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Body size, population density, and the Energetic Equivalence Rule

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Summary

1. We critically evaluated the Energetic Equivalence Rule (EER) with regard to its underlying theoretical framework, its dependence of a particular relationship between population density and body size, and the way it is calculated.
2. We found it to be theoretically incorrect, not supported by empirical data on maximum population density and body size relationships, and that its calculation is misleading. In particular, we found a general pattern underlying the allometry of maximum population density, which stresses the correspondence between the documented linear patterns and triangular relationships between both variables.
3. Two independent data sets, one for mammals and another for intertidal invertebrates, showed that medium-size species attain higher population densities, and that population density decreases towards larger and smaller sizes.
4. A more direct calculation of population energy use for mammalian primary consumers, based on measured metabolic rates, showed that populations' energy use fluctuates widely among species and that its upper limit is not independent of body size but peaks at a body size of about 100 g, and decreases toward both smaller and larger body sizes.
5. Diet also has a strong effect on this relationship. Omnivores show a positive relationship between population energy use and body size, while this is negative for carnivores and insectivores.

Key-words: allometry, body size, density, energy use, intertidal.

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Introduction

The Energetic Equivalence Rule (EER; Damuth 1981; Nee *et al.* 1991) states that the amount of energy each species uses per unit area of its habitat is independent of body mass. This rule is based on an allometric argument first proposed by Damuth (1981). He assembled data on the population density and body size of 307 mammal primary consumers around the world, and showed that average population density (D) was related to body mass (W) as $D \propto W^{-0.75}$. He also noted that since individual metabolic requirements (M) scale with body size as $M \propto W^{0.75}$, population energy use (PEU) was independent of body size. That is, $PEU = (D \times M) \propto W^0$. Later, Damuth (1987) extended the results of his previous analysis to both mammal primary and secondary consumers, and terrestrial organisms as a whole (see also Carrascal &

Telleria 1991; Nee *et al.* 1991 for birds; and Cotgreave 1993 for a review). Even though Damuth (1981, 1987) showed that the EER holds for local communities as well as for regional and world-wide collections of organisms, evidence presented by Brown & Maurer (1986), and recently by Nee *et al.* (1991), shows that within guilds and within groups of closely related organisms, such as those belonging to the same genus or tribe, a different pattern emerges. These later authors found that within these assemblages the scaling of population density has an allometric exponent greater than -0.75 , and it can even be positive, suggesting that larger species use more energy than their smaller relatives. However, Griffiths (1992) has recently pointed out that the allometric exponent of the relationship between population density and body size is close to -1.0 when the reduced major axis regression method is used, suggesting that small organisms use more energy than large organisms within communities.

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The above controversy has centred on the empirical value of the allometric exponent relating population density to body size, and the methods used for its estimation. However, the discussion has detracted attention from three important issues. The first relates to the theoretical framework underlying the EER. The second involves the form of the relationship between population density and body size, and the third the validity of the allometric argument employed in calculating the relationship between population energy use and body size. An additional issue that deserves attention (and which we will deal with elsewhere) is that since most analyses are cross-species there may be some of the usual problems of non-independence that confound comparative studies (Harvey & Pagel 1991; Cotgreave & Harvey 1992).

The theoretical framework underlying the EER

Damuth originally envisioned the EER as the result of biotic interactions over macroevolutionary time (Damuth 1981; Van Valen 1983), entailing a process of macroevolutionary coevolution (J. Damuth, personal communication). This mechanism is explained by Maiorana & Van Valen (1990) as: 'Diffuse interactions may maintain the upper bound of energy use. Any species expanding too much [i.e. increasing in density] gets its toes stepped on by an increasingly large number of other species while creating increasing selective pressure on them to respond to its advance; after a while it becomes impossible to outrun all potential competitors and predators and one's expansion is stopped. Species with very low rates of population energy flow, on the other hand, are susceptible to random-like fluctuations and thus suffer higher extinction.' The result of this process would be a negative relationship between population density and body size with a slope of -0.75 , thus making population energy use independent of body size. Although this explanation is appealing, we think it suffers from two major flaws.

