availability, the perceived resource availability is smaller for the larger individual (see Eq. 2 below for further details). This effect has been modeled as a major determinant of inter-specific coexistence (Basset and DeAngelis 2007).

Larger individuals need higher ingestion rates than their smaller competitors in order to sustain their metabolic needs. Therefore it is likely that the former become limited at a higher level of available resources than the latter. In order to quantitatively describe this basic idea, we make an explicit distinction between "resource availability" and "perceived resource availability" (see Eq. 2 below for further details). Clearly, any individual trait affecting search behavior may have an influence on the perceived resource availability. Some of those traits may also be body-size dependent. As we argue below, if the perceived resource limitation is size dependent, then simple power laws might not be adequate to explain the quantitative relationship between individual tropho-energetic rates (e.g., resource ingestion rate, assimilation rate, absorption rate) and individual body size. This hypothesis has not been tested because the body size dependency of resource availability has not yet been

incorporated into a quantitative model relating resource ingestion rates to body mass.

Here we propose a mathematical model that links individual resource ingestion rates with both body size and resource availability. The model merges a Kleiber-like (Kleiber 1932) scaling law for individual ingestion rates, a scaling law linking the perceived level of available resources with body size and Holling's functional responses (Holling 1959*a, b*) into a single framework, adding a mechanistic component to previous implicit formulations (Basset and DeAngelis 2007) which explains the body size dependency of resource availability. The aim of the paper is to investigate the actual adequacy of simple power laws to describe the relationships between tropho-energetic individual traits and individual body size and to metabolic theory with greater ecological detail and realism. In fact, by taking explicit account of the body-size dependency of resource limitation, the model incorporates ecological interactions in metabolic theory and provides a stronger theoretical framework for decoding the body size patterns characterizing guilds in nature.

Empirical evidence from a laboratory experiment on benthic macro-invertebrates and metadata from the available literature on body size scaling of resource ingestion rates are used to evaluate the realism of the model's results.

THE MODEL

Scaling laws linking aspects of individual metabolism to body size, such as basal, standard and field metabolic rates, resource ingestion and absorption rates, are all based on Kleiber's well-known equation linking metabolism to the body size of individual living organisms (Peters 1983, Nagy 2005). Kleiber's law can be written in the following form:

$$\frac{dE}{dt} = P_0 \left(\frac{M}{M_0} \right)^\alpha \quad (1)$$

where E is the energy required by an individual for its metabolic needs; P_0 is a baseline power, which determines the elevation of the scaling law; M is the mass of the organism (or 'body size'); M_0 is a baseline mass (so that the power law is applied to a non-dimensional quantity); and α is a positive constant, often taken to be

equal to 3/4 (e.g., Peters 1983).

Writing Kleiber's law using a non-dimensional argument has the immediate advantage that the proportionality factor P_0 has the same units as the left-hand side of the equation (e.g., watts).

There is very strong consensus that M and dE/dt are functionally related, but considerable debate on the nature of this relationship. A few theoretical models are consistent in deriving the power-law in Eq. 1 but they have spurred much controversy about the underlying mechanisms (West et al. 1997, Banavar et al. 1999, Makarieva et al. 2004, Glazier 2005).

The debate has often focused on the exact value to be given to the scaling exponent, and even though $\alpha = 3/4$ is the most commonly cited value, α has been observed to vary within mammals (White and Seymour 2005) as well as among mammals, birds and plants (Reich et al. 2006, Enquist et al. 2007, Starostová et al. 2009, Hendriks 2007) and the adequacy of a pure power law to describe the relationship between individual mass and metabolic rate was questioned (Dodds et al. 2001, Kolokotronis et al. 2010). Moreover, temperature is a major factor affecting individual energetics, whose role has been incorporated into Kleiber's equation by adding a Boltzmann-like temperature dependency to the term P_0 (Brown et al. 2004). A more comprehensive account of the dependency on temperature and on other factors has been recently proposed (Glazier 2010).

When applied to resource ingestion rate, Eq. 1 overlooks the role of individual adjustments to scarcity of resources in natural environments. Indeed, power-law scaling of resource ingestion rates with individual body-size assumes an unlimited supply of resources across the whole of the size range under consideration. In principle, the scaling law may persist under limiting conditions if the perception of resource limitation were invariant with body size, but this hypothesis has already been shown to be false at least for fractal spatial resource distribution (Haskell et al. 2002). In this case, the resource density encountered by a consumer has been shown to be an inverse function of the consumer sampling volume and body size at the home range scale (Haskell et al. 2002); indeed, the ratio between encountered resource density and individual sampling volume is conceptually analogous to

that between absolute resource availability and individual's metabolic requirement.

