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Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **The Paradox of Energy Equivalence**

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4 Isaac, N.J.B.¹, Storch, D.^{2,3} & Carbone, C.⁴

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6 Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford,

7 OX10 8BB, UK

8 Center for Theoretical Study, Charles University & Academy of Sciences of the CR. Prague, Czech

9 Republic

10 Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic

11 Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK.

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16 **Keywords**

17 Null models, ecology, abundance, macroecology, metabolic scaling, Damuth's rule, energetics, size-

18 density relationship, invariance

19

20 **Running head**

21 Paradox of energy equivalence

22

23 **Abstract**

24 Energy equivalence, the notion that population energy flux is independent of mass, has become a key
25 concept in ecology. We argue that energy equivalence is not an ecological ‘rule’, as claimed, but a
26 flawed concept beset by circular reasoning. In fact, the independence of mass and energy flux is a null
27 hypothesis. We show that our mechanistic understanding of size-density relationships (SDRs) follows
28 directly from this null model and the assumption that energy limits abundance. Paradoxically, without
29 this assumption energy equivalence has no meaning and we lack a mechanistic understanding for
30 SDRs. We derive an expression for the strength (r^2) of SDRs under the null model, which provides a
31 framework within which to compare published SDRs. This confirms that tight correlations between
32 mass and abundance are a trivial consequence of the span of body masses considered. Our model
33 implies that energy flux varies by 5-6 orders of magnitude among similarly sized mammals and to a far
34 greater extent in birds. We conclude that the energetic paradigm can be strengthened by considering
35 alternative, non-energetic, hypotheses.

36

37 **Introduction**

38 The relationship between body size and abundance is a key focus of research in ecology (White *et al.*,
39 2007). Damuth reported a size-density relationship (SDR) following a power law with a scaling
40 exponent close to $-3/4$ (Eqn 1a), first among mammals (Damuth, 1981) and later across a wide range of
41 vertebrate taxa (Damuth, 1987). He realized that this value was the inverse of Kleiber’s metabolic
42 scaling exponent $3/4$ (Eqn 1b), which implies that the population energy flux per unit area, estimated as
43 the product of metabolic rate and abundance, will be independent of body mass (Eqn 1c). In the scaling
44 jargon, energy flux is said to be ‘invariant’ with respect to mass, M . Nee *et al.* (1991) reported the same
45 pattern among British birds, and coined the phrase ‘energetic equivalence rule’ for situations where the
46 allometric scaling exponents for whole-organism metabolic rate, I , and population density, N , sum to
47 zero. This was formalised as part of the Metabolic Theory of Ecology (Brown *et al.*, 2004) in the
48 context of the availability (supply rate) of resources, R :

49
$$N \propto M^{-b} \quad I \propto M^b \quad R \propto I.N \propto M^0 \quad \text{Equation 1a-c}$$

50 This set of relationships constitutes the general concept of Energy Equivalence (EE), which has
51 become a cornerstone of macroecology and formed the basis of theories about population dynamics
52 (Savage *et al.*, 2004) and biodiversity patterns (Allen *et al.*, 2002). EE is underpinned by the assertion
53 that abundance is directly dependent on energy available to the population: an increase in energy input
54 leads to an increase in abundance, mediated by the energy requirements of each individual (Brown *et*
55 *al.*, 2004; Ernest *et al.*, 2008; Ernest *et al.*, 2009). We refer to this paradigm as the ‘energetic view of
56 abundance’ (see also Taper & Marquet, 1996; Morlon *et al.*, 2009).

57 Some authors considered the independence of mass and energy flux to be a fundamental rule.
58 For example, it has been stated that EE “reflects mechanistic connections ... and the partitioning of
59 available energy among species in a community” (Allen *et al.*, 2002), and “suggests that some

60 combination of physiological and ecological processes results in energetic tradeoffs, such that
61 resources are divided equally across species” (White *et al.*, 2007). However, there is no strong
62 theoretical basis for EE across species (Damuth, 1981; Brown, 1995; Brown *et al.*, 2004; Carbone *et*
63 *al.*, 2007; White *et al.*, 2007), although there have been several attempts to fill this gap. Charnov *et al.*
64 (2001) suggested that EE in mammals is a consequence of life history trade-offs (between fecundity
65 and longevity) and population dynamics (including density dependent juvenile survival). Damuth
66 (2007) developed a simulation model that produced EE through competitive interactions between pairs
67 of species. Harte *et al.* (2008) have argued that EE may be a consequence of the maximum entropy
68 principle, i.e. that it results from the most probable statistical distributions of body sizes, species, and
69 individuals in space within particular constraints given by total number of individuals, total number of
70 species, and total energy available within given area.