1. Like other coevolutionary models (e.g. Stenseth & Maynard Smith 1984), Damuth's EER model requires that organisms make use of, and therefore interact through the use of, a common energy (resource) base within a common uniform ecosystem type through evolutionary time. However, the population density–body size relationship holds even when the organisms under analysis come from different ecosystem types on different continents (Damuth 1981, 1987; Currie & Fritz 1993). As pointed out by Marquet, Navarrete & Castilla (1990), these organisms clearly do not make use of the same resource base, and therefore cannot interact to affect each other's evolution by the mechanism postulated by Damuth. Moreover, there is no reason to expect species of similar body mass coming from different ecosystems to be constrained to the same upper maximum energy use, given the different productivities of the environments they inhabit

(Maurer & Brown 1988; Brown & Maurer 1989; Currie & Fritz 1993) and the different sets of species with which they share this energy. Additionally, even species that occur within a continent or a geographic region are usually not restricted to a single community; they occur in different habitats and coexist at varying densities with many different combinations of species across their geographic ranges (Brown 1984; Brown & Kurzius 1987) and over evolutionary time (Graham 1986). Thus, it is difficult to attribute the evolution of a species to a particular spatially and temporally restricted set of biotic interactions.

2. Energy limitation may not be responsible for the observed -0.75 slope in the relationship between population density and body size. First, Currie & Fritz (1993) found a negative correlation between population density and a measure of available energy, which is inconsistent with the idea of a simple limitation by energy. In areas where more energy is available one would expect population densities to be higher, if simple energy limitation is involved. Secondly, the relationship between population density and body size could be the result of the underlying species' size and species' abundance distributions (Blackburn, Lawton & Pimm 1993b). Thirdly, a similar -0.75 slope was reported by Marquet *et al.* (1990) in a study of a multiphyletic assemblage of intertidal invertebrates. In these intertidal systems, explanations relying exclusively on the way energy is allocated or partitioned might not be directly applicable since space is the main limiting resource competed for, and whose appropriation is the main constraint on population density (see also Nee, Harvey & Cotgreave 1992 for a discussion of the effect of physical packing). Moreover, unlike the pattern observed in terrestrial animals, the scaling of metabolic rate with body mass in intertidal invertebrates varies between 0.47 and 1.28, and there is no clear clustering around 0.65 or 0.75 (Patterson 1992).

What is the relationship between population density and body size?

As stated by Damuth (1991), we are just beginning to discern the general importance of body size and its role as a major organizing factor of the world biota. Part of this understanding requires an explicit consideration of scatter around allometric relationships and its ecological and evolutionary meaning. In studying the relationships between body size and ecological or evolutionary traits, scientists have been more preoccupied with central patterns, and have explicitly or implicitly assumed that scatter around regression lines, or error variance, is associated with measurement error. However, recent empirical and theoretical evidence points out that part of the perceived scatter is due to real differences of species from predictions, because of their particular evolutionary history, ecology and physiology (Riska 1991; Harvey & Pagel

1991). A case in point is the relationship between population density and body size. Two different types of patterns have been found when $\log_{10}(D)$ is regressed against $\log_{10}(W)$. Most studies report simple linear relationships (Damuth 1981, 1987; Peters & Wassenberg 1983; Peters & Raelson 1984; Marquet *et al.* 1990; Currie & Fritz 1993), in which both variables are significantly and negatively correlated with the scatter concentrated along a narrow region surrounding the best-fit line. We call this the Linear Constraint Pattern (LCP). On the other hand, using independent data sets, Brown & Maurer (1987), Morse, Stork & Lawton (1988), Lawton (1989, 1990) and Blackburn *et al.* (1993a) found that the negative relationship between D and W is either weak or absent, and that the best descriptor of this scaling pattern is a surface or polygonal region enclosing observed combinations of both variables. We call this the Constraint Envelope Pattern (CEP). Typically, the CEP will have a well-defined upper boundary with opposite slopes on either sides of a maximum value of population density occurring at intermediate body sizes (Fig. 1). Supporters of this hypothesis have pointed out that the LCP may correspond to the right upper boundary of this CEP (a, in Fig. 1), suggesting that the LCP suffers from sampling biases against rare species, and small-bodied, rare species in particular (Brown & Maurer 1987; Lawton 1989). This particularly applies to the pattern described by Damuth (1981, 1987) who used ecological densities reported in the literature. Since most ecologists tend to study populations where they are abundant, these data may therefore be biased toward maximum densities (Lawton 1989). Under this view, the LCP is the result of a biased sample of the body size–abundance space (Currie 1993 for the opposite argument). However, despite the dissimilarities, we show here that they share a qualitatively similar relationship between maximum population density and body size, which points out that the EER does not hold for small organisms. We used the data presented by Damuth (1987) and Marquet *et al.* (1990) on mammal primary consumers and rocky intertidal invertebrates, respectively, and carried out the procedure proposed by Blackburn, Lawton & Perry (1992) to determine the slopes of the upper boundary (maximum densities) of the relationship between population density and body size. The procedure involves dividing the x -axis into intervals of equal length and recording the maximum value of the variable on the y -axis for each x interval. Because the value of the slope depends on the interval size, we applied this analysis over a range of interval sizes from 0.1 units of body size, up to a value that rendered at least three density values. After carrying out this procedure, the data were split into maximum density data for small and large organisms. The splitting point between small and large organisms was set to that body size at which the highest density value was observed. This data point was not included in the