In a homogeneous environment, characterized by a given amount R_a of available resources, the abundance of resources R_p perceived by any individual organism is a function of its size: when the tropho-energetics of large organisms start to be resource limited, smaller organisms still have a subjective perception of resource abundance. In this context, a 'homogeneous environment' is a place where the spatial location of resources is unimportant, and a single number (R_a) is sufficient to characterize the resources available in that environment. We shall assume that the functional link between perceived resources and mass is a power law:

$$R_p = cR_a \left(\frac{M}{M_0} \right)^{-x} \quad (2)$$

where the value of the constant x probably ranges from 1/4 to 3/4 (Basset and DeAngelis 2007), and c is the normalization factor required to match the available level of resources R_a to the perceived level of resources of an individual having exactly the baseline mass M_0 . Eq. 2 can be seen as the ratio of R_a to the non-dimensional, mass-dependent quantity $c^{-1}(M/M_0)^x$, showing explicitly that the perceived resource availability is the absolute availability scaled by every individual according to its energetic requirements. The scaling process gives a quantitative assessment of the relevance of a fixed resource density to the energetic requirements of an individual of a fixed body size. An inverse relationship such as Eq. 2 has already been implicitly incorporated into various models dealing with individual patch choice dynamics (Ritchie 1998), and coexistence relationships (Basset and DeAngelis 2007), but it has not yet been explicitly modeled. Individual-based perception of resources dates back to the environmental grain concept (MacArthur and Levins 1964) and is not limited to body-size dependency. Other factors affecting the perception of resource availability include resource distribution (Haskell et al. 2002), resource defense mechanisms (Abrams and Walters 1996), individual consumer niche breadth (Rossi 1985), search and pursuit ability (Krebs and Davies 1997) and risk-averse behavioral strategy (Werner et al. 1981). However, body size has a systematic effect on perceived resource availability, and its influence can be modeled as a scaling law. In our

model, body-size independent forcing factors are described by allowing for variations in the coefficients c and x of the scaling law (Eq. 2). Accounting for the allometric variation of perceived resource availability increases the realism of the resource availability assessment, even though it does not completely resolve all the other biases listed above.

How does an individual react to resource scarcity? The traditional approach is to use Holling's functional response models (Holling 1959a, b), where a prescribed function I links resource ingestion to resource availability, although several other reasonable choices may be available to I (May 1972). In accordance with the cited recent evidence suggesting that individual behavior is primarily affected by perceived resource availability rather than by absolute availability, Holling's responses can be formulated as:

$$I = \frac{R_p^\gamma}{b_\gamma + R_p^\gamma} \tag{3}$$

where $\gamma \geq 1$ ($\gamma = 1$ is Holling type II, $\gamma = 2$ is Holling type III). The independent variable is the perceived resource level R_p , and the half-saturation coefficient b does not depend on body size. In this formulation, the function I is a non-dimensional quantity and is normalized in such a way as to range between zero and one rather than from zero to T/T_m (where T is the total time, T_m is the handling time) as in Holling's original formulation; the two formulations have the same behavior. The former, in which the handling time is incorporated into the half-saturation coefficient b , expresses the quantity of ingested food as a fraction of the optimal ingestion level. It is therefore the appropriate formulation for our purposes. The same function may be expressed in a mathematically equivalent way by using R_a as the independent variable, which is operationally more convenient since R_a is easier to quantify experimentally than R_p . Indeed, by substituting Eq. 2 in Eq. 3 we obtain:

$$I = \frac{R_a^\gamma}{[b(M/M_0)^x c^{-1}]^\gamma + R_a^\gamma} \tag{4}$$

where, in this case, the half-saturation coefficient is the mass-dependent function:

$$b_a(M) = b(M/M_0)^x c^{-1}. \tag{5}$$

Under resource limiting conditions an individual will ingest only a fraction I of the resources that it would otherwise ingest. Therefore the allometric scaling law (Eq. 1), intended as a model of the resource ingestion rate, needs to be corrected as follows:

$$\frac{dQ}{dt} = P_0 \left(\frac{M}{M_0}\right)^\alpha I(M) \tag{6}$$

where Q (which replaces E) is the mass of ingested resources, and I is referred to as $I(M)$ in order to make explicit the dependency on body size. Other authors have already included size-dependency of behavioral (Brose 2010) or interactive (Weitz and Levin 2006, Brose et al. 2008) components of consumer intake rates in the Holling functional responses in predator-prey systems; the approach described by Eq. 6 is less detailed but more general than these earlier investigations on the body-size dependence of ingestion rates and equilibrium population densities.