71 Energy Equivalence has been challenged on both empirical and conceptual grounds. Marquet *et*
72 *al.* (1995) described problems with both the assumptions of EE and the statistical approaches to testing
73 EE. A growing number of studies have reported patterns inconsistent with EE at a variety of spatial
74 scales (Blackburn & Gaston, 1997; Russo *et al.*, 2003; Hayward *et al.*, 2009; Morlon *et al.*, 2009; Isaac
75 *et al.*, 2011b), although Carbone *et al.* (2007) showed that geometric considerations could lead to a
76 range of SDR exponents even when mass and energy flux are uncorrelated. Others have proposed non-
77 energetic explanations for the SDR (Blackburn *et al.*, 1993; Cotgreave, 1993).

78 Here we argue that EE is not a useful a concept in ecology. We highlight logical flaws in the
79 concept of EE itself, and of the evidence used to test it. We discuss what insights might be possible
80 from the SDR, and suggest new directions for research in this field.

81 **The Paradox**

82 We contend that the concept of EE is at best misunderstood, at worst fundamentally flawed. Equation
83 1c does not imply that all species use equal amounts of energy, merely that energy flux is independent
84 of mass. The absence of a correlation between mass and energy should not be surprising: it is, after all,
85 a null hypothesis which does not require any specific mechanism. Accepting EE as the null has two
86 important implications: 1) that neither resource partitioning nor interspecific competition need to be
87 invoked; 2) that authors claiming to find support for EE have fallen into that most basic statistical trap,
88 namely of accepting the null hypothesis rather than failing to reject it.

89 Such shortcomings of logic might be explained by the fact that energy flux is never measured,
90 but is inferred as the sum of individual metabolic rates (Eqn 1c). The ‘evidence’ (or lack thereof) for
91 EE is usually based on a simple comparison of the SDR exponent with some nominal value of the
92 metabolic scaling exponent (usually 3/4). This too is flawed: the coincidence of scaling exponents (Eqn
93 1a and 1b) does not constitute evidence, either for EE or for the wider energetic paradigm, unless
94 alternate hypotheses can be rejected. However, without the energetic view of abundance we lack a
95 mechanistic understanding for SDRs: by assuming that abundance is driven by energy availability, the
96 coincidence of scaling exponents becomes a trivial consequence of the fact that population energy flux
97 is unbiased with respect to body size. From this it follows, paradoxically, that energy equivalence is a
98 trivial and uninformative pattern under the energetic view of abundance, but is a meaningless concept if
99 we take the opposing (non-energetic) view.

100 **Tight-fitting size-density relationships are not surprising**

101 Inferences about energy partitioning are usually based on the tightness (or lack thereof) of the SDR.
102 The tightness of SDRs is strongly related to the range of body sizes considered (Tilman *et al.*, 2004;

103 Hayward *et al.*, 2010): we extend this observation to emphasise that EE is trivial, and that it has no real
104 predictive power.

105 We derived an analytical expression (see Appendix) for the predictive power of body mass in
106 SDRs under the strict version of the energetic paradigm and the null expectation of no correlation
107 between species' body mass, M , and energy flux, R . In our model, M and R are independent random
108 variables, but species abundance, N , is wholly determined by $R/M^{3/4}$. We refer to this as the 'energetic
109 null model'. Our model reveals that tight relationships occur when the variance in mass is high relative
110 to the variance in energy flux (or resource availability). Indeed, high r^2 is inevitable with a large
111 enough span in body mass (>10 orders of magnitude, figure 1), regardless of the distribution of energy
112 flux (c.f. Hayward *et al.*, 2010).