analysis, to avoid correlation biases. Regression statistics for all intervals used (Table 1) showed a consistent pattern of negative values for the slope of the upper boundary of large organisms (ranging from -1.14 to -0.95 for mammals, and from -1.36 to -0.81 for intertidal invertebrates), and of positive values for small organisms (ranging from 0.28 to 0.68 for mammals, and from 0.45 to 0.69 for intertidal invertebrates). Figure 2a (based on an interval equal to 0.4 units of body size on the x -axis; recommended by Blackburn *et al.* 1992) shows graphically how the shape of this upper boundary matches the shape reported for the upper boundary of the relationship between population density and body size of the CEP; a positive slope for small organisms and a negative slope for the larger ones (compare with Fig. 1). Furthermore, the similarity between the scaling for such distant clades as mammals and rocky intertidal invertebrates, which live in widely different ecosystem types, supports the existence of a general pattern in the scaling of maximum population density under both the LCP and the CEP, which can be characterized as a piece-wise allometric relationship.

For both mammal primary consumers and intertidal invertebrates, the positive slopes found for small organisms did not conform to the EER under the allometric argument proposed by Damuth (1981, 1987). However, the scaling of maximum population density for large species indicated that they may be limited by energetic requirements (Blackburn *et al.* 1993b), in agreement with the EER (but see Blackburn *et al.* 1993a and the next section).

Typically, small species reach lower maximum densities than medium-size species (b, in Fig. 1; Brown & Maurer 1987; Lawton 1989, 1990). This pattern has several possible explanations. On the one hand, Blackburn, Harvey & Pagel (1990) showed that a positive slope characterizing the scaling of maximum population density of small organisms may be a sampling effect resulting from there being more intermediate-sized species in the communities, which will cause the

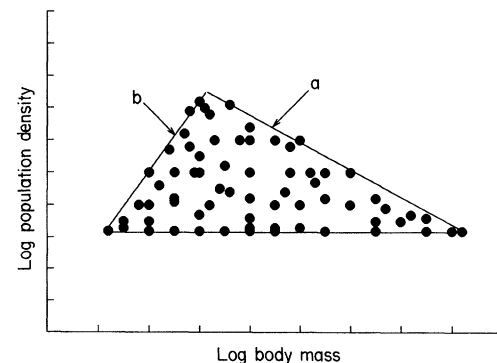


Fig. 1. Schematic representation of the relationship between population density and body size. The upper bound of the relationship peaks at a medium body size and decreases toward larger and smaller species. The lower boundary follows Currie & Fritz (1993).

Table 1. Statistics for the relationship between maximum population density and body size of mammals and intertidal invertebrates (I = interval length, a = intercept, b = slope)

I	Small				Large			
	a	b	r^2	n	a	b	r^2	n
Mammals								
0.1	3.16	0.30	0.09	12 ^{ns}	5.54	-0.95	0.73	28**
0.2	2.77	0.68	0.70	7*	5.86	-0.98	0.78	17**
0.3	2.81	0.68	0.70	5 ^{ns}	6.05	-0.99	0.93	12**
0.4	3.50	0.33	0.54	4 ^{ns}	6.60	-1.10	0.97	9**
0.5	3.53	0.28	0.74	3 ^{ns}	6.47	-1.05	0.98	8**
0.6	3.45	0.35	0.57	3 ^{ns}	6.78	-1.12	0.98	6**
0.7	—	—	—	—	6.79	-1.12	0.99	6**
0.8	—	—	—	—	6.62	-1.09	0.98	5**
0.9	—	—	—	—	6.24	-0.97	0.96	4*
1.0	—	—	—	—	6.78	-1.14	0.99	4**
Intertidal invertebrates								
0.1	4.14	0.45	0.14	7 ^{ns}	1.77	-0.81	0.41	22**
0.2	4.43	0.54	0.20	6 ^{ns}	2.00	-1.02	0.52	14**
0.3	4.90	0.69	0.29	5 ^{ns}	2.26	-1.05	0.55	11**
0.4	4.90	0.69	0.29	5 ^{ns}	2.59	-1.18	0.74	9**
0.5	5.19	0.65	0.68	4 ^{ns}	2.80	-1.28	0.82	7**
0.6	4.31	0.51	0.19	4 ^{ns}	3.01	-1.32	0.85	6**
0.7	5.19	0.65	0.68	4 ^{ns}	2.73	-1.36	0.84	5**