At this point, we rewrite Eq. 6 using Eq. 4 to describe the quantitative relationship between the ingestion rate, mass and available resources:

$$\frac{dQ}{dt} = P_0 \frac{\hat{M}^{(\alpha-\gamma x)}}{\hat{R}_a^\gamma + \hat{M}^{-\gamma x}} \tag{7}$$

where for convenience we define $\hat{M} = M/M_0$ and $\hat{R}_a = cR_a/b$ as non-dimensional masses and resources. In Eq. 7 the ingestion rate depends on both body size and resource availability. For every small interval of \hat{M} values, the function can be approximated by a scaling law, whose scaling exponent is lower than the one in Eq. 1, and decreases with increasing \hat{M} . This new relationship has the following two interesting limits, both expressed by scaling laws:

$$\hat{M} \rightarrow 0 \Rightarrow \left[\frac{dQ}{dt}\right]_{Abundant} \sim P_0 \hat{M}^\alpha \tag{8}$$

$$\hat{M} \rightarrow \infty \Rightarrow \left[\frac{dQ}{dt}\right]_{Scarce} \sim P_0 \hat{R}_a^\gamma \hat{M}^{\alpha-\gamma x} \tag{9}$$

where the symbol “ \sim ” is used with its formal mathematical meaning of “asymptotic to” and the labels “Abundant” and “Scarce” refer to size-dependent perceived resource availability. The asymptotic limit (Expression 8) is an upper bound for Eq. 7. More importantly, it coincides

with the allometric law (Eq. 1). This fact has a straightforward interpretation: for any assigned value of the resources \hat{R}_a , individuals with small enough body sizes perceive a resource-unlimited environment. The asymptotic limit (Expression 9) holds at the opposite end of the size spectrum, i.e., for individuals large enough to be strongly limited by perceived resource abundance. Expression 9 is a scaling law in which the ingestion rate is proportional to the $(\alpha - \gamma x)$ -power of the body size, and also depends on the overall amount of available resources (Fig. 1). For large γx values, the scarcity regime may even yield a power law in which the ingestion rate decreases with the mass. As we shall discuss below, this limit will not generally be observed in the field.

The thin black lines in Fig. 1 represent the ingestion rates of individuals of varying masses, as predicted by Eq. 7, in a hypothetical experiment in which the level of available resources is kept constant by replenishing the resources as the organism consumes them (for example with a chemostat-like set-up). Here, the quantity Q represents the ingested mass, dQ/dt the ingested mass per unit of time, M_0 is set at 1 g, and P_0 is approximated to 0.15 g/day in accordance with experimental evidence (Peters 1983, Basset 1992). To mirror the uncertainty in the value of x , we show the following three cases: $x = 1/4$; $x = 2/4$; $x = 3/4$. The different curves plotted in each graph correspond to a different value of \hat{R}_a . The exponent γ is set at 2, i.e., we are using the Holling type III functional response.

For intermediate body sizes, where neither Expression 8 nor Expression 9 apply, the relationship between resource ingestion and body size deviates from power-law behavior. The deviation becomes more evident as the value of the exponent x increases. This is due to the nonlinearity of the response function (Eq. 3) combined with the inverse allometric scaling of perceived resource availability described by Eq. 2, at every fixed level of \hat{R}_a .

For $\gamma x > \alpha$, if the body size exceeds the threshold value:

$$\hat{M}_T = \left(\frac{\alpha \hat{R}_a^\gamma}{\gamma x - \alpha} \right)^{\frac{1}{\gamma x}} \quad (10)$$

the model predicts decreasing individual ingestion rates with increasing body size. This

counter-intuitive pattern arises from the opposite influence of individual body size on perceived resource availability and energy requirements: above a certain individual body size, the decrease in perceived resource availability with increasing individual body size affects the ingestion rate more strongly than the increasing energy requirements. In some instances, large individuals may increase their perceived resource availability and maintain a higher ingestion rate than model expectations by improving their search behavior (Dukas and Kamil 2001), by learning (Ishii and Shimada 2010), and by optimizing their pursuit and handling behaviors (Catania and Rempel 2005). It could be argued that these adaptations and behavioral changes amount to body-size dependent changes in their functional response. These changes could be incorporated into our model by allowing the exponent γ in Eq. 3 to be a suitable function of body size. This amounts to modifying the shape of the intake function in a way analogous to what has already been proposed for handling time and instantaneous searching coefficients (Vucic-Pestic et al. 2010) or attack rate coefficients (Brose 2010). The dependence of γ on factors related to resource levels, such as the spatial scale (Morgan et al. 1997) and individual body size (Brose 2010), has also been discussed in the literature and can easily be incorporated into the model.