113 Our energetic null model provides a framework within which to compare the fit of published
114 SDRs whilst controlling for the span in body mass. Not surprisingly, the best-fitting SDRs (relative to
115 the mass range) are found among studies that controlled for key factors influencing underlying
116 variation in organism abundance, such as access to resources. For example, Carbone & Gittleman
117 (2002) showed that prey biomass is a key determinant of abundance among mammalian carnivores:
118 controlling for prey availability provides a dramatic improvement in the predictive power of body
119 mass. Likewise, a study based on carrying capacity in single-species stands of plants (i.e. without
120 interspecific competition) showed a similarly tight-fitting SDR (Enquist *et al.*, 1998).

121 Damuth's classic mammalian SDR (Damuth, 1981; Damuth, 1987) has $r^2=0.65$ across nearly
122 six orders of magnitude in body mass: random subsets with smaller mass ranges have correspondingly
123 weaker fits (figure 2). These patterns are consistent with the energetic null model in which $\log_{10}(\text{energy}$
124 $\text{flux})$ is a random normal deviate with a standard deviation in the range 1.25 - 1.65, corresponding to
125 95% confidence intervals of 80,000 and 3,000,000 fold variation in energy flux for each size class. This

126 magnitude of variation seems at odds with the notion of EE as an ecological ‘rule’ with predictive
127 power, even after accounting for error variance in estimating the abundance of wild mammal
128 populations, many of which are probably below carrying capacity. The much weaker fit among bird
129 SDRs implies still higher levels of variation (7-8 orders of magnitude variation in energy flux). Overall,
130 given the implied range of variation in energy flux, it seems reasonable to reject the notion that these
131 patterns emerge from “resource partitioning” or “energetic trade-offs“ (Allen *et al.*, 2002).

132 **The Way Ahead**

133 The problems associated with EE should not be interpreted as an attack on the energetic view of
134 abundance, which has contributed much to our understanding of large-scale patterns in community
135 structure (Brown *et al.*, 2004; Ernest *et al.*, 2008; McGill, 2008; Ernest *et al.*, 2009), and which we find
136 to be plausible in the broadest sense. Rather we urge researchers to discard the notion of energy
137 equivalence as an ecological ‘rule’, to focus instead on the mechanisms underpinning abundance-
138 energy relationships, and to consider alternative (i.e. non-energetic) determinants of species’
139 abundance.

140 To some degree, this is already happening, using data on abundances within communities. New
141 applications of species abundance distributions, using currencies of energy and biomass, have provided
142 novel insights into the partitioning of resources among species (Connolly *et al.*, 2005; Reuman *et al.*,
143 2008; Morlon *et al.*, 2009; Henderson & Magurran, 2010). A related example is the concept of zero-
144 sum dynamics, in which the energy flux of communities remains stable whilst the abundance (and body
145 size) of individual species fluctuates in a way that reflects individual metabolic requirements (Ernest *et*
146 *al.*, 2008; Ernest *et al.*, 2009). Another prediction of the energetic paradigm is that abundance should
147 increase with available energy: evidence supporting this prediction has been reported for a range of
148 taxa (Mcnaughton *et al.*, 1989; Meehan *et al.*, 2004; Meehan, 2006; Barton & Zalewski, 2007;

149 Pettorelli *et al.*, 2009; Kaspari & Weiser, 2012), but counter-examples also exist (Currie & Fritz, 1993;
150 Isaac *et al.*, 2011a).

151 Studies taking the energetic view of abundance should be more explicit about their assumptions.
152 A good example is how individual energy requirements are estimated: most studies use basal metabolic
153 rates, rather than field rates (which scale more steeply, Nagy, 2005). Many studies approximate
154 metabolic rates as $M^{3/4}$ (Ernest *et al.*, 2008; Ernest *et al.*, 2009): this is reasonable for a large range in
155 mass, but for small (<1 order of magnitude) ranges the predictive power of Kleiber's 'law' is much
156 reduced (Isaac & Carbone, 2010). In addition, correlations between mass and energy flux should be
157 accompanied by an estimate of the power to reject the null model (with specific reference to the span of
158 body masses under consideration).