^{ns} $P > 0.05$; * $P < 0.05$; ** $P < 0.01$.

size categories containing more species to be most likely to contain the largest density value. This effect could be amplified if we consider that small species, by virtue of their size, may be consistently less efficiently collected (Lawton 1989; Blackburn *et al.* 1993a). On the other hand, Currie (1993) showed that the observed positive upper slope found for small organisms may be due to incomplete sampling of a global density–body size relationship displaying the LCP pattern. However, our results show that this positive upper slope is a characteristic of both the CEP and the LCP patterns, suggesting that the former is not just produced by subsampling the latter. Although we cannot rule out sampling effects (Blackburn *et al.* 1990) we concur with Brown & Maurer (1987) and Marquet (1993) in pointing out that the observed positive upper slope characterizing the relationship between maximum density and body size for small organisms has a biological explanation. In a recent paper, Brown, Marquet & Taper (1993) showed that the triangular shape of the upper boundary of the population density–body size relationship may be the reflection of an underlying general physiological constraint linked to organismal size. Brown *et al.* (1993) introduce a simple model which shows that the effect of body size on energy acquisition and conversion processes favours medium-size species within major taxonomic groups in both ecological and evolutionary scales, in agreement with patterns of body size evolution and size-related extinction of species on islands (Brown *et al.* 1993; Marquet 1993). Their model explains why medium-size species are more diverse and can potentially achieve higher population den-

sities than their larger or smaller relatives (compare Fig. 2a and b). Under this model, both the species' size distribution and the relationship between size and density are the direct result of the same process. This is an alternative to the sampling effect hypothesis proposed by Blackburn *et al.* (1990).

In summary, in this section we propose that there is a qualitative agreement between the LCP and the CEP patterns, at least with regard to the allometry of maximum densities, and that the positive slope characterizing the allometry of maximum densities for small organisms is a general pattern with biological basis which clearly violates the EER expectations.

The validity of the allometric argument to calculate PEU

The use of two allometric relationships to obtain a third one is a widespread practice (e.g. Peters 1983; Calder 1984). However, this procedure is not free of restrictive assumptions and in no circumstances should it be used at the expense of available data. The algebraic manipulation of the allometric relationships between population density and body size, and between metabolic rate and body size in herbivorous mammals, predicts that population energy use of species is independent of body mass ($PEU = D \times M \alpha W^{-0.75} \times W^{0.75} \alpha W^{0.0}$). However, this does not mean that all species use equal amounts of energy as predicted by the EER, because the error variances associated with both allometric relationships can propagate, causing population energy use to vary dramatically among species (Currie & Fritz 1993; Blackburn & Gaston 1994). This