Giving-up behavior and large-scale dispersal away from the resource-depleted region are additional but progressively more expensive options that individuals may adopt in order to avoid starvation and individual death. In fact, by increasing size while the absolute resource density remains constant, individuals need to cope with increasingly strong resource limitation, by adopting suitable patch selection and departure behavior, by home range expansion (Carbone and Gittleman 2002), or by restricting the range of colonized ecosystems in accordance with ecosystem size and overall productivity (Marquet et al. 2005), matching the required area to their energy demand (Arim et al. 2010). This hierarchy of implications arising from the size dependency of resource limitation is thus consistent with observed patterns of increasing extinction risk with increasing body size in vertebrates (Clauset et al. 2009). It also supports a conceptual framework to the recent application of size

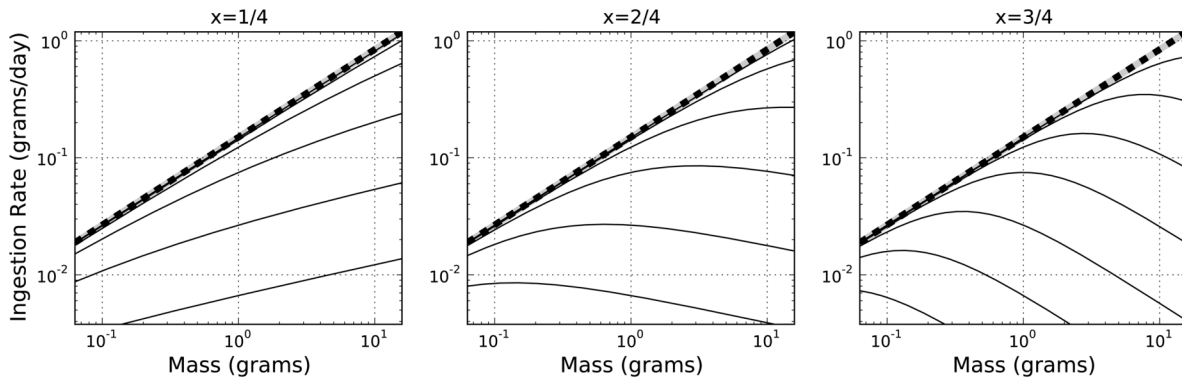


Fig. 1. Plot of Eq. 7 for $\hat{R}_a = 10^{-1}, 10^{-2/3}, 10^{-1/3}, \dots, 10^1$ (thin black lines, \hat{R}_a increasing upward). The thick dashed line is the asymptotic law (Eq. 8); the exponent of the perceived resources, from the left to the right panel is $x = 1/4, 2/4, 3/4$.

spectra patterns in the assessment of the ecological status of aquatic ecosystems (Basset et al. 2012).

We also observe that in the present formulation, the relevant measure of available resources is \hat{R}_a , not R_a . Since $\hat{R}_a = cR_a/b$, it follows that among species with individuals of comparable size, those characterized by a low half-saturation coefficient b remain closer to the allometric law (Eq. 1) than those having a larger b value. In this sense, organisms with low b cope better with scarcity of resources. A similar argument holds for c .

The model embodied by Eq. 7 is not a power law. When applied to a large range of body masses it predicts the humped curves of Fig. 1. As a consequence, we argue that a simple power law is not adequate to describe the functional relationship of resource ingestion with individual body size, when large body size intervals are considered. The model could be approximated by a power law with a body-size dependent exponent only for restricted ranges of individual body sizes. The model describes a theoretical pattern, which is expected under fixed conditions of resource supply and individual niche breadth and under competitive conditions where only indirect, exploitative, competition occurs.

When examining experimental data, departures from the theoretically expected concave-down relationship may arise from pooling large-scale biogeographical data, where resource supply is very likely to vary among ecosystems. Evolutionary and behavioral adaptations to

body-size dependent limiting conditions may also cause deviations from the theoretical pattern, for example: (1) the allometric scaling of individual home range size (Haskell et al. 2002, Jetz et al. 2004); (2) the observation that large species tend to have broader niches than small species, resulting in niche inclusiveness rather than niche partitioning along a gradient of body size variation (Wilson 1975); (3) short-term niche breadth responses to resource limitation, which include increasingly sub-optimal resources in the diet (Roughgarden 1979); (4) the shift from allometric to isometric variation of the basal metabolism with body size, as predicted by the metabolic-level boundaries (MLB) hypothesis (Glazier 2005, 2010). However, home range variations do not affect the perceived resource availability or the resulting limitation of resource ingestion rates, which occur at the patch rather than at the home range level. Niche breadth variations are generally paid for by decreasing efficiency and shifts in basal metabolism may affect ingestion rates only by forcing the individual to adopt one of the above strategies. Therefore, it is unlikely that evolutionary and behavioral adaptations can completely overcome the body size dependency of resource limitation.

EMPIRICAL EVIDENCE

As we argued in the previous section, the perceived resource availability (Eq. 2) is a more realistic but less tractable measure of resource availability than overall biomass or units of