159 We have alluded to the fact that the energetic view of abundance is not universally accepted.
160 Blackburn *et al.* (1993) presented an explanation for the SDR based on the distribution of species body
161 sizes and the fact that rare species tend to go unrecorded. An alternative "non-energetic" view is that
162 abundance could be conceived as a random variable between hard boundaries (Marquet *et al.*, 1995).
163 Cotgreave (1993) has pointed out that body size imposes a physical limit on population density, and
164 that space-filling would generate a scaling in the upper boundary of $-2/3$ (contrast this with the $-3/4$
165 upper boundary that would be expected from energy monopolisation: Blackburn & Gaston, 2001). We
166 could equally envisage a lower boundary of ecological abundance based on the fact that individuals
167 must be able to meet each other to reproduce. Minimum density can be defined as the density at which
168 population growth rate becomes negative due to Allee effects (Courchamp *et al.*, 1999). We expect that
169 minimum density would be related to daily distance traversed, which itself scales with body size
170 (Carbone *et al.*, 2005). Estimating extreme population densities is problematic, and probably prevents
171 this idea from being seriously tested (but see Silva & Downing, 1994). However, similar non-energetic

172 models might derive testable predictions. We believe that macroecology will be advanced by
173 considering both energetic and non-energetic hypotheses in concert, and comparing the predictions of
174 these divergent perspectives.

175 **Acknowledgments**

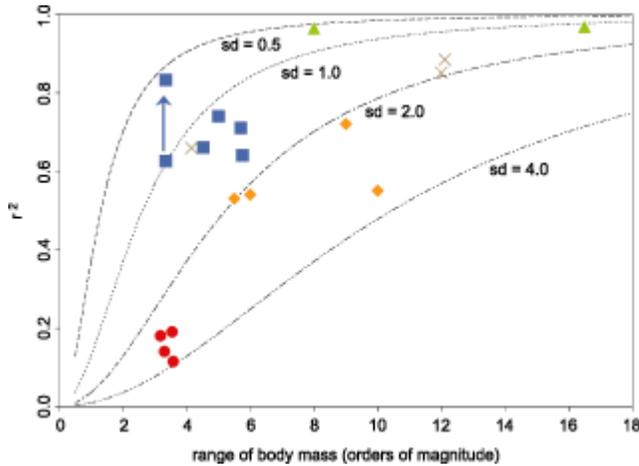
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179

180 **Figures**

181 Figure 1. Explanatory power of body mass in size-density relationships (expressed as r^2) plotted
182 against the number of orders of magnitude in mass range. Lines are derived from our expression (see
183 Appendix) for the energetic null model with differing amounts of variation (expressed as standard
184 deviations) in $\log_{10}(\text{energy flux})$ among species. The points are SDRs reported in the literature for birds
185 (circles), mammals (squares), invertebrates (diamonds), animals (crosses) and plants and phytoplankton
186 (triangles) (Data from Damuth, 1981; Peters, 1983; Damuth, 1987; Marquet *et al.*, 1990; Cotgreave &
187 Harvey, 1992; Ebenman *et al.*, 1995; Enquist *et al.*, 1998; Belgrano *et al.*, 2002; Carbone & Gittleman,
188 2002). The arrow links two points for mammalian carnivores (Carbone & Gittleman, 2002): the lower
189 point is raw abundance data, the upper is corrected for prey abundance.

