

Notes and Comments

The Scaling of Abundance in Consumers and Their Resources: Implications for the Energy Equivalence Rule

Chris Carbone,^{*} J. Marcus Rowcliffe,[†] Guy Cowlshaw,[‡] and Nick J. B. Isaac[§]

Institute of Zoology, Zoological Society of London, Regent's Park,
London NW1 4RY, United Kingdom

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ABSTRACT: The negative scaling of plant and animal abundance with body mass is one of the most fundamental relationships in ecology. However, theoretical approaches to explain this phenomenon make the unrealistic assumption that species share a homogeneous resource. Here we present a simple model linking mass and metabolism with density that includes the effects of consumer size on resource characteristics (particle size, density, and distribution). We predict patterns consistent with the energy equivalence rule (EER) under some scenarios. However, deviations from EER occur as a result of variation in resource distribution and productivity (e.g., due to the clumping of prey or variation in food particle size selection). We also predict that abundance scaling exponents change with the dimensionality of the foraging habitat. Our model predictions explain several inconsistencies in the observed scaling of vertebrate abundance among ecological and taxonomic groups and provide a broad framework for understanding variation in abundance.

Keywords: population density, diet, allometry, energy equivalence rule.

Understanding the relationship between the abundance of organisms and their resources is a key challenge in ecology (Brown 1995; Gaston and Blackburn 2000). One of the most widely used measures of abundance is population density (McNab 1963; Damuth 1981; Peters and Raelson 1984; Lindstedt et al. 1986; Silva et al. 2001). There is

extensive empirical evidence for negative scaling of species population density in relation to body size (Damuth 1987; Duarte et al. 1987; Enquist et al. 1998). Many have also found support for invariance in population energy use across taxa within a trophic level (Damuth 1981, 1998; Enquist et al. 1998; Ackerman et al. 2004), a phenomenon known as the energy equivalence rule (EER; Nee et al. 1991). However, we still have a poor understanding of how these relationships emerge given the complexity of interactions among members of ecological communities. Many previous theoretical frameworks used to predict density do not take into account the characteristics of the resources, including particle size and availability (Damuth 1987; Bohlin et al. 1994; Enquist et al. 1998; Carbone and Gittleman 2002; Haskell et al. 2002; Jetz et al. 2004). Most species within communities do not share common resources: consumers exploit different resources according to their ecological function (diet strategy and trophic level), body size, and phylogeny (Demment and Van Soest 1985; Vezina 1985; Shine 1991; Illius and Gordon 1992; Carbone et al. 1999; Schmid et al. 2000). Thus, in order to fully understand patterns in animal abundance, we need to understand the scaling of population density not only in relation to metabolic rate (resource need) but also in relation to the characteristics of the resources (particle size, distribution, and availability; Schmid et al. 2000).

Here we develop a simple model of the scaling of animal abundance (measured as population density) in relation to the scaling of resource needs (metabolic rate) based on simple allometric assumptions about how consumer body mass influences resource characteristics. We use this approach to predict abundance scaling for carnivorous and herbivorous consumers under a range of scenarios. We then discuss how our model predictions compare with patterns reported in the literature.

Model of Animal Density

We begin by defining the population based on the geometric relationship between the long-term distribution of

^{*} E-mail: chris.carbone@ioz.ac.uk.

[†] E-mail: marcus.rowcliffe@ioz.ac.uk.

[‡] E-mail: guy.cowlshaw@ioz.ac.uk.