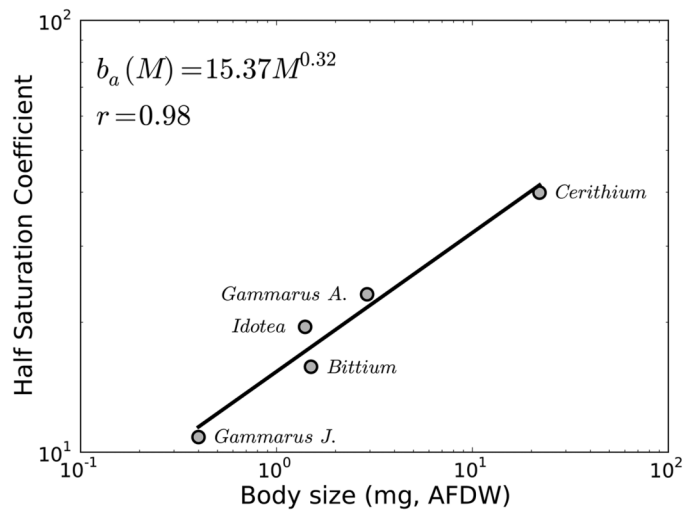


Fig. 2. Allometric variation of the half saturation coefficient b_a of Holling Type III functional response with body size in a guild of benthic detritivores. Data are from laboratory experiments carried out using ^{32}P labeled resources. For every taxon or size class, food intake rate was assessed as the ^{32}P body burden in laboratory experiments where resource availability ranged from 2 to 256 units of resources. Each unit was represented by a single alder leaf disc, fully conditioned by micro-organisms, which was previously labeled with ^{32}P orthophosphate. Techniques for ^{32}P labeling of alder leaf discs are described in Basset (1993). In this model (4) the size-dependent half saturation coefficient is $b_a(M) = b(M/M_0)^x c^{-1}$.

potential resources per unit of space. In our conceptual framework, the scaling of perceived resources with body size implies that the half-saturation coefficient of Holling's functional responses also scales as a power law of body size (Eqs. 3 and 2 combine to give Eq. 4). Therefore, we consider the half-saturation coefficient of Holling's functional responses as a quantifiable proxy for the perception of resource availability as a function of body size.

In a case study we ran experiments under laboratory conditions with benthic macro-invertebrates in order to evaluate the change of functional response parameters with body size along a gradient of resource availability; in the experimental plots resource availability ranged geometrically from 2 to 256 resource units per individual (Basset et al., in preparation). With the Holling Type III functional response used in our model, the half saturation coefficient was found to scale positively with individual body size, with a scaling factor not statistically different from a range of scaling factors lower than 1/2 and including 1/4 (i.e., $x = 0.32$, Fig. 2; comparison between slopes, t-test, ns). This direct relationship was independent of the functional response

equation used; depending on the type of Holling's functional response used for the fit, the half-saturation coefficient scaled with species body-size with a positive exponent in a range between 1/4 and 1/2. A positive scaling factor of the half-saturation coefficient with individual cell size was also found with phytoplankton, where available data ($x = 0.17$; Valeila 1984) also showed a scaling factor close to 1/4. A range of values between 1/4 and 3/4 was recently used to investigate the influence of size dependent space use consumer behavior on species interaction and coexistence within competitive guilds (Basset and DeAngelis, 2007).

The occurrence of an inverse scaling of perceived resource availability with body size is also derived from the analysis of published data on patch departure behavior, using the resource giving-up density as a proxy for perceived resource availability: i.e., everything else being equal, higher giving-up densities (GUDs) indicate lower perceived availability. Actually, GUD data for seed-eating rodent guilds showed higher GUDs for higher individual body masses and metabolism (Brown 1988, Brown et al. 1994, Kotler et al. 2002; but see also Kotler et al. 1993 for