190



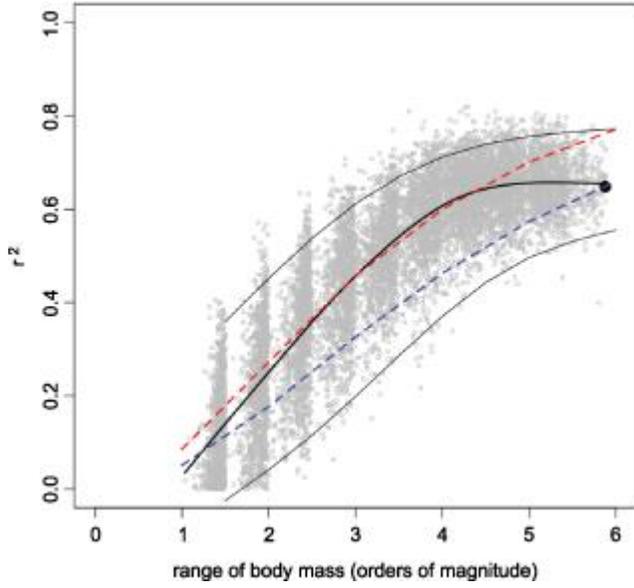
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193 Figure 2. Explanatory power of the mammalian size-density relationship (expressed as r^2) is strongly
194 related to the range of body masses considered. Grey points are 10,000 random subsets of 50 species,
195 each with a constrained range of body mass: solid black lines indicate the mean and 95% confidence
196 intervals. The black circle is the unconstrained dataset of 467 species. Data are taken from Damuth

197 (1987). The upper and lower dashed lines are the expected r^2 derived from our analytical expression of
198 the null model, with standard deviations in $\log(\text{energy flux})$ of 1.25 and 1.65 respectively (see appendix
199 for further details).

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- 314
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316

317 **Biosketches**

318 Nick Isaac conducts research on species' distribution and abundance over large scales, using data on
319 insects, mammals and birds. Of particular interest is the relative contribution of traits and
320 environmental factors in shaping biodiversity, and how these patterns change with scale.

321

322 David Storch is interested in macroecology, evolutionary ecology and ecological theory, with particular
323 emphasis on patterns of species distribution and diversity.

324

325 Chris Carbone researches the role of body size and consumer-resource relationships in shaping
326 organism ecology and population processes, focusing on mammalian and dinosaurian carnivores.

327

The Paradox of Energy Equivalence

Nick J.B. Isaac, David Storch & Chris Carbone

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Appendix S1: Analytical derivation for the expected explanatory power (r^2) of the size-density relationship under the energetic null model

We start from the simple expression for r^2 , found in basic statistical texts:

$$r^2 = 1 - \text{SSE} / \text{SST} \quad \text{Eqn A1}$$

In equation A1, SSE and SST are the sum of squared errors and the sum of squares of the dependent variable (logged abundance, $\log N$), respectively. Under the null model of energy equivalence (no correlation between energy flux and mass), the error variance is simply the variance in $\log(\text{energy flux})$. Here, we follow Brown *et al.* (2004) in using R (for ‘resource availability’) in place of energy flux:

$$\text{SSE} = \text{Var}(\log R) \quad \text{Eqn A2}$$

$$\text{SST} = \text{Var}(\log N) \quad \text{Eqn A3}$$

$$r^2 = 1 - \text{Var}(\log R) / \text{Var}(\log N) \quad \text{Eqn A4}$$

Under the energetic paradigm, abundance is simply the energy available divided by the energy requirements of each individual:

$$N = R / I \quad \text{Eqn A5}$$

$$\log N = \log(R / I) = \log R - \log I \quad \text{Eqn A6}$$

Substituting Eqn 6 into Eqn 4:

$$r^2 = 1 - \text{Var}(\log R) / \text{Var}(\log R - \log I) \quad \text{Eqn A7}$$

$$= 1 - \text{Var}(\log R) / [\text{Var}(\log R) + \text{Var}(\log I)] \quad \text{Eqn A8}$$

Substituting I for M :

$$\log I \propto b \cdot \log M \quad \text{Eqn A9}$$

$$r^2 = 1 - \text{Var}(\log R) / [\text{Var}(\log R) + \text{Var}(b \cdot \log M)] \quad \text{Eqn A10}$$

$$= 1 - \text{Var}(\log R) / [\text{Var}(\log R) + b^2 \cdot \text{Var}(\log M)] \quad \text{Eqn A11}$$

Finally, we substitute the variance in $\log M$ with the span in M ($\text{span}M$, in orders of magnitude), by assuming a lognormal distribution of body masses, with 95% confidence limits equal to the observed span:

$$r^2 = 1 - \text{Var}(\log R) / [\text{Var}(\log R) + (b \cdot \text{span}M / 1.96)^2] \quad \text{Eqn A12}$$

References

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.