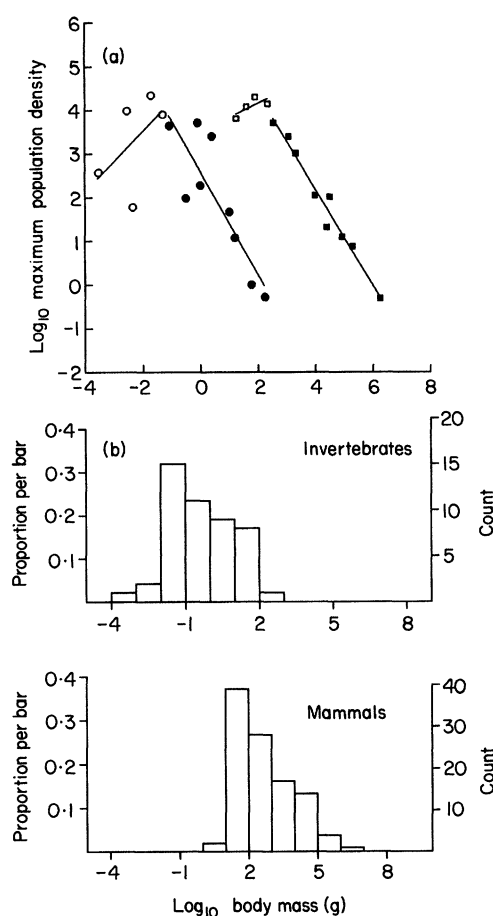


Fig. 2. (a) The upper boundary of the relationship between population density and body size for intertidal invertebrates (circles), and terrestrial herbivorous mammals (squares). Open symbols denote small species, closed symbols denote large species. Density values are individuals m^{-2} and individuals km^{-2} , for intertidal invertebrates and mammals, respectively. (b) Frequency distribution of body size for the complete data sets for mammals and intertidal invertebrates.

variability is lost under the algebraic manipulation of allometric equations. Since this has been the standard way population energy use is calculated (Damuth 1981, 1987, 1993; Peters 1983, Brown & Maurer 1986; Griffiths 1992; Currie & Fritz 1993), it is worth assessing how this variance affects the scaling of population energy use. To capture part of the variance associated with the estimates of PEU and avoid using the algebraic manipulation pointed out above, we calculated PEU directly for mammal species for which body size, density and basal metabolic rate data were available (Fig. 3). Ideally, one should use field metabolic rates instead of basal; however, field metabolic data are not yet available for enough species of mammals to allow for a statistical analysis (Nagy 1987 and Koteja 1991 present data for only 39 different species, of which 19 have density values listed in Damuth 1987). Data on population density, body size and diet were obtained from Robinson & Redford (1986), Damuth (1987), Brown & Nicoletto (1991) and P.A. Marquet (unpublished data); data for metabolic rate

were obtained from Elgar & Harvey (1987), McNab (1988) and Bozinovic & Rosenmann (1988).

As expected, population energy use varied widely among species of mammals. The slope of this relationship is not different from 0.0 for mammalian primary consumers, as expected under the EER, but it is positive for omnivores and negative for insectivores (Table 2). More important, however, is the fact that, qualitatively, the shape of the upper boundary found for population density (Fig. 2) also characterizes the relationship between population energy use and body size for herbivorous mammals. Population energy use attains its maximum value at a body size of around 100 g, the same as population density, and tends to decrease towards larger and smaller body sizes. The decrease towards large body size, although expected, should be viewed with caution, since logistic constraints make it difficult to take metabolic measurements of large organisms; more data could potentially reveal a different pattern for large mammals. Slope values for the upper boundary of this relationship ranged from 1.6 to 2.08 for the small species, and from -0.22 to -0.08 for the large ones. The large variability detected in population energy use, and in particular the shape of the upper boundary of this relationship, suggests that different species use different amounts of energy (this difference could reach more than three orders of magnitude) and that maximum population energy use is not independent of body size. This clearly violates the EER, in agreement with the recent findings reported by Damuth (1993). Further, variability in population energy use, even for species of similar size, is likely to be the result of different amounts of energy being available to them.

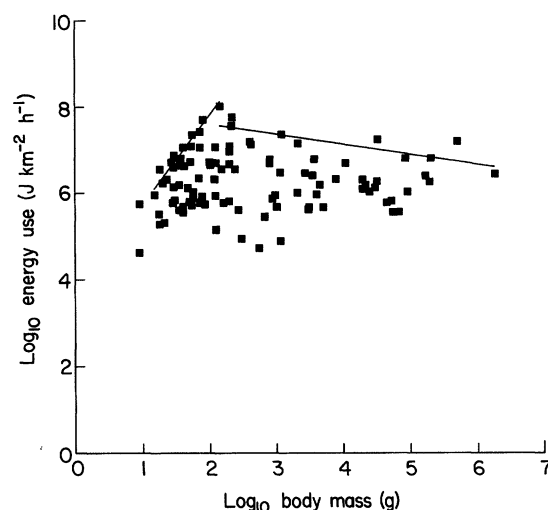


Fig. 3. The relationship between population energy use and body size for terrestrial herbivorous mammals. Lines are least-square fitted slopes for maximum values of population energy use (see text for further details). The regression equation for the upper boundary of small organisms is $\text{PEU} = 3.67 + 2.08 W$ ($n = 5$, $r^2 = 0.97$; $P < 0.003$); for large organisms $\text{PEU} = 7.5 + -0.13 W$ ($n = 8$, $r^2 = 0.24$; $P > 0.05$).