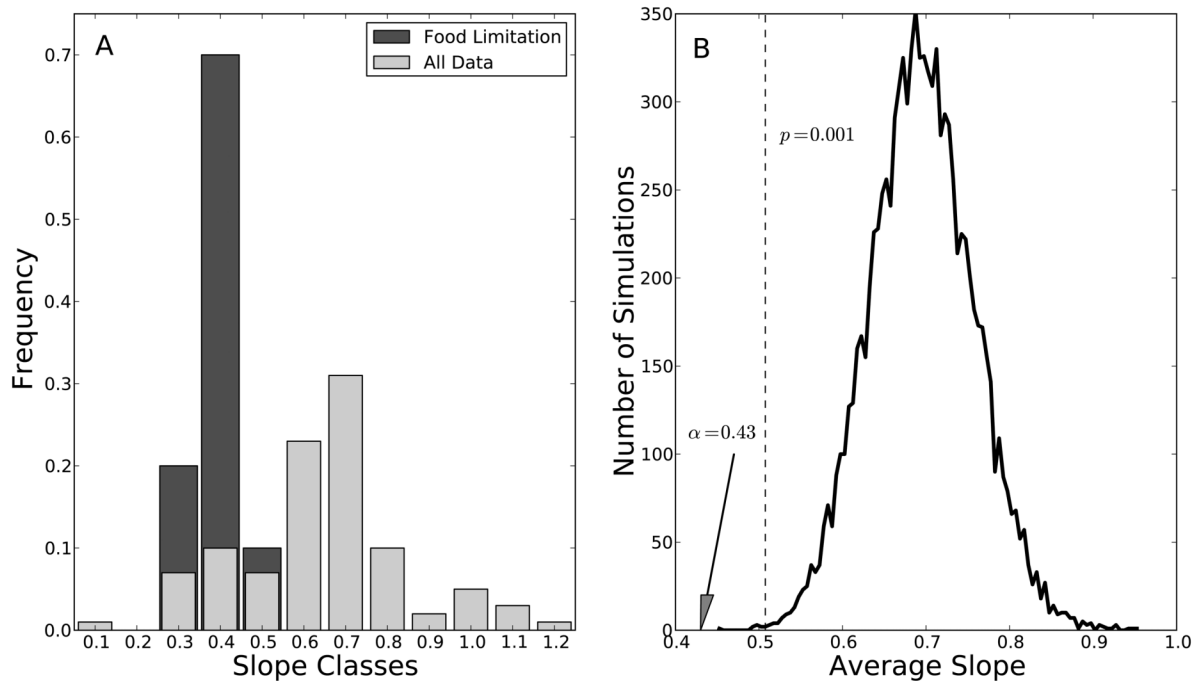


Fig. 3. Meta-analysis of published data on the allometric relationships between ingestion rates and body size in consumers including aquatic and terrestrial groups, invertebrates and vertebrates. Data are from 100 allometric regressions reported in the 51 published papers listed in Table 1. Ten regressions explicitly refer to limiting conditions. (A) The frequency distribution of slope values α of the allometric regressions are plotted, comparing food limitation conditions with the overall data set. (B) Statistical comparison of the observed average slope under food limitation conditions with the results of 10,000 Monte Carlo simulations of 10 cases randomly selected from the overall dataset. Slopes on the left of the vertical dashed line have a probability of less than 1/1000.

opposing evidence). Predation risks (manipulation of predators: Mohr et al. 2003; availability of refugia and intensity of light: Brown et al. 1988) were other factors found to affect the GUD of seed-eating rodents. Therefore, the assumption underlying Eq. 2 is supported by a specific laboratory case study and by literature data from guilds including invertebrate and vertebrate species.

Eq. 7 is a new model for the relationship between ingestion rates and individual body-size, which accounts for dependency on resource availability. It is not a power law, but it tends to a Kleiber-like law for unlimited resource availability. Furthermore, for small mass intervals, it can be approximated by power laws having an exponent which decreases with increasing mass. Experimental data is most often analyzed by assuming an underlying power law. Therefore it is interesting to observe whether there is a significant difference in exponents of power laws

fitted to data measured in limited and unlimited resource conditions. Literature data show a large variability in the scaling exponents of resource ingestion rates versus individual body-size, which range from $\alpha = 0.1$ to $\alpha = 1.2$, as shown in Fig. 3A. The dataset is based on 51 papers retrieved from a literature search for allometric scaling laws relating individual body size to ingestion rates, describing 100 experimental cases/conditions where allometric relationships between individual body size and ingestion rates were reported (Tables 1 and 2). The data refer to cases/conditions covering terrestrial and aquatic conditions, and invertebrate and vertebrate guilds. Of these, 10% were originally referred to as cases/conditions of resource shortage. If the ingestion rate always mirrored Kleiber's allometric law, such a large range of experimental conditions would not be relevant to the observed variability, since this law is supposed to cover a

Table 1. Key information on the allometric scaling of individual resource ingestion rate with individual body-size is shown by listing the taxonomic group considered (“Group”); the slope value of the allometric relationship (“ α ”), which is an average if the paper reports several regressions, as detailed in Table 2; the number of regressions computed in the paper (“ N ”); the number of declared occurrences of resource limitation to consumers (“ N_L ”) and the reference source (“Reference”).