[§] E-mail: nick.isaac@ioz.ac.uk.

consumers and the distribution, size, and productivity of its resources, assuming the space used is sufficient to provide the consumer with its energy requirements. We define consumer density N_c , in relation to the consumer resource requirements Q_c , and the characteristics of the resource and habitat dimensionality (defined below). Food items are qualitatively different entities for predators and herbivores, and the densities of items are accordingly defined differently for these two groups. For predators, we assume resources are quantified in terms of the mass of the food item M_i (which is related to consumer body mass), the prey item group size G_i (assuming only one individual is taken per group), and item density N_i . For herbivores, we define a food item as a bite, and the density of items is therefore calculated as the quotient of total available plant biomass B_i and bite size M_i . In addition, the scaling exponents of density will be affected by the dimensions of the foraging habitat, f (where $f = 2$ for terrestrial resources and 3 for some arboreal, aerial, or aquatic resources; Carbone et al. 2005). We assume for both predators and herbivores that N_c is also dependent on the long-term productivity of resources U_i . Thus,

$$N_c \propto \left(\frac{M_i N_i U_i}{Q_c G_i} \right)^{2/f}, \tag{1a}$$

$$N_c \propto \left(\frac{B_i U_i}{Q_c} \right)^{2/f}, \tag{1b}$$

for predators and herbivores, respectively.

Given these relationships, we use known scaling rules to derive a predicted scaling relationship for the characteristics of the consumer and its resources. First, food requirements of the consumer scale with body mass M_c according to

$$Q_c \propto M_c^q. \tag{2}$$

For predators, prey item mass scales with predator body mass according to

$$M_i \propto M_c^p, \tag{3}$$

prey density scales with prey mass according to

$$N_i \propto M_i^d, \tag{4}$$

and prey group size scales with prey mass according to

$$G_i \propto M_i^g. \tag{5}$$

For predators, individual prey productivity scales with prey mass according to

$$U_i \propto M_i^u. \tag{6}$$

For herbivores, we expect the biomass of food plants to scale positively with consumer mass, reflecting greater selectivity for more digestible, less abundant plant parts in smaller herbivores:

$$B_i \propto M_c^b. \tag{7}$$

We expect the same selectivity to lead to negative scaling of productivity with herbivore mass because the more digestible plant parts selected by smaller herbivores regenerate more rapidly (Demment and Van Soest 1985):

$$U_i \propto M_c^u. \tag{8}$$

Substituting equations (2)–(8) into the scaling relationships in equation (1) gives

$$N_c \propto \left(\frac{M_c^p M_c^{pd} M_c^{pu}}{M_c^q M_c^{pg}} \right)^{2/f} \propto M_c^{[p(1+d+u-g)-q]2/f} \tag{9a}$$

for predators and

$$N_c \propto \left(\frac{M_c^b M_c^u}{M_c^q} \right)^{2/f} \propto M_c^{(b+u-q)2/f} \tag{9b}$$

for herbivores.

Parameter Values

We are interested in applying our model to a very broad range of taxonomic groups. In order to do so, we fit parameter values derived from empirical studies in the literature to our model and assess whether our emergent predictions are consistent with the density–body mass scaling exponents reported for different taxonomic groups of consumers. The scaling exponents of metabolic rate q have been found to vary with normalization constants (Glazier 2005), so we use a range of exponents from 0.67 to 1.0 representing the range of variation described in previous studies (Peters 1983; Clarke and Johnston 1999; Nagy et al. 1999; Glazier 2006).

For the predator model, we explore the special case where M_i^u is proportional to the prey mass–specific metabolic rate (Brown et al. 2000; Charnov 2001; Ernest et al. 2003) and the prey density exponent d equals the negative of the prey metabolic rate exponent. Thus, total population production rates across prey types remain constant (i.e., energy equivalence) and the exponent term $1 + d + u$ in equation (9a) equals zero (Farlow 1976; Damuth 1981; Peters 1983). This simplification allow us to focus our analysis on other factors

affecting the scaling of consumer density, but the effect of varying each exponent independently can easily be seen in equation (9a) and is discussed further below.

We assume that prey mass is directly proportional to predator mass ($p = 1$), as has commonly been described (Peters 1983; Vezina 1985; Cohen et al. 2003). We were unable to find studies estimating the scaling of prey group size with body mass except in African bovids, where $g = 0.66$ (Brashares et al. 2000). Since some prey types may not show a grouping effect with mass (e.g., invertebrate prey), we present predictions with and without this effect ($g = 0$ or 0.66), but we expect this exponent may vary within this range.