Table 2. The relationship between population energy use and body size for mammals. Values in parentheses are one standard error. Symbols as in Table 1.

Group	<i>n</i>	<i>b</i>	<i>a</i>	<i>r</i> ²	<i>P</i>
All mammals	141	−0.08(0.06)	6.2	0.012	0.191
Herbivores	102	0.08(0.19)	2.12	0.002	0.645
Carnivores	10	−0.46(0.48)	5.40	0.103	0.365
Insectivores	23	−0.71(0.29)	6.44	0.216	0.025
Omnivores	6	1.26(0.57)	−3.45	0.55	0.090

This is also contrary to the EER, which assumes energy to be equally available to species of all sizes (Brown & Maurer 1987; Lawton 1989; Blackburn *et al.* 1993b).

It is not at all unexpected that mammals of around 100 g attain both greater population densities and use larger amounts of energy than smaller or larger mammals. In fact, Brown *et al.* (1993) show that under close examination most allometric relationships are not simple straight lines but change direction around a body mass of 100 g in mammals. These authors propose that this body size is the optimum body size for mammals in both evolutionary and ecological time scales (Maurer, Brown & Rusler 1992; Brown *et al.* 1993; Marquet 1993), and that it is the result of physiological constraints related to the rate at which resources, in excess of those required for self-maintenance, are obtained from the environment and transformed into energy to do reproductive work (Brown *et al.* 1993; Marquet 1993). Furthermore, the agreement between the population density and the population energy-use patterns shown in Figs 2 and 3 supports the view that the species which extract more energy from the environment are also the ones that put more individuals into it. That is, the way in which individuals are distributed among species within communities (i.e. relative abundance patterns) should parallel the way energy is distributed. This empirical observation agrees with the theoretical arguments recently proposed by Marquet (1993) (see discussion by Harvey & Godfray 1987; Sugihara 1989; Pagel, Harvey & Godfray 1991).

Unfortunately, there is no extensive and standardized information on the metabolic rates of intertidal invertebrates in general, and in particular for the species considered in this study. This precludes the estimation of the population energy use for these assemblages. However, the similitude between maximum population density and body size for small and large intertidal invertebrates and mammals is remarkable; in both cases the body size at which maximum density is attained is also where the maximum number of species is found (Fig. 2). Although, this can be explained by the sampling effect hypothesis (Blackburn *et al.* 1990), we interpret it as reflecting the action of the same underlying process favouring medium-size species (Brown *et al.* 1993; Marquet 1993). Nevertheless, the detection of an opti-

mal body size in the multiphyletic intertidal communities studied could reflect more the effect of an ecosystem/habitat-related evolutionary constraint. However, it is suggestive that among the species that attain this optimal body size are the successful barnacles (Cirripedia, Balanomorphs), in particular the chthamaloid and balanoid forms such as species of the genera *Chthamalus*, *Jehlius*, *Balanus* and *Notobalanus* (Castilla 1981; Navarrete & Castilla 1990). On the one hand, Balanomorphs barnacles such as above, or related genera, are found in virtually all contemporary shores, exhibiting specialized adaptations to a wide variety of rocky shore intertidal environments. On the other, they show a long-standing late Mesozoic and Cenozoic fossil record (Newman & Hessler 1989) with remarkable adaptive radiations (e.g. Balanoidea during the Cenozoic Era; Newman & Stanley 1981).

Conclusions

We critically evaluated the EER with regard to its underlying theoretical framework, its dependence of a particular relationship between population density and body size, and the way it is calculated. We found it to be theoretically incorrect, not supported by empirical data on population density and body size relationships, and that its calculation is misleading. In particular, we found a general pattern underlying the allometry of maximum population density, which stresses the correspondence between the two alternative allometric patterns found in natural assemblages. The empirical calculation of population energy use for mammalian primary consumers shows that this fluctuates widely among species, and that its upper limit is not independent of body size but peaks at a body size of about 100 g, and decreases towards both smaller and larger body sizes. Diet also has a strong effect on this relationship. Omnivores show a positive relationship between population energy use and body size, while this is negative for carnivores and insectivores. This empirical evidence, coupled with a reassessment of the relationship between population density and body size, does not support the EER.

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