| Group | α | N | N_L | Reference |
|---|----------|-----|-------|---------------------------------|
| Grazer mammals | 0.36 | 1 | 1 | Clutton-Brock and Harvey (1983) |
| Grazer ruminants | 0.36 | 1 | 1 | Illius and Gordon (1987) |
| <i>Mytilus edulis</i> | 0.41 | 1 | 1 | Thompson (1984) |
| Rotifers | 0.42 | 1 | 1 | Stemberger and Gilbert (1987) |
| Daphniids | 0.42 | 1 | 1 | Jeyasingh (2007) |
| Pinniped adults | 0.44 | 1 | 0 | Innes et al. (1987) |
| Subantarctic copepods | 0.46 | 4 | 4 | Atkinson (1996) |
| Grazers mammals | 0.48 | 1 | 1 | Conradt et al. (2000) |
| <i>Crassostrea gigas</i> | 0.49 | 15 | 0 | Bougrier et al. (1995) |
| <i>Ursus arctos horribilis</i> | 0.51 | 2 | 0 | Rode et al. (2001) |
| Mustelidae adults | 0.58 | 1 | 0 | Innes et al. (1987) |
| Terrestrial carnivora adult | 0.58 | 1 | 0 | Innes et al. (1987) |
| Arid zone marsupials | 0.60 | 1 | 0 | Nagy and Bradshaw (2000) |
| <i>Chlamys nobilis</i> | 0.60 | 1 | 0 | Pan and Wang (2008) |
| <i>Dreissena polymorpha</i> | 0.61 | 1 | 0 | Schneider et al. (1988) |
| <i>Alces alces calves</i> | 0.62 | 1 | 0 | Andersen and Saether (1992) |
| <i>Chlamys farreri</i> | 0.62 | 1 | 0 | Bacher et al. (2003) |
| Copepods | 0.62 | 1 | 0 | Ikeda (1977) |
| Daphniids | 0.63 | 1 | 0 | Jeyasingh (2007) |
| Pinniped adults and terrestrial carnivora | 0.63 | 1 | 0 | Innes et al. (1987) |
| Raptorial birds | 0.63 | 1 | 0 | Calder and King (1974) |
| Raptorial birds | 0.63 | 1 | 0 | Schoener (1968) |
| Herbivorous caecum fermenters | 0.64 | 1 | 0 | Clauss et al. (2007) |
| Delphinoidea | 0.67 | 1 | 0 | Innes et al. (1986) |
| Forest floor arthropods | 0.68 | 1 | 0 | Reichle (1968) |
| Mammals | 0.68 | 1 | 0 | Harestad and Bunnell (1979) |
| <i>Pleuronectes platessa</i> | 0.68 | 1 | 0 | Van der Veer et al. (2009) |
| Sea ducks | 0.69 | 1 | 0 | Goudie and Ankney (1986) |
| Carnivorous homeotherms | 0.69 | 1 | 0 | Farlow (1976) |
| Invertebrates | 0.69 | 1 | 0 | Capriulo (1982) |
| Carnivorous mammals | 0.70 | 1 | 0 | Farlow (1976) |
| Herbivorous mammals | 0.70 | 1 | 0 | Shiple et al. (1994) |
| Passerine birds | 0.70 | 1 | 0 | Lindstrom and Kvist (1995) |
| <i>Styela plicata</i> | 0.70 | 1 | 0 | Fisher (1977) |
| <i>Capitella</i> sp. | 0.70 | 1 | 0 | Forbes and Lopez (1987) |
| Homeotherms | 0.70 | 1 | 0 | Farlow (1976) |
| Marine calanoid copepods | 0.70 | 1 | 0 | Saiz and Calbet (2007) |
| Herbivorous homeotherms | 0.72 | 1 | 0 | Farlow (1976) |
| Mammals and birds | 0.72 | 1 | 0 | Kirkwood (1983) |
| Herbivorous mammals | 0.73 | 1 | 0 | Farlow (1976) |
| <i>Alces alces</i> adults | 0.73 | 1 | 0 | Andersen and Saether (1992) |
| Phocidae juveniles | 0.73 | 2 | 0 | Innes et al. (1987) |
| Terrestrial mammals | 0.73 | 1 | 0 | Nagy et al. (1999) |
| Deposit-feeders | 0.74 | 1 | 0 | Cammen (1980a) |
| Cattles | 0.75 | 1 | 0 | Murray (1991) |
| Marine amphipods | 0.75 | 1 | 0 | Dagg (1976) |
| Whales | 0.75 | 1 | 0 | Hinga (1979) |
| Zoo mammals | 0.75 | 1 | 0 | Evans and Miller (1968) |
| Herbivorous non-ruminant foregut fermenters | 0.76 | 1 | 0 | Clauss et al. (2007) |
| Herbivorous mammals | 0.77 | 2 | 0 | Clauss et al. (2007) |
| Phocidae adults | 0.77 | 3 | 0 | Innes et al. (1987) |
| Carnivores | 0.77 | 1 | 0 | Carbone et al. (2007) |
| Ungulates | 0.77 | 1 | 0 | Clauss et al. (2007) |
| Zooplankton | 0.77 | 1 | 0 | Hansen et al. (1997) |
| Geese | 0.78 | 1 | 0 | Durant et al. (2003) |
| Herbivorous colon fermenters | 0.79 | 1 | 0 | Clauss et al. (2007) |
| Crustacea | 0.8 | 1 | 0 | Conover (1978) |
| Carnivorous poikilotherms | 0.82 | 1 | 0 | Farlow (1976) |
| Periphyton | 0.83 | 1 | 0 | Cattaneo and Mosseau (1995) |
| Ciliates | 0.84 | 1 | 0 | Fenchel (1980) |
| Fishes | 0.84 | 1 | 0 | McCann (1998) |

Table 1. Continued.