For the herbivore model, the relationship between biomass scaling exponent b and plant productivity u is complicated by the fact that herbivores eat only parts of plants, so we take a different approach to that used in the predator model. We expect plant food biomass to scale positively with body mass ($b > 0$; Demment and Van Soest 1985). There is little published information on the scaling of available plant biomass with herbivore mass (taking into account selectivity and digestibility). However, two studies estimate a positive scaling in North American herbivores (Belovsky 1997) and grazers in Tanzania (Wilmschurst et al. 2000) of 0.21–0.22, so we set $b = 0.22$. We also have no empirical

estimates of the productivity of different plant parts, u , consumed by herbivores. However, bite mass in herbivores scales approximately to the 0.62 of herbivore mass (Shiple et al. 1994), and if we assume that the production rates of these parts are similar to the production rates of whole plants ($\text{mass}^{-0.25}$; Enquist et al. 1999), we would predict scaling production rates of $u = -0.16$ (0.62×-0.25). The estimated b and u values for the herbivore model do not differ substantially from the equivalent terms in the predator model ($1 + d = 0.25$, $u = -0.25$), and with these exponent values, the herbivore and predator models (without prey grouping) make the same predictions.

Results and Discussion

Our model is used to make predictions of animal density scaling in relation to body mass given variation between consumers in the scaling of resource needs (related to the scaling of metabolism), the characteristics of the resource (related to consumer size and dietary strategy), and the dimensionality of the foraging habitat. Given the observed range of the parameters used in our model, we inevitably predict a wide range of density-mass scaling exponents, and these predictions are explored in the next sections.

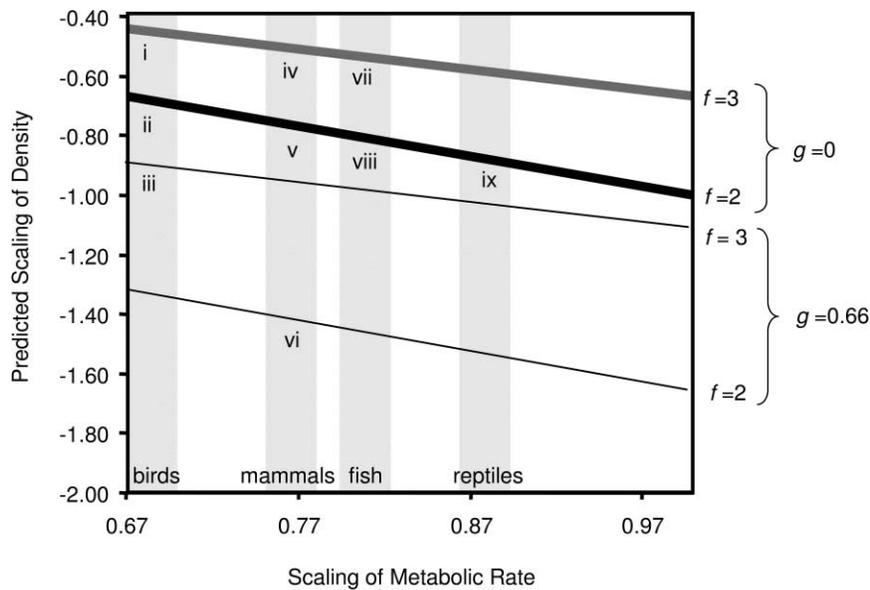


Figure 1: Predictions of the predator model for the scaling exponent of population density in relation to the scaling of metabolic rate, q (related to resource need), in environments of two and three dimensions ($f = 2$ and $f = 3$, respectively), and without or with the scaling of prey grouping ($g = 0$ and $g = 0.66$, respectively). Vertical shaded areas designate different vertebrate groups (birds, mammals, fish, and reptiles). Their positions with respect to metabolic rate scaling are based on mean estimates by Nagy et al. (1999) and Clarke and Johnston (1999). i = flying birds, ii = nonflying and terrestrial feeding birds, iii = predatory flying birds, iv = arboreal mammals, v = terrestrial mammals, vi = predatory terrestrial mammals (with prey grouping), vii = pelagic fish, $viii$ = benthic fish, ix = terrestrial reptiles. Predictions approximately matching the energy equivalence rule are emphasized by heavy lines (black for two dimensions, gray for three dimensions).

Different Routes to the Same Exponent

Under a range of different underlying conditions, the model predicts similar exponents for the scaling of density. For example, we predict -0.67 density scaling for predators (without prey grouping) living in a two-dimensional environment, with a metabolic rate scaling of 0.67 . We predict the same exponent with a metabolic rate scaling of 1.0 with no prey grouping in a three-dimensional environment. The predator model (in three-dimensional habitats) can also predict a density scaling exponent near -0.75 across the full range of metabolic rate scaling exponents (0.67 – 1.0), with intermediate values of the prey grouping exponent g (varying between 0 and 0.66 ; fig. 1). The potential for overlap in the model predictions has implications for our understanding of energy equivalence, particularly tests of EER based on comparisons of the scaling exponents.

Prey Characteristics and Habitat Dimensionality

In order to simplify the analysis, we presented a special case of the predator model in which the exponent terms $1 + d$ and u canceled out (see eq. [9a]), and there was energy equivalence in prey population energy use and production rates (Damuth 1981). Under these conditions, the predator model predicts energy equivalence without prey grouping in two dimensions. Likewise, the herbivore model predicts energy equivalence in two dimensions when b and u cancel out. Both models predict shallower density scaling in three-dimensional foraging habitats (fig. 1), since density is usually measured in two dimensions. However, the predictions of the predator model with prey grouping ($g > 0$) can deviate strongly from energy equivalence (table 1; fig. 1). This is because an increase in prey group size leads to an increase in the distance between kills, thus reducing predator density. Deviations from energy equivalence in this model could also be amplified by increasing the prey size scaling exponent p (eqq. [9a], [9b]). The simplified conditions for prey energy use illustrate the effects of varying p , g , and f , but the influence of the remaining exponents can easily be seen in equations (9a), (9b).

Abundance Scaling in Vertebrates

Considering both the habitat dimensions and the scaling of resource requirements, we can make broad comparisons between our predictions and the observed density scaling exponents for ecological and taxonomic groups of vertebrates cited in the literature (see fig. 1). The published studies differ greatly in the nature of the data and the methods used for estimating density and census area (Blackburn and Gaston 1996), and they are biased in the selection of taxonomic groups, so our comparisons should be interpreted with caution.

In birds, based on our model predictions, we would expect to see less negative density-mass scaling exponents. This is because of the potentially three-dimensional nature of their habitat and because the metabolic rate exponents of birds are near 0.67 and significantly lower than 0.75 (Bennett and Harvey 1987; Nagy 2005). Scrutiny of the literature indicates that the scaling of density relationships in birds is highly variable (Gaston and Blackburn 2000; Russo et al. 2003) but that the exponents are indeed lower than those found in mammals and other taxonomic groups, with slopes ranging from -0.31 to -0.60 (Ebenman et al. 1995; Russo et al. 2003; -0.66 for maximum density, Brown and Maurer 1987). There is also a tendency for both flightless birds (those living in two-dimensional environments) and predators like raptors to have more negative scaling exponents (Ebenman et al. 1995; Russo et al. 2003). Thus, bird abundance scaling is qualitatively consistent with our model predictions.