| Group | α | N | N_L | Reference |
|----------------------------------|----------|-----|-------|-------------------------|
| <i>Ursus americanus</i> | 0.86 | 1 | 0 | Welch et al. (1997) |
| Non-mustelid carnivora adults | 0.88 | 2 | 0 | Innes et al. (1987) |
| Benthic detritivores | 0.88 | 3 | 0 | Cammen (1980b) |
| <i>Daphnia ambigua</i> | 0.99 | 1 | 0 | Lynch et al. (1986) |
| Larval fish | 1.00 | 3 | 0 | MacKenzie et al. (1990) |
| <i>Odocoileus hemionus</i> | 1.00 | 1 | 0 | Hobbs (1989) |
| <i>Sus</i> sp. | 1.00 | 1 | 0 | Wellock et al. (2003) |
| <i>Daphnia parvula</i> | 1.00 | 1 | 0 | Lynch et al. (1986) |
| Finches | 1.02 | 1 | 0 | Calder and King (1974) |
| <i>Acartia tonsa</i> | 1.08 | 1 | 0 | Berggreen et al. (1988) |
| <i>Daphnia pulex</i> | 1.20 | 1 | 0 | Lynch et al. (1986) |
| <i>Daphnia galathea mendotae</i> | 1.24 | 1 | 0 | Innes et al. (1987) |

wide range of sizes and taxonomic variability, and it is proposed as a universal law. In our model for resource ingestion rates, a Kleiber-like allometric law is merely an upper threshold for unlimited conditions. Furthermore, the model predicts that for conditions of resource shortage the slope of the best fitting power-law should be lower than for unlimited resource conditions, since the ingestion rate of large individuals is expected to be limited earlier and more strongly than that of small individuals.

The subsample of ten experimental cases specifically referring to limiting conditions shows an average exponent $\alpha = 0.43$, much lower than the average exponent of the complete data set. A Monte Carlo simulation carried out by extracting 10,000 randomly chosen subsamples of ten elements shows, with an extremely high confidence level, that the difference between the averages is statistically significant, and is not due to stochastic fluctuations (Fig. 3B). Recent evidence of positive scaling of the exponent α of a freshwater crayfish with nutrient and organic matter supply seems to support this point (McFeeters et al. 2011). Therefore, our model appears to be consistent with the evidence available in the literature, although direct experimental tests of individual resource intake variability with integrated variation of absolute resource availability and individual body size are still required.

CONCLUSIONS

The model described in this paper incorporates into a single equation three main factors in the process of animal resource ingestion: (1) the

Table 2. Individual regressions for papers reporting multiple regressions for the same group. In the case of subantarctic copepods the author states that conditions were resource-limited in all four cases. In all other cases there is no explicit indication of resource limitation.

| Group | Regression value | Reference |
|--------------------------------|------------------|-------------------------|
| <i>Crassostrea gigas</i> | 0.19 | Bougrier et al. (1995) |
| | 0.31 | |
| | 0.31 | |
| | 0.33 | |
| | 0.35 | |
| | 0.36 | |
| | 0.42 | |
| | 0.54 | |
| | 0.54 | |
| | 0.59 | |
| Subartic copepods | 0.64 | Atkinson (1996) |
| | 0.66 | |
| | 0.67 | |
| | 0.69 | |
| <i>Ursus arctos horribilis</i> | 0.71 | Rode et al. (2001) |
| | 0.72 | |
| Phocidae juveniles | 0.42 | Innes et al. (1987) |
| | 0.43 | |
| Herbivorous mammals | 0.49 | Clauss et al. (2007) |
| | 0.51 | |
| | 0.57 | |
| Phocidae adults | 0.44 | Innes et al. (1987) |
| | 0.74 | |
| Non-mustelid carnivora adults | 0.76 | Innes et al. (1987) |
| | 0.77 | |
| | 0.87 | |
| Benthic detritivores | 0.71 | Cammen (1980b) |
| | 0.87 | |
| Larval fish | 0.89 | MacKenzie et al. (1990) |
| | 0.74 | |
| | 0.79 | |
| | 1.12 | |
| | 0.84 | |
| | 0.99 | |
| | 1.16 | |

dependence of individual metabolic requirements on individual body size; (2) the dependence of individual resource ingestion rates on resource availability; and, finally (3) the dependence of resource availability perceived at the individual level on individual body size. It builds on previous findings (Basset and DeAngelis 2007), extends the field of application of both Holling and Kleiber-like equations and helps to explain the deviations from the 3/4 scaling of metabolism with body size that is often seen in data from wild populations, restricting this expectation to conditions where food is sufficiently available. The substitution of the term “resource availability” with the body-size dependent term “perceived availability” extends the application of Holling’s functional responses to the analysis of intra-guild competition and coexistence. The introduction of the normalized functional response I to the Kleiber-like equation extends the latter to limiting conditions, conceptually incorporating size dependency into the allometric scaling coefficient. However, the model proposed here is no longer a scaling law. Finally, by unifying the body-size and resource availability components of ingestion-rate variability, the model contributes to the integration of metabolic and resource-perception theory with population dynamics of both resources and consumers.

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