Across a wide range of mammals, most of which are terrestrial, population density scales with the inverse of the metabolic rate (scaling exponent of -0.78 , Damuth 1981, 1987; Nagy et al. 1999). However, studies on primates and other arboreal mammals that have a three-dimensional environment find less negative density scaling exponents between -0.54 and -0.61 (Robinson and Redford 1986; Fa and Purvis 1997; Carbone et al. 2005). In addition, carnivorous mammals have significantly more negative density scaling exponents than herbivores (Marquet 2002; see also Damuth 1987; Jetz et al. 2004). Both of these findings are consistent with our model predictions. In the latter example, we believe that larger carnivores

Table 1: Some predictions of the models in relation to the characteristics of prey distribution and dimensions of habitat

| Habitat dimensions | Herbivore ($b = .22$; $u = -.16$) | Predator—no prey groups (g or $p = 0$) | Predator-prey grouping ($g = .66$, $p = 1.0$) |
|-----------------------------------|---|---|---|
| Two (e.g., terrestrial) | $-.69$ | $-.75^a$ | -1.41 |
| Three (aerial, arboreal, aquatic) | $-.44$ | $-.50^b$ | $-.94$ |

Note: The metabolic rates scaling exponent $q = 0.75$.

^a Predictions consistent with the energy equivalence rule in two dimensions.

^b Predictions consistent with the energy equivalence rule in three dimensions.

deviate from the EER because of the greater tendency for large prey to form groups (i.e., $g > 0$).

For lizards, the scaling of density with body mass is significantly steeper than that of mammals (scaling exponent of -1.03 ± 0.14 SE; data from Damuth 1987), but this is consistent with the observed scaling of metabolic rate of 0.92 (significantly higher than 0.75) in this group (Nagy 2005). These results are also consistent with our model predictions for predators with little or no prey grouping ($g \approx 0$) living in a two-dimensional environment.

Among fish, the scaling of density and metabolism are well studied in salmonids. In this group, the scaling is generally strongly negative, with an average of -0.90 (Grant et al. 1998), and this is consistent with the relatively steep average scaling of metabolism of 0.87 (Steingrimsson and Grant 1999). These relationships have been used to represent support for the EER (Bohlin et al. 1994). Our model would predict a shallower scaling of density given the three-dimensional nature of aquatic environments, but there may also be an effect of prey grouping on predatory fish that counteracts the effect on environment dimensionality (fig. 1). In salmonid guilds across sites, scaling exponents become less negative with increasing water depth (Steingrimsson and Grant 1999), which may reflect the fact that in deep water, there is greater potential to use different strata. The scaling of density in reef fish was shallower than in salmonids, near -0.75 , which was justified by Ackerman et al. (2004) as support for the EER. Without a clearer understanding of the scaling of fish metabolism, their ecology, and other potential conflicting factors, it is hard to interpret whether the observed patterns in density scaling support our model predictions or the EER.

Conclusions

Overall, our model predictions highlight the need for a better understanding of factors affecting the scaling of density, such as resource characteristics (e.g., prey choice), habitat dimensions, and metabolic rate scaling. However, there appears to be consistent variation in density scaling exponents related to major taxonomic and ecological groups and habitat types, and our predictions are broadly consistent with these observed patterns.

Abundance is one of the most widely used measures of how animals use their environment and has been studied at a range of spatial and temporal scales. While abundance is often linked with resource requirements and availability (East 1984; Gregory and Gaston 2000; Carbone and Gittleman 2002; Gaston et al. 2003; Etienne and Olff 2004), there has been a lack of a clear theoretical framework to understand how broadscale interspecific population density patterns might emerge from complex communities given that most species do not share common resources.

We believe that the key to understanding how resources affect the scaling of animal abundance is to understand the partitioning of resources and, critically, how the size and distribution of food items scale with consumer size. Having achieved this, we will be better able to understand the influence of both metabolism and resources on global patterns in the scaling of animal abundance. In this article, we have used our model in a very broad context, although it could easily be adapted to explore factors affecting specific settings on finer spatial scales and as such provides a general framework for understanding patterns in the scaling of animal abundance.

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